

13 Paleosols

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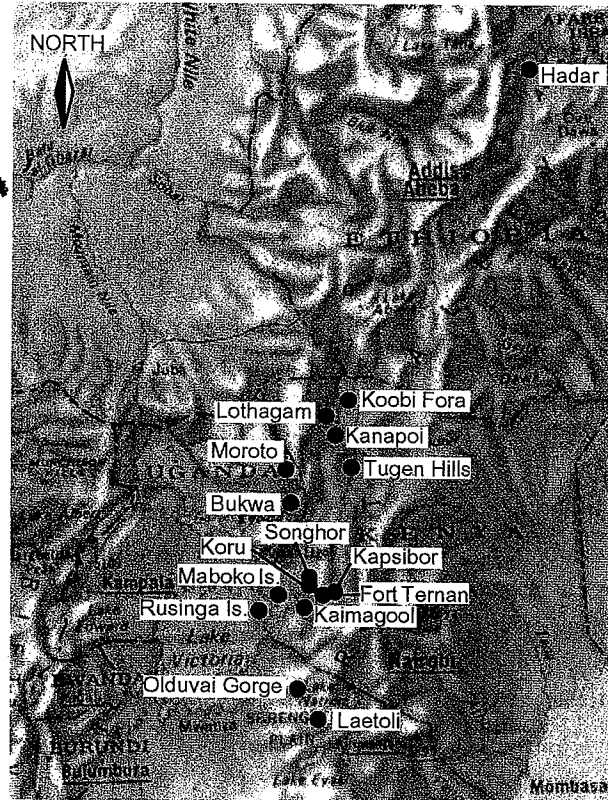
Abstract

Soils are known to be products of environmental factors such as climate, vegetation, topographic setting, parent material, and time for formation so that paleosols, or fossil soils, can potentially reveal changing environments of the past. Evidence from paleosols for past climate and vegetation in East Africa does not support traditional narratives of human evolution during a single transition from primeval forest to dry climate and open grassland. Instead, paleosols indicate climatic oscillations between wet and dry, and alternating expansion of woodland and grassland, since at least 18 Ma (million years ago). Acquisition of dry grassland adaptations such as thick enamel by 18 Ma, adducted hallux by 14 Ma, and cursorial legs by 1.8 Ma, alternated with woodland adaptations such as short stiff back by 16 Ma, erect stance by 6 Ma, and flat face by 3.5 Ma. Our ancestors survived profoundly changing climate and vegetation, with some adaptations lasting only to the next environmental shift, but others proving to be of lasting value.

13.1 Introduction

Our species, and its ancestors of millions of years ago, evolved on the soils of Africa (Darwin 1872; Fleagle 1998). Many of those soils have been eroded or altered beyond recognition by deep burial, but many paleosols are buried within floodplain, volcanic, lacustrine, alluvial plain, and cave deposits of Africa (Retallack 2001a). These paleosols provide much of the colorful banding and mottling seen in East African badlands and dongas, including many fossil hominoid localities (● *Figure 13.1*). Many fossils of human ancestors come from paleosols (Retallack et al. 1995, 2002; Radosovich et al. 1997; Wynn 2004a, b), which are also records of past environments of our evolutionary antecedents (● *Figure 13.1*). Modern soils are known to be products of environmental factors such as climate, vegetation, parent materials, topographic setting, and time for formation (Jenny 1941). These formative factors can be interpreted from fossiliferous paleosols to provide hitherto unavailable details of the habitats of fossil apes and humans.

■ Figure 13.1
Localities for paleosol studies in East Africa



The vegetation of fossil ape and human sites is central to long-standing theories for the evolution of upright stance. “The hands and arms could hardly have become perfect enough to have manufactured weapons, or to have hurled stones and spears with a true aim, ‘... so long as they were especially fitted to climbing trees’” (Darwin 1872). Other ideas are that grasslands selected for upright stance because of the need to be vigilant against predators (Dart 1926), to manipulate small seeds (Jolly 1970), to minimize exposure to the sun (Wheeler 1984), or to cover long distances with less energy by walking (Rodman and McHenry 1980) or running (Bramble and Lieberman 2004). Wooded grasslands and open woodlands are also plausible sites for evolution of upright stance from squat feeding on the ground (Kingdon 2003) or moving between scattered fruiting bushes (Sanford 2003). Alternatively, upright stance may have evolved in forests because it allowed erect-back climbing (Tuttle 1981), hands free to care for premature infants (Lovejoy 1981), phallic display to females (Tanner 1981), or intimidation displays to rivals (Jablonski and Chaplin 1993).

Paleosols are relevant to these questions because the fine root traces and crumb structure of grassland soils are distinct from the thick clayey subsurface horizons of both woodland and forest soils (Jenny 1941). Woodland and forest soils differ markedly in their clay minerals and chemical composition (Retallack 1997). Even the aquatic theory of human origins (Morgan 1982) can be evaluated from paleosols because mangal, littoral, lake margin, and streamside paleosols are distinguished by virtue of relict bedding and common burrows of crabs and clams (Retallack 2001).

Paleoclimate also is of interest as a selective pressure on hominoid evolution through drought and other hardships. Paleoclimate was also a primary control of past vegetation in which hominoids found food and shelter. Paleoclimatic shifts to drier climate and more open grassy vegetation have been held responsible for major evolutionary innovations in hominoids and bovids (Vrba 1999), as have changes in degree of climatic variability (Potts 1996). Soils of dry climate have calcareous nodules at a shallower depth than soils of humid climate (Retallack 2004) and also are less leached of cationic nutrients (Ca^{2+} , Mg^{2+} , K^+ , Na^+) than humid-climate soils (Sheldon et al. 2002). Paleosols can thus provide paleoclimatic records at the very sites of early human ancestors rather than inferred from remote records of deep-sea cores (de Menocal 2004).

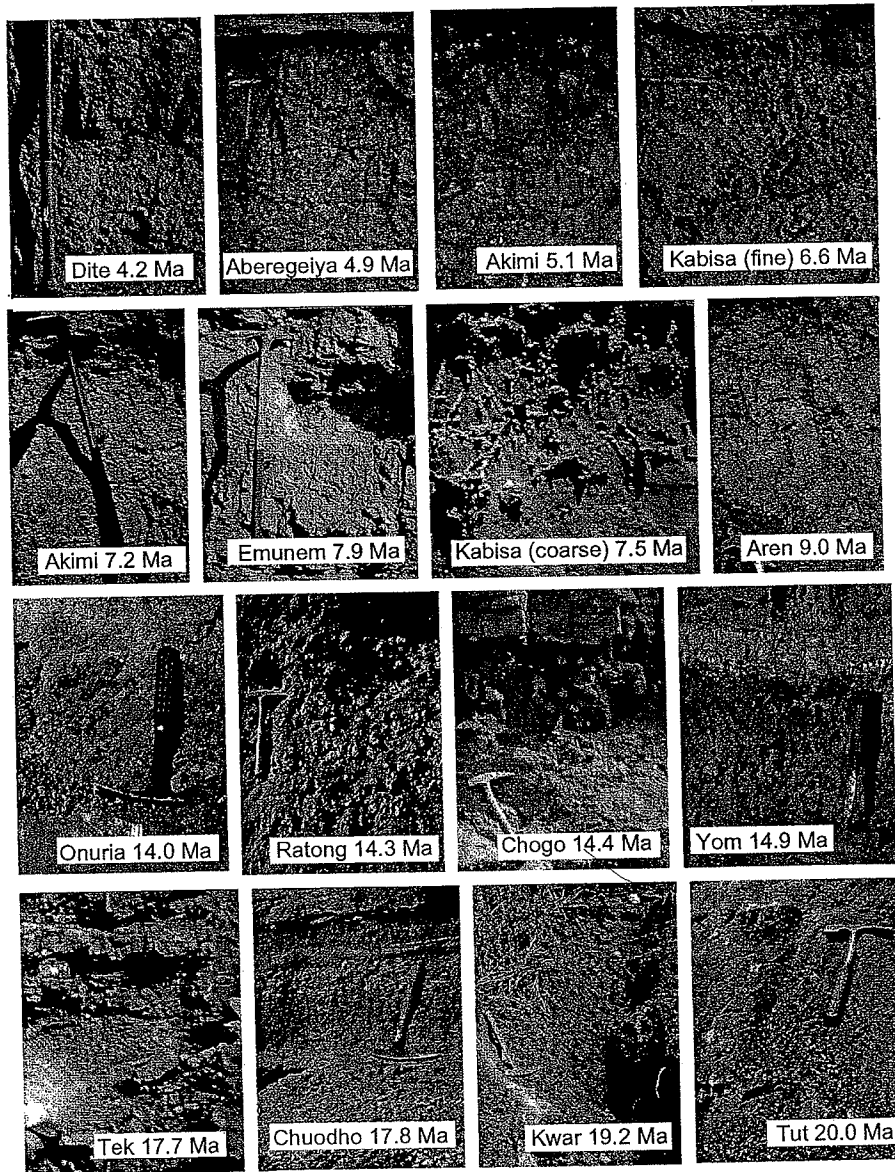
This review emphasizes climate and vegetation, but other soil forming factors of parent material, topographic position, and duration of soil formation can also be inferred from paleosols. Highly calcareous and saline carbonatite volcanics are an unusual parent material of many African hominid sites (Retallack 1991a), fortunate because of their remarkable preservative effects for fossil bones, seeds, and insects (Retallack et al. 1995). Many East African paleosols preserve a record of well-drained fluvial terraces, infrequently flooded, and some volcanic apron paleosols represent foothills environments (Retallack 1991a), thus revealing environments beyond the usual lowland constraints of sedimentary environments. Degree of soil development can also be used to infer duration of paleosol formation and rates of sediment accumulation, with implications for the geochronology of ape and human ancestor sites (Retallack et al. 1995, 2002).

13.2 Recognition of paleosols

Paleosols are often distinctive and striking bands of red clay (Bt horizon), calcareous nodules (Bk horizon), or coal (O horizon) in sedimentary and volcanic sequences (● Figure 13.2). Three general classes of observations are especially helpful in paleosol recognition: root traces, soil horizons, and soil texture (Retallack 1997).

Figure 13.2

Kenyan Miocene paleosols have been given field names using local Luo and Turkana languages. These pedotypes are objective field mapping units for paleosols: their interpretation and classification requires laboratory study



Root traces are the most diagnostic evidence of paleosols and sometimes are obvious because cemented and erosion-resistant (Kabisa pedotype of **Figure 13.2**). Difficulties arise in recognition of root traces because they are often replaced by other minerals and ramify in three dimensions in such a way that one rock face reveals little of the overall pattern. Few fossil roots are carbonaceous or reveal histological structures like fossil wood (Retallack 1997). The original root has commonly rotted out, and the hole it occupied is filled with claystone or siltstone, or encrusted with iron oxide or calcium carbonate. Drab haloed root traces are very distinct, green gray mottles, in reddish paleosol matrix, formed during early burial chemical reduction by microbes fueled by consumption of root organic matter (Retallack 1991b). In all these cases, root traces are truncated at the surface of the paleosol, and branch and taper downward. These features distinguish root traces from most kinds of burrows in soils, although the relationship between burrows and roots can be complex. Roots may preferentially follow soft fill of burrows rather than hard soil matrix, and burrows may congregate around roots on which the burrowing animals fed (Retallack 1991a).

Soil horizons develop through thousands of years whereas sedimentary beds are deposited in days. Unlike sedimentary beds, which have sharp bottoms and usually sharp tops as well, paleosols have a sharp top, representing the ancient land surface, but gradational lower contacts (Retallack 2001a). Sedimentary beds also include a variety of sedimentary structures, such as lamination, cross bedding, and ripple marks (as in Tek pedotype of **Figure 13.2**), whereas soil horizons develop with obliteration of these original features (Tut pedotype of **Figure 13.2**). Similarly, soil formation progressively destroys the original crystalline structure of volcanic or granitic parent materials (Retallack 1991a). In dry climate soils (Aridisols), primary sedimentary or volcanic structures are obscured at first by filaments and soft, small carbonate masses, then large, hard, carbonate nodules (calcic or Bk horizon of Chogo pedotype in **Figure 13.2**), and finally thick carbonate layers (petrocalcic or K horizon of Soil Survey Staff 2000). In sod-grassland soils (Mollisols), primary lamination and crystalline structure is broken up by fine roots and replaced by dark, fecal pellets of earthworms to create a crumb-textured, organic surface horizon (mollic epipedon of Dite, Chogo, Yom, and Onuria pedotypes of **Figure 13.2**). A variety of other kinds of soil horizons are recognized and important to soil classification (Retallack 1997, 2001a; Soil Survey Staff 2000).

Soil structure also develops within soil horizons and is very distinct from sedimentary bedding and igneous crystalline texture. The fundamental elements of soil structure are modified cracks and other surfaces (cutans), and the clods they define (peds). Cutans include clay skins (argillans) lining cracks in the soil

and rusty weathering rinds (sesquans) around clods and pebbles in soil (Retallack 2001a). Peds have a variety of shapes: lenticular in swelling-clay soils (Vertisols: Aberegaiya pedotype of ● *Figure 13.2*), blocky subangular in fertile forest soils (Alfisols: Tut pedotype of ● *Figure 13.2*), and crumb shaped (small and ellipsoidal) in grassland soils (Mollisols: Dite, Chogo, Yom, and Onuria pedotypes of ● *Figure 13.2*). Although cracks and other voids are not preserved in paleosols due to compaction by overburden, peds, and cutans are common and conspicuous (Retallack 1991a). Other soil structures less diagnostic of soils include concretions, nodules, and crystals (Retallack 2001a).

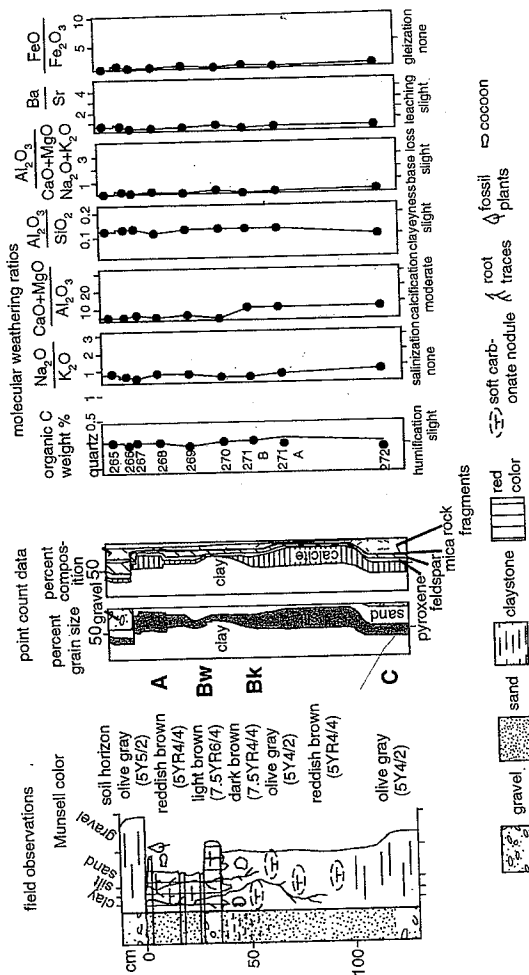
13.3 Methods for the study of paleosols

Just as soil individuals (pedons) are studied as soil columns in soil pits, paleosols are studied in columnar stratigraphic sections of the sort also used in sedimentology and stratigraphy (● *Figure 13.3*). Grain size is emphasized because it is important to soil formation, as weathering transforms sand and silt grains to clay. A graphical representation of grain size profiles conveys important information on the abruptness of horizon transitions. Color from a Munsell chart should also be represented, as redness denotes the degree of chemical oxidation and drainage of soils and paleosols. Calcareousness determined by relative effervescence with dilute hydrochloric acid also is important as a guide to chemical leaching and soil nutrient status (Retallack 1997).

Laboratory studies of paleosols do not employ all the same techniques used in soil science because some important soil measures, such as base saturation, are altered upon burial of soils (Retallack 1991b). Petrographic thin sections are especially useful for revealing soil microfabrics, and the point counting of thin sections furnishes estimates of changes in grain size and mineral composition of paleosols. For example, increased subsurface clayeyness can be used to recognize diagnostic horizons (argillic horizon) for forest soils (Alfisols and Ultisols), whereas traces of nutrient-rich minerals, such as calcite and feldspar, distinguish fertile forest soils (Alfisols) from infertile forest soils (Ultisols; Retallack 1997).

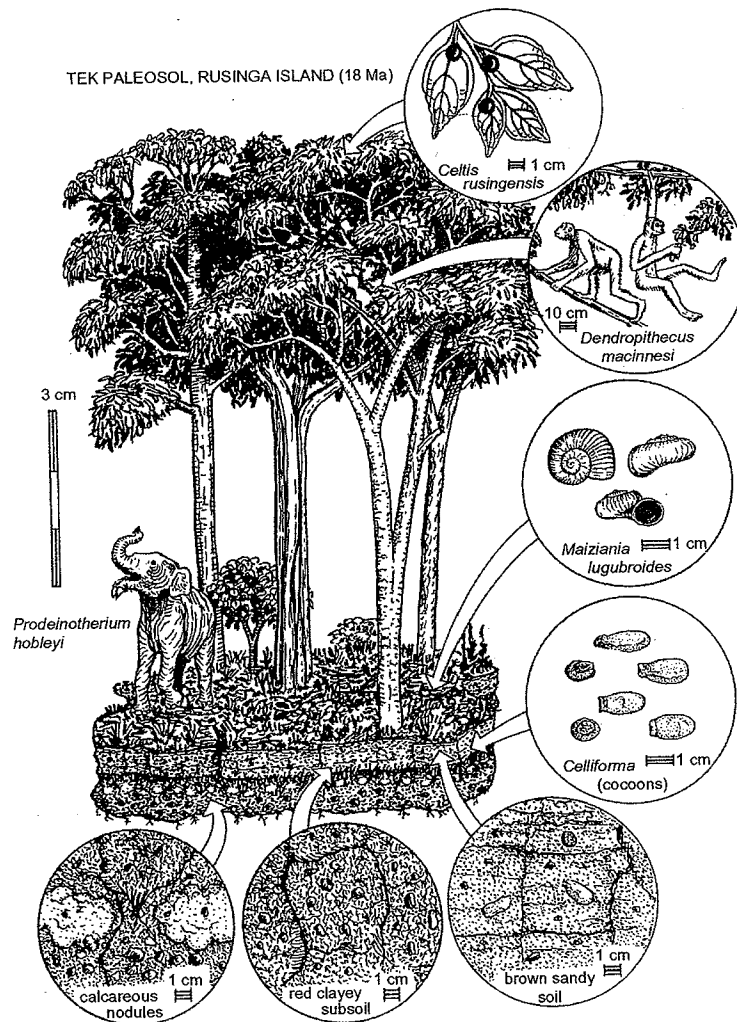
Chemical analyses also are useful in characterizing and classifying paleosols, especially molar ratios designed to gauge the progress of common soil-forming chemical reactions. The hydrolysis reaction common in silicate weathering leaches cationic bases (Ca^{2+} , Mg^{2+} , K^+ , Na^+) from host minerals, such as feldspar, to create clay (Al rich) and is thus indicated by high ratios of alumina/bases. An alumina/base ratio higher than 2 is a good proxy for the transition from fertile forest soils (Alfisols) to infertile forest soils (Ultisols). Soda/potash molar ratios in excess of 1 indicate unusually salty soils. Ferrous/ferric molar ratios in

Figure 13.3 Petrographic and chemical data for the Tek paleosol from the 18 Ma Hiwegi Formation of Rusinga Island, Kenya [data from Retallack et al. (1995)]



excess of 1 indicate well-drained soils (Retallack 1997). By these criteria, the petrographic and chemical data on the 18 Ma Tek paleosol from Rusinga Island Kenya (● Figure 13.3) indicate a fertile Inceptisol that was nonsaline and well-drained. These data allow identification of analogous modern soils (Retallack et al. 1995) and refine understanding of the ancient landscape and its ecosystem (● Figure 13.4).

■ Figure 13.4
Reconstruction of Tek paleosol from the 18 Ma Hiwegi Formation of Rusinga Island, Kenya
[data from Retallack et al. (1995)]



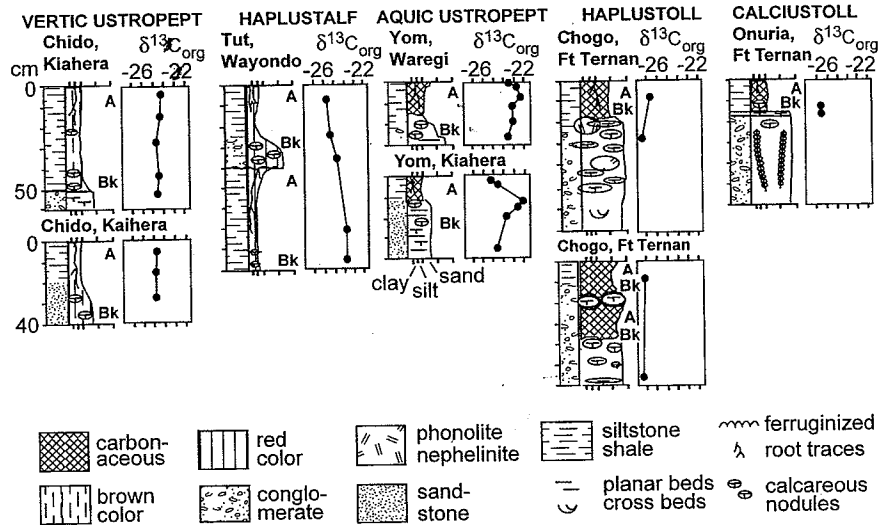
Carbon isotopic compositions of paleosol carbonate were at first thought to be useful indicators of grasslands because most tropical grasses have a C_4 photosynthetic pathway which creates isotopically heavy carbon (Cerling 1992). The most prominent failure of this technique was application to the Middle Miocene (14.4 Ma) locality of Fort Ternan, with paleosol carbonate isotopically like rain forest (Cerling et al. 1997a), but fossil soils, grasses, trees, and antelope like those of a mosaic of wooded grassland and grassy woodland (Retallack 1991a, 1992; Koch 1998; Turner and Antón 2004). Subsequently it was found that even tropical grasses used the C_3 photosynthetic pathway until about 7 Ma or younger (Cerling et al. 1997b; Fox and Koch 2003). The quality of graze (C_3 more nutritious than C_4) can be assessed by isotopic studies of teeth and paleosols, but the question of grass or shrub diet is better assessed from mammalian tooth microwear, hypsodonty, and cursoriality (MacFadden 2000). The advent of C_4 grasses within tropical grasslands is most likely related to declining Late Miocene atmospheric CO_2 content (Cerling et al. 1997a). Another failure of carbon isotopes to indicate past vegetation is Sikes's (1994) forest interpretation of the paleosol at Olduvai fossil locality FLK yielding *Australopithecus boisei*. This paleosol with relict bedding, zeolites, little clay, and shallow carbonate is unlike forest soils, and probably supported salt-tolerant, lake-margin shrubs (Retallack 2001a), which have a similar C_3 isotopic value to forest (Sikes 1994). Isotopic values of carbon and oxygen in paleosols and animals are controlled by so many factors that biotic and pedogenic constraints are needed (Koch 1998). Carbon isotopic studies of paleosols are now more useful for assessing atmospheric CO_2 from carbonate and organic isotopic offsets (Ekart et al. 1999) and soil productivity from isotopic depth functions (Yapp and Poths 1994). Carbon isotopic depth profiles of paleosols also provide new insights into carbon cycling within different kinds of ancient ecosystems. Grassland paleosols (Chogo and Onuria pedotype of ● Figure 13.5) show more effective humification at the surface (higher $\delta^{13}C$ values) than woodland soils (Tut of ● Figure 13.5), and swelling-clay paleosols have flat carbon isotopic profiles due to soil mixing (Chido of ● Figure 13.5). Preservation of such carbon-cycling signatures known from modern soils within different pedotypes gives additional evidence for paleosol classification and interpretation (Bestland and Krull 1999).

13.4 Paleosols as proxies of paleoprecipitation

Climatic zonation of soils was a key element in the Russian origins of soil science (Jenny 1941), and a variety of relationships between particular soil features and climatic variables can be applied to East African paleosols in order to reconstruct

■ Figure 13.5

Carbon isotopic ($\delta^{13}\text{C}_{\text{org}}$) depth profiles of Kenyan Miocene pedotypes, showing strong surface humification in grassland paleosols (Chogo and Onuria pedotypes), subsurface humification in Alfisols (Tut) and mixing in vertic Inceptisols (Chido). Carbon isotopic data is from Bestland and Krull (1999) and Cerling et al. (1997a), and paleosols described by Retallack (1991a), Retallack et al (1995), and Bestland and Krull (1999)



paleoclimate. For example, depth to carbonate horizon (D in cm) is related to mean annual precipitation (P in mm) by formula (1) below (from Retallack 2005). This depth can be corrected for compaction due to overlying sediment using geological estimates of overburden and standard formulae (Sheldon and Retallack 2001). Also related to mean annual precipitation (P) is nutrient base content ($C = \text{Al}_2\text{O}_3 / (\text{Al}_2\text{O}_3 + \text{CaO} + \text{MgO} + \text{Na}_2\text{O})$ in mol) of soil Bt horizons by formula (2) below (Sheldon et al. 2002).

$$P = 137.24 + 6.45D - 0.013D^2 \quad R^2 = 0.52, \text{ S.E.} = \pm 147 \text{ mm} \quad (1)$$

$$P = 221.12 \cdot e^{0.197C} \quad R^2 = 0.72, \text{ S.E.} = \pm 182 \text{ mm} \quad (2)$$

Chemical weathering also alters the mineral content of soils, especially their clay minerals, which begin as smectites and then lose cationic bases with further chemical weathering to become kaolinite (Retallack 2001). This indication of paleoprecipitation works best with noncalcareous soils, which are found in climates receiving more than 1,000-mm mean annual precipitation (Retallack 2004). In East Africa today, smectite is dominant in soils receiving less than 1,200-mm mean annual precipitation, and kaolinite dominant in wetter climates

(Mizota et al. 1988). Thus noncalcareous, smectitic soils define a limited paleoclimatic window of 1,000–1,200-mm mean annual precipitation.

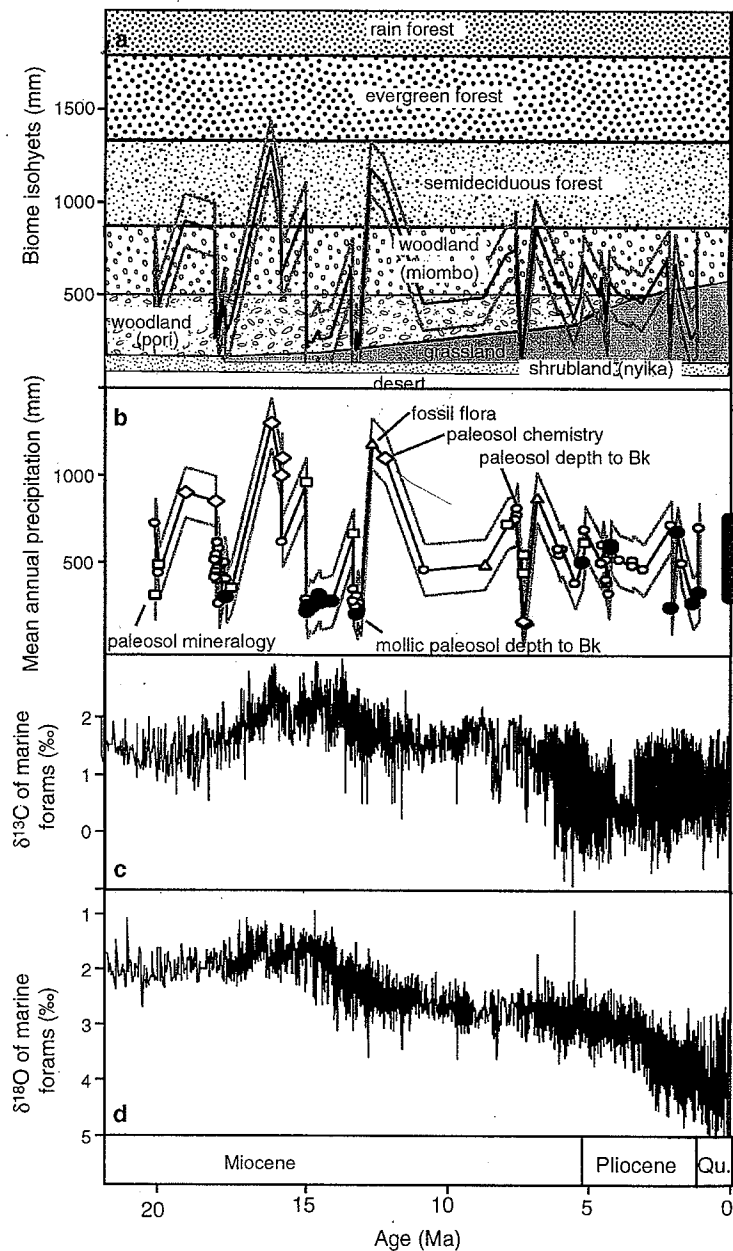
My new compilation of Kenyan paleoprecipitation over the past 20 million years (● *Figure 13.6b*) includes previously published data on African depth to Bk (Wynn 2001, 2004a,b; Wynn and Retallack 2002; Retallack 2001b; Retallack et al. 2002), and paleosol chemical (Retallack et al. 1995, 2002; Thackray 1989; Bestland 1990; Retallack 1991a; Wynn and Retallack 2002) and clay mineral composition (Retallack 1991a, Behrensmeyer et al. 2002), as well as published inferences from size and shape of fossil leaves (Jacobs 2002). This compilation is limited to data from around Lake Victoria for the early-middle Miocene, the Tugen Hills for the mid-late Miocene and the Turkana Basin for the Miocene to Quaternary. The geological time scale is from radiometric dating of these various fossil primate sites (Deino et al. 1990; Retallack 1991a, Jacobs and Deino 1996; Behrensmeyer et al. 2002; Hill et al. 2002).

These new data reveal not just one Neogene aridification event at about 7 Ma, as has long been implied by the “Tertiary pluvial hypothesis” (Leakey 1952), the “Miocene lake hypothesis” (Kent 1944), the “Miocene rain forest hypothesis” (Andrews and Van Couvering 1975; Andrews 1996), and the “Late Miocene grassland hypothesis” (Cerling 1992; Cerling et al. 1997a, b). These theories had already been discredited by discovery of Miocene desert dunes, shrubland snails, alkaline lakes, open-country grasses, grazing mammals, and grassland paleosols in East Africa (Pickford 1986a, 2002a; Retallack et al. 1990, 2002).

Instead the data (● *Figure 13.6*) reveal a Neogene paleoclimatic roller coaster of at least nine dry spells with intervening wet periods, of which humidity spikes at 16 and 13 Ma were the wettest of the last 20 million years. This new paleoprecipitation curve is similar to paleotemperature variations for Africa inferred from north–south oscillation through time of Ethiopian and Palearctic biogeographic realms (Pickford 2002a). These new data are also similar to foraminiferal oxygen isotope curves from the deep sea (Zachos et al. 2001), commonly used as a basis for evaluating human evolution in Africa (de Menocal 2004), but the match is not precise (● *Figure 13.6b* and *c*). A general trend of extreme and volatile middle Miocene values, but subdued late Miocene to Quaternary values, is evident from both isotopic and paleosol data. The paleosol record reveals much greater variation in rainfall than would be inferred from carbon isotopic values of marine foraminifera, which are damped by global oceanic mixing with time lags of several thousand years. More profound damping is seen in oxygen isotopic values of marine foraminifera, which show a long-term increase unlike local rainfall and foraminiferal carbon records. This increase is plotted on reversed axes in ● *Figure 13.6d* because it has been interpreted as a long-term temperature

■ Figure 13.6

A 20 million year record of vegetation (a) and paleoprecipitation (b) from Kenya, compared with carbon (c) and oxygen (d) isotopic composition of marine foraminifera. Paleoprecipitation data from paleosols (b) is from depth to carbonate (open ellipses), clay mineral (diamonds), and chemical composition (squares) after Retallack (1991a), Retallack et al. (1995, 2002), Wynn (2001, 2004a, b), Wynn and Retallack (2001). Paleobotanical estimates from Jacobs (2002) and Jacobs and Deino (1996). Modern vegetation precipitation limits are from Anhufer et al. (1999)



decline (Zachos et al. 2001), but part of this long-term trend is due not just to temperature but to water recycling with plate tectonics (Veizer et al. 2001). The global oxygen isotope record also shows an increase after 3 Ma due to continental icecap sequestration of isotopically light oxygen, in addition to temperature effects (Zachos et al. 2001). Despite these problems, the East African paleosol record and global isotopic records present a very different concept of climatic variation experienced by our distant ancestors than the past idea of a seminal Late Miocene climatic event. Instead of a single origin of humanity at a turning point of environmental change, the new record implies rather that our lineage responded to a gauntlet of changing conditions with a variety of adaptations (Table 13.1), as discussed later.

Table 13.1
Geological age of African climatic events, selected adaptations, and hominoid diversity (D), origination (O), and extinction (E)

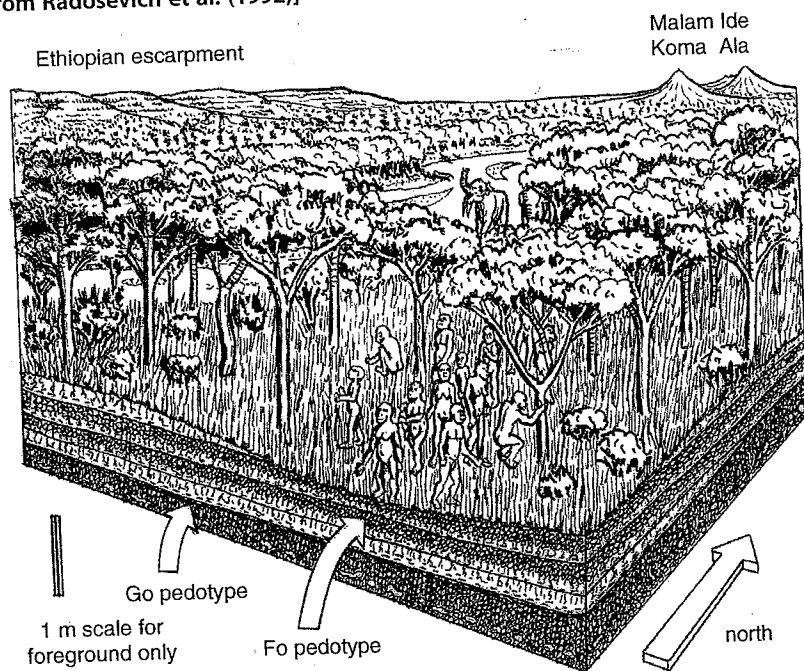
Age (Ma)	Hominoid adaptations and extinctions	D	O	E
20.2 dry	Robust mandible for hard food (<i>Rangwapithecus</i>)	10	9	0
19.1 wet	Low cusp molars for folivory (<i>Nyanzapithecus</i>)	5	0	5
17.7 dry	Thick enamel for hard food (<i>Afropithecus</i>)	6	1	2
16.1 very wet	Short back for suspension (<i>Morotopithecus</i>)	4	3	6
14.9 very dry	Adducted hallux for ground walking (<i>Kenyapithecus</i>)	7	4	2
12.6 very wet	Thin enamel molars for soft food (<i>Otaviapithecus</i>)	2	2	5
10.7 dry	Large size for ground feeding (<i>Samburupithecus</i>)	3	3	0
8.6 wet	Ape extinction with monkey radiation (<i>Microcolobus</i>)	1	1	3
7.5 very dry	Knuckle walking for ground (<i>Pan-Gorilla</i> ancestors)	1	1	1
6.8 wet	Upright stance for nest provisioning (<i>Orrorin</i>)	1	1	1
5.4 dry	Small incisiform canines for hard food (<i>Ardipithecus</i>)	3	1	2
4.2 wet	Flat face for stereoscopic vision (<i>Kenyanthropus</i>)	1	1	3
2.5 dry	Large molars for hard food (<i>Paranthropus</i>)	6	4	2
2.1 wet	Small molars for soft food (<i>Homo habilis</i>)	3	0	4
1.8 dry	Long legs for endurance running (<i>Homo ergaster</i>)	5	3	2
1.7 wet	Occipital bun for competition (<i>Homo erectus</i>)	4	0	3
1.0 dry	Globular brain for generalist roles (<i>Homo antecessor</i>)	4	2	1
0.1 wet	Magdalenian tools and culture (<i>Homo sapiens</i>)	1	1	4

13.5 Paleosols as trace fossils of ecosystems

Australopithecus afarensis is known from body fossils, such as the partial skeleton "Lucy" (Johanson et al. 1982), as well as from trace fossils, such as the footprints of Laetoli (Leakey and Harris 1987). The soils of *A. afarensis* also are known, especially at the "first family" site near Hadar, Ethiopia (Radosevich et al. 1992). Here a troop of at least 13 individuals, young and old, died, rotted, and were

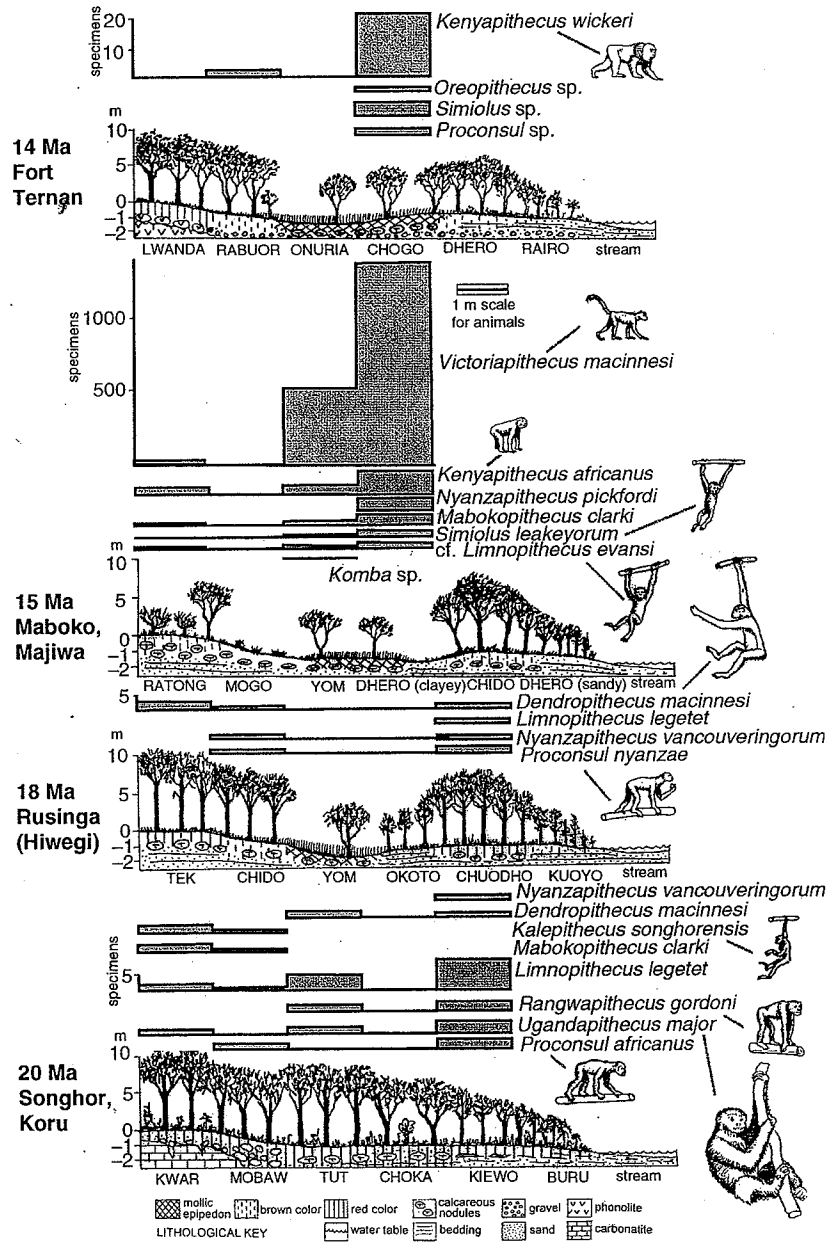
partially disarticulated, before being interred in flood deposits on a crumb-structured soil of grassy streamside woodland (● *Figure 13.7*). The paleosol is not only a matrix to the bones but a trace fossil of their ecosystem. Furthermore, paleosols by definition are in the very place they formed, not redeposited. Unlike the skeleton of “Lucy” found in the sandstone of a former river channel (Johanson et al. 1982), and thus transported some distance from its natural habitat, the first family was found where it died and had lived (Radosevich et al. 1992). Thus, paleosols give a finer resolution of primate paleoenvironments in time (● *Figure 13.6*) as well as space (● *Figure 13.7*).

■ **Figure 13.7**
Reconstruction of paleosols at the “First Family site” for *Australopithecus afarensis* at Hadar [data from Radosevich et al. (1992)]



The various paleosols containing Miocene ape fossils in southwest Kenya can also be used to constrain their habitats (● *Figure 13.8*). The fragmentary and weathered nature of most of these fossils is evidence that they accumulated through natural processes of death and decay on the paleosols in which they are found (Pickford 1986a). The great diversity of fossil apes in this region (Gommery et al. 2002; Harrison 2002; Ward and Duren 2002) is in contrast to the low diversity of great apes today (Fleagle 1998), leading to the idea that Miocene apes, defined from apelike dentition, were ecologically more like both

■ Figure 13.8
 Paleosols of Miocene apes from southwestern Kenya [data from Retallack (1991a) with
 taxonomy after Harrison (2002), Retallack et al. (2002), Ward and Duren (2002)]



apes and monkeys today (Andrews 1996). Analysis of their occurrence in paleosols shows that there was some ecological separation of different species to different soil types, but still high diversity within a soil type (● Figure 13.8). In the 20 Ma sites of Koru and Songhor, for example, one taxon (*Ugandapithecus*) shows little habitat specificity through a variety of tropical dry forest habitats, but small taxa (*Kalpipithecus*, *Mabokopithecus*) are in upland soils and larger taxa (*Proconsul*, *Rangwapithecus*, *Dendropithecus*, *Nyanzapithecus*) remained in lowland forests closer to water. One paleosol type (Kiewo pedotype) has as many as six taxa: three likely suspensory feeders (*Limnopithecus*, *Dendropithecus*, *Ugandapithecus* from small to large) and three likely overbranch feeders (*Nyanzapithecus*, *Proconsul*, *Rangwapithecus*, from small to large). The contrasting sizes and other differences between these taxa suggest niche partitioning of forest canopy tiers.

Diverse sympatric catarrhine communities persisted into the dry woodland landscapes of Rusinga Island at 17.8 Ma, when paleosols with the crumb peds and iron-manganese nodules of dambo grasslands (Yom pedotype) appear, but are rare and barren of primate fossils (Retallack et al. 1995). Other evidence for grasslands of about the same age are abundant bunch grasses at the Ugandan fossil site of Bukwa (Pickford 2002b). Yom paleosols of dambo grassland are much more common by 14.7 Ma on Maboko Island (Retallack et al. 2002), where they contain abundant vervet-like monkeys (*Victoriapithecus*: note change of scale for this exceptional collection in ● Figure 13.8). These seasonally inundated grasslands of dry climates were not encouraging to fossil apes, which were more common in riparian woodlands (*Nyanzapithecus*, *Limnopithecus*, *Mabokopithecus* and *Simiolus* of Dhero paleosols). More wide ranging was *Kenyapithecus*, found in both riparian woodland (Dhero) and nyika shrubland (Ratong), which it exploited more effectively than other apes because of its thick enameled, large molars useful for tough foods (Martin 1985) and its macaque-like limbs and feet (McCrossin et al. 1998). A similar pattern of wide ranging *Kenyapithecus* and forest-dependent other apes (*Oreopithecus*, *Simiolus*, *Proconsul*) persisted in grassland mosaics of Fort Ternan and Kapsibor at 14.4 Ma, when well-drained short-grass, wooded grassland was widespread. The appearance of grasslands so encouraging for victoriapithecine ancestors of vervets and colobines, was not so encouraging to apes, which remained rare components of the fossil fauna.

Reconstruction of rainfall from paleosols implies also vegetation belts (● Figure 13.6a), by comparison with Holocene climatic ranges of plant formations (Anhuf et al. 1999). There was rainforest in central Africa during the past 20 million years as indicated by rare finds of fossil plants (Bancroft 1932, 1933), but evidence of rain forest has not yet been found in the East African areas of hominoid fossils (Retallack 1991a, Jacobs 2002). These interpretations (● Figure 13.6a) are well in accord with indications of vegetation from paleosol classification, profile

form and root traces (Retallack 1991a), as evidence that the climatic range of most vegetation types did not change over the past 20 million years.

An exception is the evolution of grasslands, which expanded their climatic range to displace extinct kinds of woodlands (● *Figures 13.6 and 13.9*). There is not yet any East African evidence of grasslands before 17.8 Ma, when crumb-textured, brown, simple (A-Bk) profiles of dambo were rare at Rusinga Island (Retallack et al. 1995) and bunchgrasses grew luxuriantly at Bukwa (Pickford 2002b). Well-drained, short-grass, sod-grasslands were widespread by 14.4 Ma (Retallack 1991a, Retallack et al. 2002) and well-drained, tall-grass, sod-grasslands expanded their climatic range considerably by 7 Ma (Wynn 2004a, b). Grasslands were a newly coevolved ecosystem of the Cenozoic, with grasses uniquely suited to grazing by virtue of their intercalary meristems, modular growth, basal tillering, and sod formation, and grazers uniquely suited to coarse grassy fodder by virtue of their wide muzzles, hypsodont teeth, and hard hooves (Retallack 2001a). A world without grasslands was transformed over some 20 million years to a Plio-Pleistocene world with grassland covering at least a quarter of the land surface. Holocene humans spread grassy agroecosystems to almost all parts of the world (Retallack 2001a). Neogene expansion of grasslands within the paleoclimatic belt roughly defined by the 300–750 mm per annum isohyet enabled grasslands to capture the planetary modal rainfall belt and most fertile soils, with consequences for global change including a significant contribution to global cooling (Retallack 2001b).

Before the expansion of the grasslands, an extinct woody vegetation occupied their climatic range (● *Figure 13.6*). I call these extinct dry woodlands poris (● *Table 13.2*), from a Hadza word for bush (Woodburn 1968). A good example of a poris ecosystem is the Tek paleosol of Rusinga Island (● *Figures 13.3 and 13.4*), which has yielded fossil primates and other mammals, snails, and plants (Pickford 1995; Retallack et al. 1995). Other examples of poris ecosystems include Tut, Choka, and Kwar pedotypes of Songhor and Koru dated at 20 Ma (Retallack 1991a). From the soil perspective, these paleosols have no clear modern analog because they are red and clayey, with large root traces and blocky structure like woodland soils, yet have shallow calcareous horizons like those found in modern African semiarid to subhumid grassland soils. Modern African soils with such shallow carbonate have very different crumb structure, fine root traces, and dark brown organic-rich surface horizons from abundant grasses.

From the paleoanthropological perspective, these ancient communities have no modern analogs because they have so many fossil hominoids, as many as six species in the Kwar pedotype (● *Figure 13.8*). No community has so many species of hominoids today. Nor do modern hominoids live in such dry climates. Mt. Assirik in Senegal with 956 (854–1224) mm mean annual precipitation is

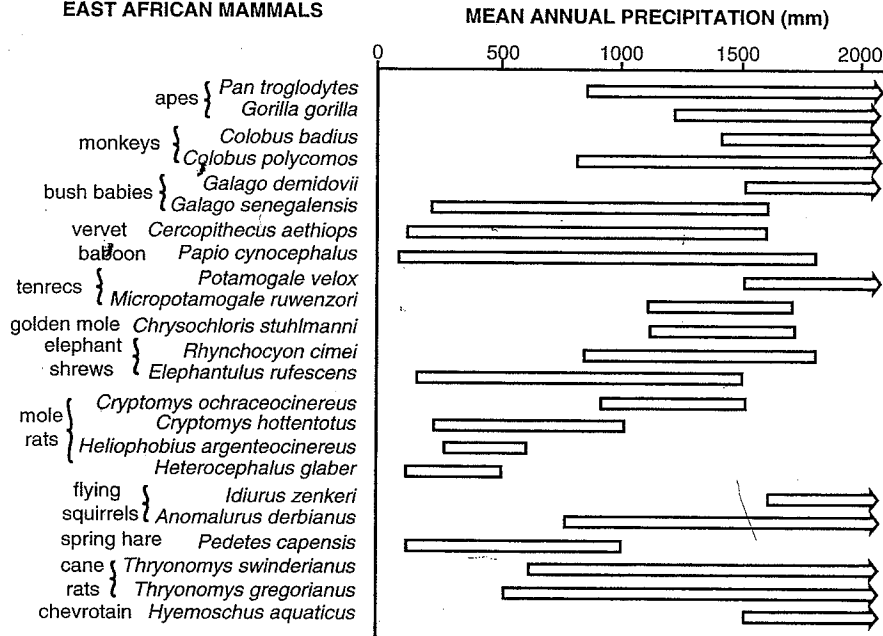
the driest climate with chimpanzees (Kappelman 1993), although Kingdon (2003) gives anecdotes of chimpanzees in wooded grassland. It is now clear that Miocene apes filled a variety of niches like those today filled by vervets, baboons, and colobines as well as apes (Retallack et al. 2002). Pori ecosystems such as the Kwar paleosol at Koru (20 Ma) also show peculiar associations of other mammals, including a mix of dry climate taxa, such as mole rats (*Bathyergoides*), with wet climate taxa such as flying squirrels (*Paranomalous*), giant elephant shrews (*Miorynthocyon clarki*), tenrecs (*Protenrec tricuspis*), golden moles (*Prochrysochloris miocaenicus*), and chevrotains (*Dorcatherium songhorensis*; Retallack 1991a). Similarly the Tut and Choka paleosols at Songhor (20 Ma) and Tek paleosols on Rusinga Island (17.8 Ma) have wet climate flying squirrels and tenrecs as well as dry climate mole rats and spring hares (Retallack 1991a; Retallack et al. 1995). These nonanalog combinations of fossil mammals can be explained by a theory of evolutionary replacement of pori with grassland within semiarid to subhumid regions. Before the advent of grasslands, woody vegetation became smaller in stature and biomass from wet to dry regions. This continuum was disrupted as grasslands evolved to usurp the climatic range of pori woodland. Grasslands expanded their range to create a biogeographic divide between Nyika shrubland and miombo woodland (● Figure 13.9).

Fossil primates of East Africa not only coped with changing mixes of animals but with changing climate and vegetation (● Figure 13.6). Wynn (2004b) has introduced the concept of evolutionary entropy to explain effects of climate and vegetation change on hominoid diversity. Climatically dry episodes encouraged grassland mosaic environments with a more varied landscape of open grassland and local woodland, and thus greater landscape disorder or negentropy. Wet episodes of forest vegetation presented more uniform landscapes of higher entropy. My compilation of hominoid diversity, originations, and extinctions (● Table 13.1, ● Figure 13.10) supports the view that dry episodes correspond with diverse primates, whereas wet episodes lead to extinctions, particularly of specialized arid-adapted taxa. The concept of ecosystem entropy in hominoid evolution is similar in some respects to Vrba's (1999) "turnover pulse hypothesis," but ecosystem entropy presents diffuse and long-term selection pressures, rather than episodic crises or "turnover pulses." Recent compilations of mammalian

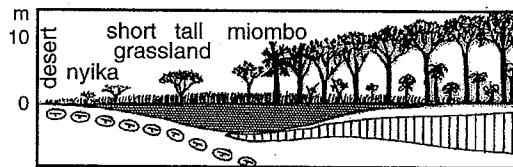
■ Figure 13.9

A scenario for stepwise evolution of East African grasslands with modern precipitation tolerances of African mammals related to those found fossilized in paleosols (Tut, Choka, Kwar) of pori woodlands that preceded the expansion of grasslands. The advent of grasslands disrupted formerly overlapping ranges of apes, bush babies, flying squirrels, mole rats and spring hares. Climatic ranges of modern mammals are from Kingdon (1971, 1974a, b, 1979) and of paleosols from Retallack (1991a); Retallack et al. (1995)

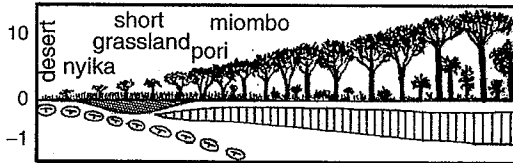
CLIMATIC RANGE OF LIVING EAST AFRICAN MAMMALS



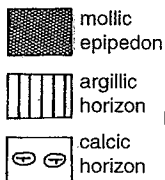
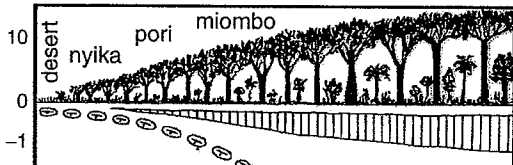
PLIOCENE-RECENT (0-7 Ma)
advent of tall sod grassland



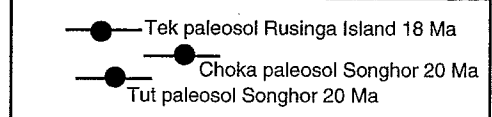
MIDDLE-LATE MIOCENE (7-18 Ma)
advent of short sod grassland



OLIGOCENE-EARLY MIOCENE (18-33 Ma)
desert rangeland and pori woodland



SELECTED NON ANALOG FOSSILIFEROUS PALEOSOLS



MEAN ANNUAL PRECIPITATION (mm)

■ Table 13.2

Comparison of extinct pori woodland with extant East African vegetation

Feature	Pori	Miombo	Nyika	Savanna
Vegetation	Dry woodland	Dry woodland	Dry bushland	Wooded grassland
Key genera	<i>Celtis</i>	<i>Brachystegia</i>	<i>Acacia</i>	<i>Combretum</i>
Floral origins	Zambezian	Zambezian	Zambezian	Eurasian
Spinosity	Unarmed	Unarmed	Spinose	Spinose
Leaf set	Semideciduous	Deciduous	Deciduous	Deciduous
Fruit size	Large	Large	Small	Small
Snails	<i>Cerastua</i>	<i>Limicolaria</i>	<i>Achatina</i>	<i>Pupoides</i>
Snail origins	Somalian	Somalian	Somalian	Somalian
Mammals	Apes, rodents	Antelope	Antelope	Antelope
Ungulates	<i>Walangania</i>	<i>Aepyceros</i>	<i>Tragelaphus</i>	<i>Connochaetes</i>
Primates	<i>Proconsul</i>	<i>Cercopithecus</i>	<i>Papio</i>	<i>Papio</i>
Mammal origin	Zambezian	Zambezian	Zambezian	Eurasian
Fire frequency	Low	High	High	High
Soil organics	Low	Low	Low	High
Soil fertility	High	Low	Low	High
Soil type	Alfisol	Oxisol, Vertisol	Aridisol	Mollisol, Vertisol
Parent material	Volcanic	Granitic	Granitic	Volcanic

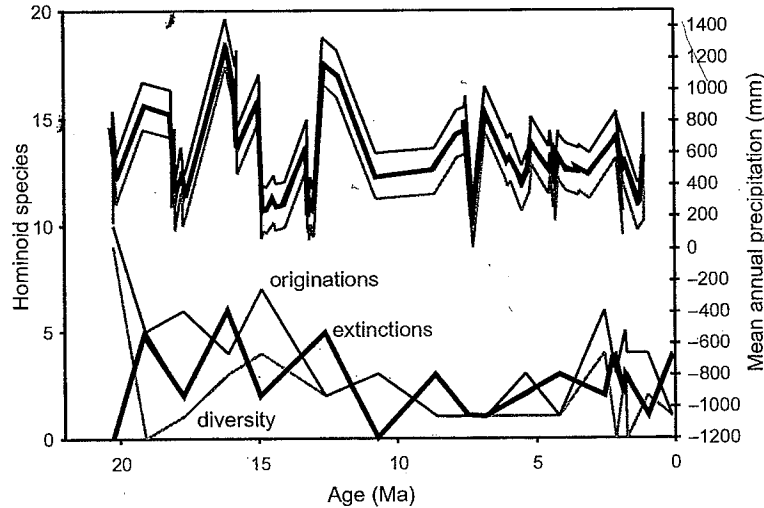
data from the Turkana region do not show such crises (Bobe et al. 2002), revealing instead an oscillating diversity compatible with less synchronized selection by ecosystem entropy.

A major caveat for such theories is the generally inferior fossil record of climatic wet phases because their soils and sediments are noncalcareous and so not favorable to the preservation of bone (Retallack 1998). We still have no primate fossil record from paleoclimatic wet phases of the early Miocene, but there are discoveries of wet climate human ancestors from 13 Ma (Hill et al. 2002), 6 Ma (Brunet et al. 2002; Galik et al. 2004) and 4–3 Ma (Carroll 2003). The soil-taphonomic bias against wet climate fossils makes the search difficult, not impossible (Peterhans 1993).

Each fluctuation in climate and vegetation presented new crises and opportunities to primates. My own correlation of climatic events with critical adaptations (● Table 13.1) is only an outline of a new research agenda, to be fleshed out with further studies of the critical intervals. The late Miocene paleosols and primate fossils of the Tugen Hills, for example, remain very poorly known compared with those of the Lake Victoria and Turkana basins. Nevertheless, there are general themes apparent from this compilation. We did not evolve from apes in one seminal event, but by a protracted process of growth and pruning of our evolutionary tree. Some specialized features such as procumbent incisors at 18 Ma evolved in dry grassy woodlands, but did not survive succeeding forest expansions (McCrossin and Benefit 1997). Some specialized features such as long arms

■ Figure 13.10

Mean annual precipitation and hominoid diversity, extinctions and originations in East Africa over the past 20 million years. The paleoprecipitation curve is from ● Figure 13.6. Hominoid data is from Pickford (1986b, 1987), Harrison (2002), Ward and Duren (2002), and Carroll (2003)



by 20 Ma for suspensory locomotion in forests did not persist through succeeding grassland expansions (Harrison 2002). Other forest adaptations such as a short-stiff back by 16 Ma (Pickford et al. 1999), erect stance by 6 Ma (Senut et al. 2001; Galik et al. 2004), and flat face by 3.5 Ma (Leakey et al. 2001) proved advantageous in the long term, just as did grassland adaptations, such as thick enamel by 18 Ma (Martin 1985; McCrossin and Benefit 1997), adducted hallux by 14.7 Ma (McCrossin et al. 1998), and long legs for endurance running by 1.8 Ma (Bramble and Lieberman 2004). Although each of these ideas could be debated individually, the general concept of human evolution as a generalist path through a gauntlet of environmental challenges (Potts 1996) is increasingly supported by a burgeoning fossil record (Carroll 2003). There will always be a need for dating and finding more human ancestor fossils, but paleosols now provide new evidence of evolutionary selection pressures with high temporal and spatial resolution.

Past hypotheses of a Miocene pluvial, lake and rain forest (Kent 1944; Leakey 1952; Andrews and Van Couvering 1976; Andrews 1996) and late Miocene grassland (Cerling 1992; Cerling et al. 1997a, b) find, as already reviewed, a counterpart in long-standing theories linking late Miocene evolution of human upright stance or large brains with hunting prowess (Darwin 1872), vigilance against predators (Dart 1926), manipulation of small seeds (Jolly 1970), minimization of sun exposure (Wheeler 1984), long-distance walking (Rodman and

McHenry 1980) or running (Bramble and Lieberman 2004), squat feeding on the ground (Kingdon 2003), or moving between scattered fruiting bushes (Sanford 2003). Forest explanations of upright stance allowing erect-back climbing (Tuttle 1974), hands free to care for premature infants (Lovejoy 1981), phallic display to females (Tanner 1981), or intimidation displays to rivals (Jablonski and Chaplin 1993) move the event back into the "Miocene rain forest" (of Andrews and Van Couvering 1975; Andrews 1996), for which there is little evidence at hominoid sites in East Africa (Figure 13.6a). All these views can be reassessed in light of the improved record of East African paleosols, which suggests that there were many alternating habitats in East Africa, not just one seminal environmental shift. Darwin's (1872) idea that erect stance was linked to tool use and brain expansion has been out of favor since the discovery of "Lucy," when it became clear that erect stance preceded tool use and brain expansion by millions of years (Johanson et al. 1982). Erect stance now appears to have occurred in wooded habitats by 6 Ma (Pickford and Senut 2001; Vignaud et al. 2002), perhaps selected by the use of hands in nest provisioning (Lovejoy 1981). We are a mosaic of a complex evolutionary history and no longer need settle for simple or single allegories of human evolution.

13.6 Conclusions

There is a copious and informative fossil record of soils at most of the fossil ape and human ancestor sites in Africa, and study of these paleosols is now giving important insights into the long evolutionary career of our ancestors. The primate evolutionary radiation of the Neogene has been a long saga of changing habitats and adaptations. The fossil record of soils now allows us to address its complexity on a scale appropriate to primate home ranges and to recognize nonanalog habitats of the past. Our ancestors have run an evolutionary gauntlet of changing climate and vegetation that have spawned many evolutionary innovations, some of them lasting only to the next shift in climate and vegetation, but others of them proven to be of lasting value.

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