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Comment on the paleoenvironment of *Kenyapithecus* at Fort Ternan

The nature of former vegetation at the well known middle Miocene fossil site near Fort Ternan, Kenya, has been considered recently by both Kappelman (1991) and Cerling *et al.* (1991). The use of carbonate and organic matter isotopic composition of paleosols as paleoenvironmental indicators by Cerling *et al.* is a new and exciting development for paleoecology and paleopedology. In this case, however, woodland vegetation at Fort Ternan has been interpreted from the isotopic composition of sparry calcite cement and organic residues remaining from an episode of early burial cementation and decay, rather than on the micrite and organic matter of the original soil.

The depth function of isotopic values within the Fort Ternan profiles is uniform as in diagenetically altered paleosols (Lander, 1990), rather than showing less negative $\delta^{13}C$ of carbonate toward the surface and more negative $\delta^{13}C$ of organic matter toward the surface, as in some modern soils (Cerling *et al.* 1989; Ambrose & Sikes, 1991). The carbon and oxygen isotopic values of carbonate also fall within a well marked mode for carbonatite tuffs in the compilation of isotopic values by Dienes (1989; whose values for oxygen can be converted by the formula $\delta^{18}O_{SMOW} = 1 \cdot 03068 . \delta^{18}O_{PDB} + 30 \cdot 86$, according to Friedman & O'Neil, 1977). Also, the carbon in both carbonate and organic matter of the paleosols is unusually light (very negative) compared to that in modern soils (Cerling *et al.*, 1991). These are mere warning signals rather than fatal flaws, because Cerling *et al.* (1991) argue (1) that these soils were so productive that diffusion of atmospheric carbon dioxide was overwhelmed by soil respiration, (2) that these communities were stable for a long period of time and had a more closed canopy than modern soils studied, and (3) that igneous petrologists have overlooked the degree of soil alteration in their isotopic analyses of carbonatite tuffs. These qualifications place their interpretation near one extreme of the range previously proposed for Fort Ternan (Table 1).

Stronger doubts about the isotopic results come from the petrographic character of the samples analysed by Cerling *et al.* (1991). Some of the samples have pedogenic micrite with displacive and replacive textures, as well as a generation of pore-filling sparry calcite that fills undeformed root holes, soil cracks and the hollow culms of fossil grasses in such a way as to suggest it formed shortly after burial (specimens FT-R2, 6, 9, 12, 13, 14, 76, 77; photomicrographs of Retallack, 1991*b*, Figures 2.14 & 2.15). Other specimens low in the paleosol profiles (pedogenic C horizons) have much more sparry calcite than pedogenic micrite (samples FT-R10, 11, 15, 16, 18, 78). Other isotopically analysed samples from the base of lahars and nephelinitic sandstones showing no sign of soil formation have only the sparry cement formed early during burial (samples FT-R1, 74; photomicrographs of Retallack, 1991*b*, Figure 3.2). Surprisingly, all these petrographically and genetically diverse samples have nearly identical carbon isotopic composition of carbonates, presumably dominated by the conspicuous sparry cement. The source of the sparry calcite is not known. It could have come from

Table 1 Summary of interpretations of middle Miocene vegetation at Fort Ternan, Kenya

Interpretation	Evidence	Shortcomings	Reference
Mosaic of wooded grassland and grassy woodland	Identification of paleosols in soil classifications, interpretation of paleosol features and a small-scale catena of Chogo paleosols	Loss of organic matter and copious calcite cementation during early burial have altered appearance of the paleosols	Retallack et al., 1990; Retallack, 1991b; Retallack et al., 1990
Mosaic of wooded grassland and grassy woodland	Root traces and stump casts in paleosols and in preserved paleosol catena of Chogo paleosols	Root traces are not well preserved, mainly clay films with some calcareous rhizoconcretions	Retallack, 1991b
Wooded grassland	Identifications of fossil grasses from Onuria paleosol, their size and phytolith vs. stomatal density	Comparisons are entirely with modern grasses: few fossil grasses are known	Dugas & Retallack, in press; Retallack, 1992
Wooded grassland	Fossil pollen from type Chogo clay paleosol	Poorly preserved and small for palynological sample (284 grains)	Bonnefille, 1984
Grassy woodland	Taxonomy and size of fruits of Chogo eroded phase paleosol	Only 15 fossils found, not including small seeds found by sieving	Shipman, 1977; Retallack, 1991b
Grassy woodland	Identification of fossil snails largely from Chogo paleosols	Dominance by subulinids indicates unusual preservation or sampling	Pickford, 1984, 1985, 1986
Wooded grassland or grassy woodland	Striated microwear on fossil antelope teeth from Chogo paleosols	Found in only one species of antelope, not on other teeth	Shipman et al., 1981
Wooded grassland or grassy woodland	Marked taxonomic modernization of middle versus early Miocene mammals	Indicates some relative opening up of vegetation from early to middle Miocene, but not its extent	Pickford, 1981, 1984, 1986
Grassy woodland or bushland	Size, feeding and locomotor adaptations of mammals from Chogo paleosols	Middle Miocene faunas may not yet have evolved modern adaptations to open habitats	Andrews et al., 1979; Evans et al., 1981
Grassy woodland or bushland	Locomotor adaptation of antelope femoral heads from Chogo paleosols	Small sample size (seven femurs) pooled from several Chogo paleosols of antelope not yet adapted to grassland	Kappelman, 1991
Grassy woodland or bushland	Taxonomic affinities of antelope in Chogo paleosols	Open country antelope may not yet have evolved during middle Miocene	Thomas, 1984
Closed woodland or Afromontane grassland	Carbon isotopic composition of carbonate and organic matter in Chogo and Onuria paleosols	Same isotopic values as sandstones where the only carbonate is sparry calcite formed during burial	Cerling et al., 1991
Forest	Fossil flying squirrels and lorises	These fossils are rare fragments	Andrews & Walker, 1976

groundwater of the nearby volcanic slopes that were presumably forested or from renewed inputs of carbonatite tuff. I suspect, however, that it came from decay of small amounts of organic matter in the buried soil whose porosity was rapidly declining as cementation proceeded. These conditions could yield the observed isotopic composition according to the models of Cerling (1991). Such a diagenetic origin may also explain the soil-like difference of about 15‰ between carbon in carbonate and co-existing organic matter in these paleosols. Walkley-Black analyses of total organic carbon in these paleosols were no more than 0·17 weight percent (Retallack, 1991b, Appendix 5), whereas comparable soils of the Serengeti Plains of Tanzania have organic carbon contents up to 9% (de Wit, 1978; Jager, 1982) and forested soils of Kenya have values up to 5·64% (Thorp et al., 1960). Loss of about an order of magnitude of organic matter in paleosols compared with well drained surface soils is common (Stevenson, 1969) and is probably due to decomposition soon after burial (Retallack, 1991a,b). These effects, together with coalification, can appreciably alter the composition of organic matter in paleosols compared with soils (Schnitzer et al., 1990). Scarce altered remnants of organic matter in these buried soils are what were analysed by Cerling et al. (1991). Although this first attempt at a bulk isotopic analysis of the Fort Ternan paleosols was confounded by pervasive burial cementation, more sophisticated approaches to the isotopic systematics of different phases of carbonate and organic matter in these paleosols can be envisaged for the future.

Unlike isotopic analysis of paleosols, fossils have been used to interpret paleoenvironments since the last century. Kappelman's (1991) study of the functional morphology of antelope femoral heads, like some other paleozoological studies at Fort Ternan (Andrews & Evans, 1979; Andrews et al., 1979; Evans et al., 1981; Pickford, 1985) concluded that the vegetation there was woodland. Taphonomic studies of mammals at Fort Ternan have revealed paleo-gullys and other elements of the paleoenvironmental mosaic (Shipman et al., 1981; Shipman, 1986), but most published paleontological studies of fossil mammals and snails from there could not have detected this mosaic because they were based on collections pooled from different kinds of what can be termed Chogo paleosols (Retallack, 1991b).

A more serious logical flaw in such functional morphological studies is the assumption that antelope of a kind now best suited to woodland necessarily lived in woodland. Various studies (Vrba, 1980; Kappelman, 1984, 1991; Thomas, 1984) demonstrate that antelope ancestors were adapted to woodland and forest and that grassland-adapted antelope had not yet evolved by the middle Miocene. Hence middle Miocene antelope fossils could not indicate grasslands even if grasslands were present. Evolution of grassland adaptations was initiated during middle Miocene time, presumably in response to somewhat more open vegetation, and this led to a mammalian fauna discernibly more like the modern East African one (Pickford, 1981).

The fossil snails at Fort Ternan can be interpreted similarly. Even today snails are most diverse in forested regions, with subsets of genera extending into wooded grasslands and deserts (Van Bruggen, 1978; Heller, 1984). Fort Ternan snails are similar to modern woodland forms but very different and less diverse than from the early Miocene in southwestern Kenya (Pickford, 1985, 1986, 1987).

While adaptations in fossil faunas may have lagged slightly behind paleoenvironmental change, which is better assessed by independent means, the fossils do provide indispensable evidence of early co-evolution of grasses and grazers. Furthermore, the information that could be gleaned from fossils at Fort Ternan is far from exhausted. The cenogram approach for comparing size variation of fossil mammalian faunas could be productively employed

at Fort Ternan, as by Legendre (1986) for European mammalian faunas at the Eocene–Oligocene boundary. Faunas with a size distribution suggestive of forest were replaced by faunas more like those of dry open rangeland, an interpretation compatible with evidence from fossil soils (Meyer *et al.*, 1980; Freytet & Plaziat, 1982), but not with the taxonomy nor functional morphology of these European mammals. Similar approaches to East African fossil faunas could also prove revealing.

Just as with functional morphology or taxonomic comparisons of antelope, it can be assumed that features and kinds of paleosols were formed in similar environments to similar features and kinds of modern soils. Paleosols are in theory more direct reflections of environment than fossil organisms, because they are uncompromised by a hidden agenda in the form of a genome. In addition, much is now known about soil-forming factors (Birkeland, 1984) and soils of the Old World tropics (F.A.O., 1977*a,b*; Murthy *et al.*, 1982; Sombroek *et al.*, 1982) and this facilitates the testing of hypotheses concerning paleosols. None of the Miocene paleosols at Fort Ternan are like the thick, non-calcareous, humic Andepts under the present Mau Escarpment forests (Mbuvi & Njeri, 1977), contrary to Andrews & Walker (1976). Also different are the thick red soils in Precambrian basement under dry woodland and wooded shrubland, locally called "nyika", as in Tsavo West National Park, Kenya (Sombroek *et al.*, 1982), suggested as an analog on the basis of fossil snails by Pickford (1987). If these soils are thicker and better developed than the paleosols of Fort Ternan, desert soils around the carbonatite–nephelinite volcano Oldoinyo Lengai, Tanzania, are much less deeply weathered and richer in salts and zeolites (Anderson, 1963; Hay, 1989). The middle Miocene paleosols at Fort Ternan are most like those of the Serengeti Plain of Tanzania, both in their classification and in paleoenvironmentally significant features such as the thickness of their mollic epipedons and depth and morphology of calcic horizons (particularly profiles NaNo-A no. 26, NaLag no. 46 and Barsek no. 44 of de Wit, 1978). In addition, the Fort Ternan deposits are no longer thought to be an isolated fault block, but form a mappable horizon over at least 9·6 km (Pickford, 1984, 1986; Retallack, 1991*b*). Lateral variation in paleosols can be seen between several badlands exposures and is especially well documented in the large fossil quarry (Andrews & Walker, 1976; Retallack, 1991*b*). These interpretations of a middle Miocene grassland mosaic are developed at length elsewhere (Retallack, 1991*b*).

Isotopic analysis, vertebrate fossils and paleosols are all more or less indirect indicators of ancient vegetation at Fort Ternan, and on this question the fossil plants themselves should have the last word. Fruits and seeds from the Chogo clay eroded phase paleosol include taxa indicative of Zambezian grassy riparian woodland (Shipman, 1977; Retallack, 1991*a*, 1992), compatible with other plant evidence of widespread Miocene open grassy woodland ("miombo", "nyika") in Africa (Axelrod & Raven, 1978). The Chogo clay eroded phase paleosol also contains poorly preserved stump casts, but they are small, more like those of grassy woodland than of forest (Retallack, 1991*b*, 1992). The fossil fruit and seed flora is small (15 specimens) and lacks the very small propagules that are commonly retrieved by seiving (Tiffney, 1985). New excavations could help here.

Fossil pollen were found in only a few of the paleosol samples at Fort Ternan. The type Chogo clay only 7 m along the strike to the east of the Chogo clay eroded phase paleosol contained mainly the pollen of grasses (54%) and sedges (27%), with a minor component of palynomorphs of dry Afromontane forest, fellfield and marsh (Bonnefille, 1984). This small (only 284 grains) and poorly preserved assemblage demonstrates that future studies may not be in vain, and is especially remarkable considering the generally low preservation potential of grass pollen (Hamilton, 1982).
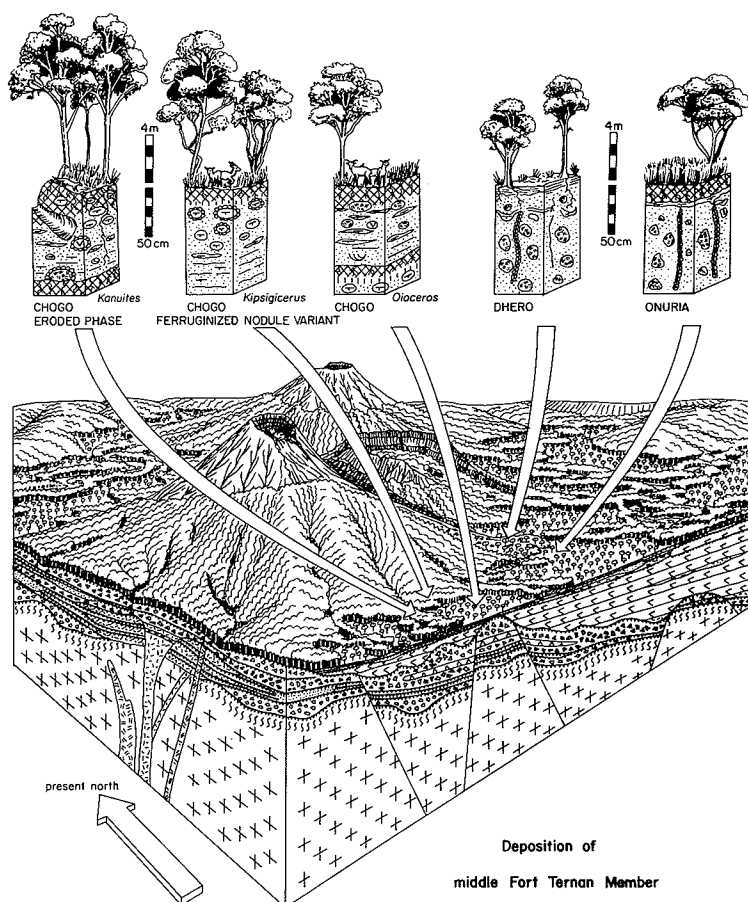
Figure 1. Interpreted paleoenvironment, soils and vegetation of southwestern Kenya during middle Miocene time some 14 million years ago (from Retallack, 1991*b*).

Finally, there are common fossil grasses at Fort Ternan, both within the Chogo clay eroded phase paleosol and above the Onuria clay paleosol, where grass fossils reach a density of $19,259/m^3$ of rock (Retallack *et al.*, 1990). The cuticles of the fossil grasses are well preserved in places and can be identified (Dugas, 1989; Dugas & Retallack, in press) using the computer identification key of Watson & Dallwitz (1989). So far, five distinctive species have been recognized belonging to or related to genera of open grassy woodland on impoverished soils (*Cleistochloa*, *Stereochlaena*), wooded grassland on clayey or rocky soils (*Pogoneura*, *Polevansia*, *Cyclostachya*), and desert and coastal open grassland on alkaline and even salty soils (*Distichlis*). The ratio of chloridoid/panicoid grasses and the percentage of chloridoids in this fossil grass flora are most like modern African grass floras of wooded grassland (Retallack, 1992). The relative density of phytoliths and stomates on three species of the fossil grasses with adequate amounts of preserved cuticle compared with 44 species of modern East African grasses all have dense phytoliths and sparse stomates found in grasses of open and wooded grasslands (Retallack, 1992). Studies of fossil grasses have been hampered in the past by their rarity (Thomasson, 1987), but this does not seem to be a problem at Fort Ternan or at several

other sites in East African Miocene volcaniclastic rocks (Hamilton, 1968; Jacobs & Kabuye, 1987).

In conclusion, there is now paleobotanical evidence for a mosaic of wooded grassland (type Chogo clay and Onuria paleosols), grassy woodland (Chogo clay eroded phase and ferruginized nodule variant paleosols), early successional woodland (Dhero clay paleosols), dry Afromontane forest, fellfield and marsh (from far travelled pollen) around the large nephelinitic-carbonatitic stratovolcano at Fort Ternan during middle Miocene time (Figure 1). This supports interpretations based on paleosols, and is not strongly contradicted by evidence of fossil insects, snails or mammals, but is at variance with evidence of carbon isotopic composition of paleosol carbonate and organic matter.

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