

Middle Miocene fossil plants from Fort Ternan (Kenya) and evolution of African grasslands

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Abstract.—New evidence from fossil plants at the Middle Miocene fossil quarry near Fort Ternan, Kenya, together with that from paleosols, allow reconstruction of a mosaic of early successional woodland (on Dhero paleosols), grassy woodland (on Chogo clay eroded phase and ferruginized nodule variant paleosols) and wooded grassland (on type Chogo and Onuria clay paleosols). This grassy open vegetation was on a high plateau of phonolite at the foot of a carbonatite-nephelinite stratovolcano, which probably supported dry Afromontane forest, alpine meadows, and marsh. This earliest savanna-mosaic vegetation yet documented from Africa, was probably recruited from dry lateritic soils elsewhere in Africa during climatic drying and cooling some 15 Ma. These early grassland ecosystems were very different from Early Miocene forest ecosystems of East Africa, but not altogether like modern grasslands either. Already present were grasses with dense growth and rich in silica bodies, and abundant antelope with moderately high crowned teeth and cursorial limb structure. These mammalian adaptations to grasslands, however, were not nearly so pronounced as they are in modern African grassland faunas, which include zebra and other Asiatic immigrants, as well as antelope. Grasses of the subfamily Chloridoideae and supertribe Panicanae were common in tropical Africa by Middle Miocene time, if not much earlier, but there is not yet evidence so far back in time for the grass supertribe Andropogonae which is now dominant in seasonally arid, overgrazed, and burned African grasslands.

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Introduction

A visit to an East African game park is like a trip back in time to the world of the Tertiary. These relatively unspoiled ungulate-grass ecosystems have formed the basis for interpreting assemblages of fossil mammals (Webb 1977, 1978) and grasses (Thomasson 1979, 1987; Crepet and Feldmann 1991) as old as Eocene in the Americas. The antiquity of such ecosystems in Africa, however, has been subject to debate, which is widely considered to have implications for the origin of human ancestors from apes (Hill and Ward 1988).

Grass pollen has been found as old as Eocene in Cameroon (Salard-Cheboldaeff 1979), when the Zaire Basin was climatically drier than at present and south of the equator (Furon 1968). Grass pollen is increasingly common in rocks of each succeeding geological epoch (Kedves 1971; Bonnefille 1984; Bonnefille et al. 1987). Possible African megafossil grasses are known as far back as Early Miocene (23 Ma) and indisputable grass fossils by Middle Miocene (14 Ma) time (Hamilton 1968; Palmer 1976; Thackray 1989; Jacobs and Kabuye 1987; Dugas and Retallack 1993).

A few grass fossils, however, do not necessarily mean that there was a grassland, because grasses are a conspicuous component of woodland and other kinds of vegetation. A case for Oligocene grasslands in Egypt has been made on the basis of sedimentological evidence, but remains unconvincing in light of more recent studies of sediments, paleosols, and fossil plants there (Bown et al. 1982). Debate continues on whether grassland appeared in Africa during Middle Miocene time (about 15 Ma) as represented by such Kenyan localities as Maboko and Fort Ternan, or did grasslands appear with hipparionine horses during Late Miocene time (9 Ma)? A Late Miocene appearance of open grassland and wooded grassland is favored by the evidence of generic composition and functional morphology of East African fossil mammals (Van Couvering 1980; Evans et al. 1981; Kappelman 1991), generic composition of fossil snail assemblages (Pickford 1985, 1987), generic composition and foliar physiognomy of Middle Miocene fossil dicot leaves (Jacobs and Kabuye 1987) and isotopic composition of paleosol carbonate (Cerling et al. 1991). Middle

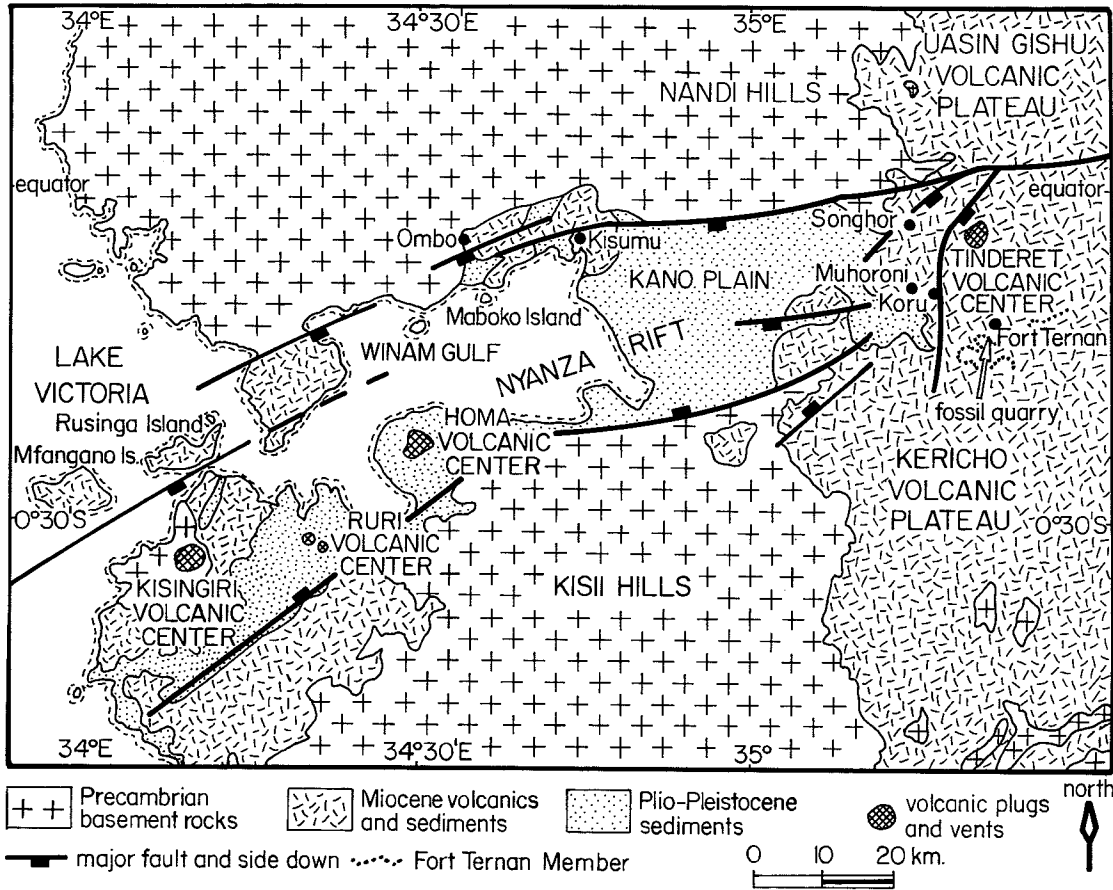


FIGURE 1. Location of Fort Ternan on the south flank of the Tinderet alkaline volcanic center, surrounded by the Middle Miocene Kericho Phonolites over Precambrian basement of southwestern Kenya.

Miocene grasslands, on the other hand, are in evidence from the suprageneric composition and tooth wear of East African fossil mammal assemblages (Shipman et al. 1981), palynological analysis of paleosols (Bonnefille 1984), and the identification and interpretation of factors in the formation of paleosols (Retallack et al. 1990; Retallack 1991). A new perspective can now be gained on this debate from the study of fossil plants from the well-known locality of Fort Ternan, Kenya.

Materials and Methods

This study concerns fossil plants from the large fossil quarry at Fort Ternan National Monument, 2 km southwest of Fort Ternan siding, on the Nairobi-Kisumu railway, in southwestern Kenya (fig. 1). The quarry is in

the Fort Ternan Member of the Kericho Phonolites (Retallack 1991). It is the best known Middle Miocene fossil site in Kenya, having yielded at least 11,000 fossil bones and teeth (Shipman et al. 1981), and 160 fossil snails (Pickford 1985), as well as millipedes, spiders, beetles, and plant remains (Pickford 1986).

Almost all of the fossils were found in two superimposed paleosols: the type Chogo clay and 7 m to the west its laterally equivalent Chogo clay eroded phase, overlying the Chogo clay ferruginized-nodule variant (Retallack et al. 1990; Retallack 1991). These paleosols have been dated from volcanic biotite at 14.4 ± 0.2 and 15.1 ± 0.7 m.y. old using the potassium-argon (K/Ar) technique, and 13.9 ± 0.3 m.y. using the $^{39}\text{Ar}/^{40}\text{Ar}$ stepwise degassing technique (Shipman et al. 1981; corrected by method of Dalrymple 1979). Poorly

preserved fossil grasses were found in Chogo paleosols, but a well-preserved assemblage of grasses was found in nephelinitic sandstone overlying an additional paleosol, the type Onuria clay, the top of which is 4 m higher within this large excavation (Retallack 1991). Chogo and Onuria paleosols are separated by sandstones, thick lahars, and two very weakly developed paleosols of the Dhero Series (Retallack 1991). These sediments were deposited rapidly, and the paleosols may not be very different in geological age. The Onuria assemblage is certainly no younger than a lava 15 m above it in the sequence, the Kericho Phonolite, which at Fort Ternan yielded biotite with ages of 12.6 ± 0.7 , 12.5 ± 0.4 , and 12.7 ± 0.15 using $^{39}\text{Ar}/^{40}\text{Ar}$ total fusion, stepwise degassing and K/Ar techniques, respectively (Shipman et al. 1981). This report concerns mainly fossil grasses above the Onuria paleosol, although some fossil fruits and seeds have been reported from this stratigraphic level as well (Shipman 1977). All the fossils are in the Paleontology Department of The International Louis Leakey Museum for African Prehistory of the Kenyan National Museums, Nairobi.

Taxonomic comparisons of the fossil flora at Fort Ternan and elsewhere in Africa were based on original reports of these fossil floras (summarized by Axelrod and Raven 1978, with additions by Jacobs and Kabuye 1987; Dugas and Retallack 1993) compared with compilations of living African vegetation by Rattray (1960) and White (1983), using also suprageneric classifications of Watson et al. (1985), Watson and Dallwitz (1989), and Heywood (1978).

Functional morphological studies included measurements of fossil grasses using a vernier micrometer. Volumes of dicot propagules were calculated from diameters and heights of approximating spheres, cones, and cylinders, as recommended by Tiffney (1985). Curve-fitting computer routines are those of Davis (1973).

Numbers of stomates and silica bodies per mm^2 were counted from grids drawn onto scanning electron micrographs of fossil grasses (Dugas and Retallack 1993) and living East African grasses (Palmer and Tucker 1981; 1983;

Palmer et al. 1985; Palmer and Gerbeth-Jones 1986, 1988). Information on habitat preferences of the species is from Clayton (1970), Clayton and Renvoize (1982), and Clayton et al. (1974). Included were all East African species with at least three illustrated areas of both intercostal stomates and costal silica bodies, and with adequate habitat information. Stomatal index (%) and phytolith index (%) were calculated according to the formula $100 \cdot D / (C + D)$, where D is the density of the feature per mm^2 and C is the density of cells per mm^2 (Kerp 1990). Both stomatal and phytolith densities were normalized to a mean of three or more estimates of costal cell density. These indices remove biases introduced by variation in cell size, which can be a problem for taxa as rich in polyploids as grasses.

Taxonomic Comparisons of Fort Ternan Fossil Plants

A well-established approach for reconstructing Neogene vegetation is the comparison of lists of fossil genera or families with living floras, and particularly the use of indicator taxa. This approach assumes that genera and families have not changed their habit, habitat or, associated taxa for some 14 m.y.: assumptions that may not be warranted for plants currently as rich in genera, species, and varieties as legumes and grasses.

Generic Comparison of Dicot Megafossils.—A small fossil flora of fruits, seeds, twigs, stipular spines, and grasses has been found in the Chogo clay eroded-phase paleosol (Shipman 1977; Retallack 1991). Like similar better-known fossil floras from Rusinga Island (Chesters 1957; Collinson 1983), few of these genera are especially good indicator taxa, and related living plants include a variety of trees, shrubs, and vines of rain forest to wooded grassland. As a group however, this assemblage is most like that of Zambezian woodland or wetter parts of the Somali-Masai *Acacia-Commiphora* wooded grasslands, particularly their riparian gallery woodland (table 1). This modern vegetation also now includes *Sterculia*: tentatively identified from an isolated leaf impression in tuffs below the Chogo clay ferruginized-nodule paleosol (by Andrews and Walker 1976).

TABLE 1. Comparison of the Middle Miocene fruit, seed, and twig fossil flora of the Chogo clay eroded phase paleosol with modern African vegetation (data from Shipman 1977; White 1983; Retallack 1991).

Fossil genus and species	Part found	Volume (mm ³)	Similar living plants	Habit	Habitat and vegetation
<i>Annonospermum</i> sp.	ruminant seed	394, 338	Annonaceae (custard apple family)	trees and shrubs, some vines	form genus: family common in Guineo-Congolian area and tropics worldwide
<i>Celtis rusingensis</i>	endocarp	463, 268, 268	<i>Celtis</i> spp. hackberry, Ulmaceae	trees and shrubs	Guineo-Congolian colonizing forest, Zambebian to Sudanian woodland, Somalia to Ponderland wooded grassland
Indeterminate	knobby exocarp	2623	cf. <i>Myrmecosycos messorius</i> Cucurbitaceae (gourds)	perennial herb, family also with vines	Somalia-Masai wooded grassland, around harvester ant nests; family widespread, tropical, temperate
Indeterminate	curved stipular spine		cf. <i>Acacia</i> spp. Leguminosae (pea family)	"thorn" trees and shrubs	Zambebian and Sudanian woodland, Somalia-Masai wooded grassland, Saharan and Namibian desert
<i>Acacia</i> sp.	curved pod		cf. <i>Acacia dolichocephala</i> Leguminosae	trees, shrubs	Sudanian riparian woodland: genus as above
<i>Icacinocarya</i> sp.	endocarp	1016	Icaninaceae (icacina vines)	trees, shrubs and vines	extinct genus, common in tropical forests
<i>Euphorbiotheca pulchra</i>	capsule	1175, 1175, 1042	Euphorbiaceae (spurge family)	trees, shrubs, herbs and succulents	form genus; family widespread, tropical and temperate
<i>Berchemia pseudo-discolor</i>	dried exocarp	326	<i>Berchemia discolor</i> bird plum (Rhamnaceae)	mainly shrubs, some trees	Zambebian dry deciduous and riparian forest, Somalia-Masai to Tongaland-Ponderland wooded grassland
<i>Zizyphus rusingensis</i>	dried exocarp	589, 589	<i>Zizyphus mauritana</i> , <i>Z. abyssinica</i> (Rhamnaceae)	"thorn" trees and shrubs	Zambebian and Sudanian dry woodland, Somalia-Masai wooded grassland, Saharan wadi shrubland
<i>Cnestis</i> sp.	endocarp	5532	<i>Cnestis ferruginea</i> (itch pod, Connaraceae)	tree; other species shrubs and vines	Guinea-Congolian rain and dry forests; other species in Zambebian woodland
<i>Leakeyia vesiculosa</i>	endocarp	838	<i>Ochrosia</i> sp. (Apocynaceae, oleanders)	tree; family with shrubs, herbs, succulents)	fossil genus; living genus, tropical forest in Australia and New Caledonia; family tropical and temperate
Indeterminate	culm		Gramineae	grass	widespread tropical to frigid

TABLE 2. Comparison of the Middle Miocene fossil palynoflora of the type Chogo clay with modern African vegetation (data from Heywood 1978; White 1983; Bonnefille 1984).

Similar living plants	No. of grains	Habit	Habitat
<i>Botryococcus</i> (Algae)	—	microscopic	aquatic blooms of colonies of unicells
Pteridophyta indet. (monolete spores)	2	ferns or club mosses	epiphytes and ground cover in moist places
<i>Juniperus</i> (conifer Cupressaceae)	4	trees and shrubs	in tropical Africa primarily in Afromontane shrubland; forest to desert elsewhere
<i>Podocarpus</i> (conifer, Podocarpaceae)	9	trees and shrubs	in tropical Africa primarily in Afromontane forest; lowland forests elsewhere
Amaranthaceae or Chenopodiaceae (cockscombs, pokeweeds)	7	mainly weedy herbs, some vines, shrubs	forest understory to alpine and desert vegetation, including salt-tolerant forms
<i>Celtis</i> (hackberry, Ulmaceae)	3	trees and shrubs	Guineo-Congolian colonizing forest, Zambezi-an to Sudanian woodland, Somalia-Masai to Pondoland-Tongaland wooded grassland
Urticaceae (nettles)	9	herbs, trees	forest to grassland, worldwide
Combretaceae (bush willows)	1	trees, shrubs, and vines	forest to wooded grassland, especially prominent in wooded grassland and mangal
<i>Acalypha</i> (Euphorbiaceae)	3	shrubs, trees, some herbs	Guineo-Congolian forest, Zambezi-an to Sudanian woodland, Somalia-Masai to Pondoland-Tongaland wooded grassland
cf. <i>Croton</i> (Euphorbiaceae)	1	trees	Guineo-Congolian forest, Zambezi-an woodland, Tongaland-Pondoland bushland
cf. <i>Lannea</i> (Anacardiaceae)	1	trees and shrubs	Guineo-Congolian forest, Zambezi-an woodland, Somalia-Masai to Tongaland-Pondoland wooded grassland
<i>Olea</i> sp. cf. <i>O. africana</i> (olive, Oleaceae)	2	tree	in tropical Africa primarily in dry Afromontane woodland; lowland forest elsewhere
<i>Plantago</i> sp. cf. <i>P. coronopus</i> (plantain, Plantaginaceae)	1	herb	species of sea cliffs in Europe; other species, including those of Africa, widespread colonists of disturbed, open ground
<i>Anthospermum</i> sp. (Rubiaceae, coffee family)	1	trees, shrubs, herbs	Afromontane grassland and heath; Zambezi-an and Sudanian woodland and clearings
Compositae or Tubiflorae (daisies, eyebrights)	2	herbs, some shrubs	common in lowland and montane grasslands, woodlands and forests worldwide
<i>Potamogeton</i> sp. cf. <i>P. pectinatus</i> (pondweed, Potamogetonaceae)	1	pondweed	submerged aquatic with some floating leaves, in ponds and lakes
Gramineae (grasses)	154	herbs, bamboos	common in grasslands, including montane and marsh, also in woodland and forest
Cyperaceae (sedges)	76	herbs	common in grasslands, including montane and marsh, also in woodland and forest
<i>Typha</i> sp. (Typhaceae, cattails)	2	herbs	emergent aquatic reeds of marsh, pond, river, and lake

Generic Comparison of Palynomorphs.—The type Chogo clay paleosol has yielded a small assemblage (only 284 grains) of pollen and spores (Bonnefille 1984). Especially noteworthy is the abundance of grasses (54%), because grass and other thin-walled pollen, such as that of *Acacia*, are seldom prominent in palynological assemblages (Hamilton 1982). This fossil assemblage of grasses and tropical woody dicots, is most like the wetter parts of Somalia-Masai *Acacia-Commiphora* wooded grassland or an open patch within Zambezi-an woodland (table 2). Also present were small

amounts of indicator taxa for dry montane forest (*Olea*, *Juniperus*, *Podocarpus*), alpine herbfield (*Artemisia* found in a separate palynomorph sample), and marsh (*Potamogeton*, *Typha*, *Botryococcus*). These kinds of vegetation may also have been nearby.

Generic Comparison of Fossil Grasses.—The nephelinitic sandstone above the type Onuria clay at Fort Ternan has yielded abundant fossil grasses. Among the well-preserved fossil grass cuticles are recognized five species (fig. 2): two of them comparable with *Cleistochloa*, another with *Stereochlaena*, a fourth with *Dis-*

TABLE 3. Taxonomic, physiological and habitat implications of taxa comparable to Middle Miocene fossil grasses and dicot from sandstone above the type Onuria paleosol (data from Watson and Dallwitz 1989)

Taxon	Classification	DIST statistic, related taxon	C _{3/4}	Distribution	No. of species	Habitats
Unknown	dicot		C ₃	unknown	—	mesophytic woody plant
<i>Cleistochloa</i>	Panicanae	0.0455 <i>Calyptochloa</i>	C ₃	Australasia (New South Wales, Queensland, New Guinea)	2	open habitats, dry sandstone, xerophytic
<i>Stereochlaena</i>	Panicanae	0.0308 <i>Digitaria</i>	C ₄	tropical Africa (Tanzania, Mozambique, Botswana, Transvaal)	6	open habitats, wooded grassland, grassy woodland, mesophytic, glycophytic, not commonly adventive
<i>Distichlis</i>	Chloridoideae	0.0322 <i>Reederochloa</i>	C ₄	Australia (Tasmania, Victoria, South Australia) and New World (Patagonia through Central America, USA to Canada)	12	open habitats, grassland, wooded grassland, seashore, coast, desert, halophytic, not commonly adventive
<i>Pogoneura</i>	Chloridoideae	0.0457 <i>Chloris</i>	C ₄	East Africa (Uganda, Tanzania)	1	wooded grassland, heavy clay soil, not commonly adventive
<i>Polevansia</i>	Chloridoideae	0.0517 <i>Microchloa</i>	C ₄	South Africa (Orange Free State, Cape, Lesotho)	1	open habitats, mountain grassland, mesophytic, glycophytic, not commonly adventive
<i>Cyclostachya</i>	Chloridoideae	0.0692 <i>Cathestechum</i>	C ₄	Mexico	1	open habitats, dry grassy woodland, not commonly adventive

tichlis, and a fifth indeterminate, but a chloridoid most like *Pogoneura*, *Polevansia*, and *Cyclostachya* (table 3). Only two of these genera still live in Africa: *Stereochlaena* as an understory to open *Brachystegia* woodlands on lateritic soils of southeast Africa (Clayton 1978; Clayton and Renvoize 1982) and *Pogoneura* in wooded grasslands in heavy clay soils in East Africa (Clayton et al. 1974). It is conceivable that fossils identified with *Cleistochloa* and *Distichlis* are really extinct genera, but this would not alter the conclusion that there is no modern African grassland comparable with this flora at the generic level. Nevertheless, these genera can be taken as an indication of dry, perhaps saline, open woodland to grassland that was not early in ecological succession after disturbance.

Most of the living genera comparable to the Fort Ternan fossils use the Hatch-Slack (C₄) photosynthetic pathway, as is universal

in African lowland tropical grasslands, as opposed to montane, temperate, and marsh grasslands and to woody dicots in which the Calvin cycle (C₃) is dominant. There are also two likely C₃ grass species in the Fort Ternan fossil flora (Dugas and Retallack 1993). However, the carbon isotopic composition of carbonates ($\delta^{13}\text{C}$ vs. PDB of -11.1‰ to -14.9‰) and of associated organic matter ($\delta^{13}\text{C}$ vs. PDB of -26.6‰ to -30.5‰) from my samples of type Onuria and Chogo paleosols from Fort Ternan (Cerling et al. 1991) indicates less than 10% C₄ grasses. I am uneasy with these isotopic results because similar isotopic values were obtained deep within the paleosols and in overlying sediments, where all the carbonate observed in thin section (Retallack 1991: fig. 3.2) is a nonpedogenic cavity-filling sparry calcite cement that probably postdates burial because it is similar to cement of associated lahars. Thus, the isotopic values re-

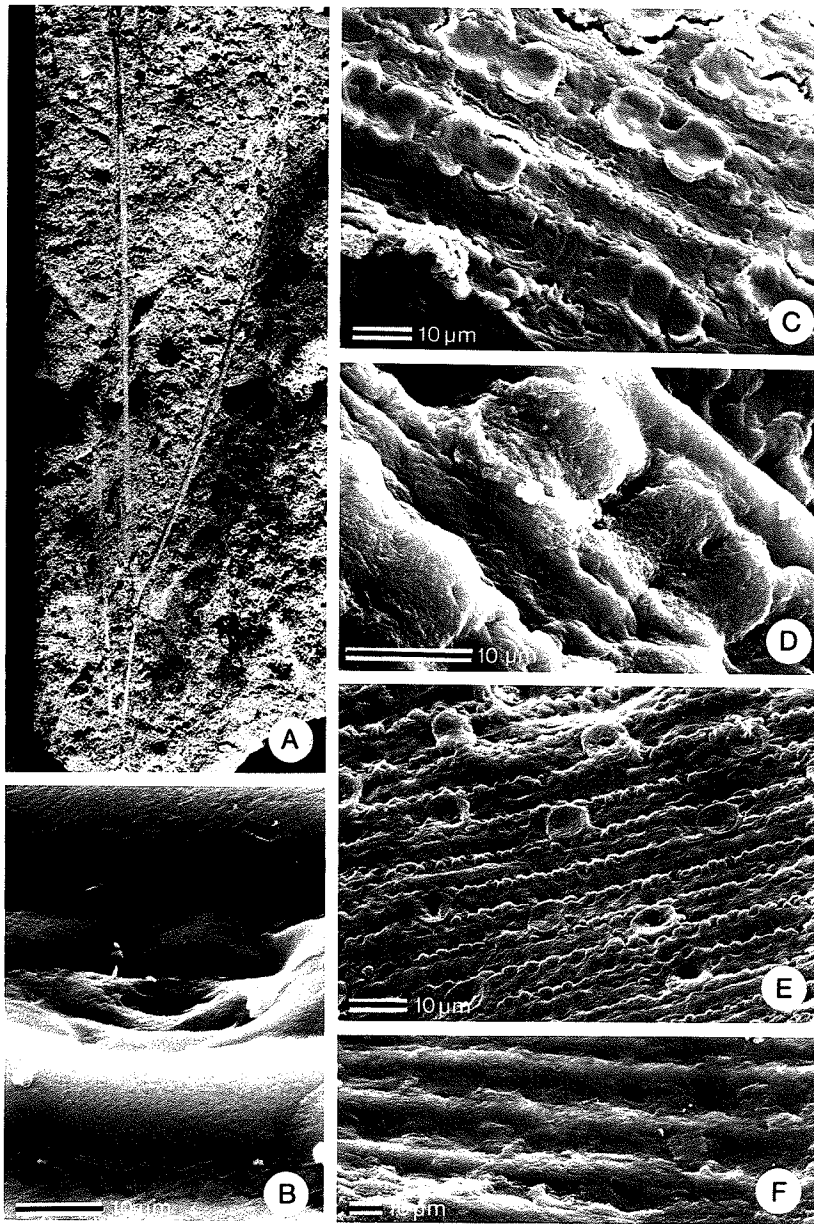


FIGURE 2. The five known Middle Miocene fossil grasses from Fort Ternan, Kenya, described by Dugas and Retallack 1993: A, B, *Stereochlaena miocenica*, branching culm and stomate from adaxial leaf sheath (KNMP-FT-F13126); C, *Cleistochloa kabuyis*, dumbbell-shaped silica bodies on abaxial leaf epidermis (KNMP-FT-F13130); D, *Cleistochloa shipmanae*, dumbbell-shaped silica body and accompanying cork cell on abaxial leaf epidermis (KNMP-FT-F13123); E, *Distichlis africana*, round silica bodies on abaxial leaf epidermis (KNMP-FT-F13127); F, Chloridoideae gen. et sp. indet., saddle-shaped silica bodies on abaxial leaf epidermis (KNMP-FT-F13128). Scale for A in cm; bars for all others 10 μm .

flect burial rather than soil formation, and future research needs to disentangle these signals with more careful attention to the nature of analyzed carbonate (Retallack in press).

Nevertheless, a significant C_3 component by comparison with modern Kenyan vegetation (Tieszen et al. 1979) could be an indication of forest, or of grassland that was seasonally wa-

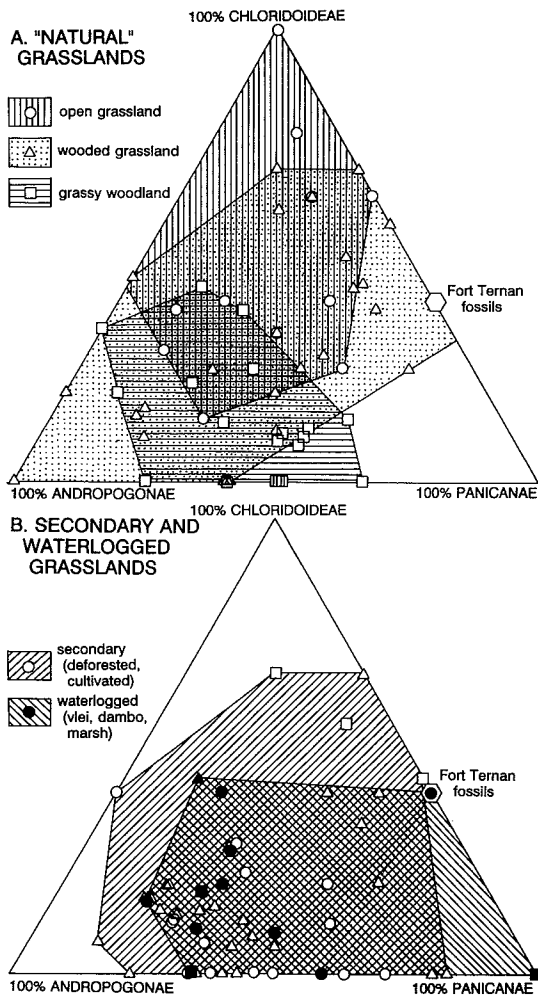


FIGURE 3. The proportion of species within Chloridoideae, Panicanae, and Andropogonae for "natural" lowland African grasslands (A) and for disturbed and marshy grasslands (B). Only lists of more than five species of these taxa from Rattray (1960) were used, with assignment to taxonomic categories following Watson and Dallwitz (1989).

terlogged or at elevations of 2000 to 3000 m. Of these alternatives, the lack of other grass subfamilies and chemical composition of the Onuria paleosol are evidence against the first two (Retallack et al. 1990). High elevation is likely, considering evidence of fossil pollen (Bonfille 1984) and snails found at Fort Ternan (Pickford 1985). The Tinderet volcanic center has not been active for 5 m.y. and the Nyanza Rift may still be subsiding (Pickford 1982), yet the Fort Ternan locality is still at 1660 m elevation.

Suprageneric Comparison of Fossil Grasses.— While the combination of grass genera above the Onuria paleosol is not typical in Africa today, the combination of Chloridoid and Panicoid subfamilies (in this latter case, all supertribe Panicanae) is typical for African tropical grasslands, as opposed to desert, marsh, and montane grasslands, or woodlands and forests, in which Pooideae, Arundinoideae and Bambusoideae are commonly present. Only above 3000 m, in marshes and in rain forests, are these other subfamilies abundant and diverse, so that most African grasslands can be considered to include only three suprageneric components: the subfamily Chloridoideae, and the supertribes Panicanae and Andropogonae of the subfamily Panicoideae. Comparison of proportions of these taxonomic elements for various modern grass floras listed by Rattray (1960), reveals some interesting generalizations (fig. 3). For example, most grasslands disturbed by fire, overgrazing, or cultivation include abundant and diverse Andropogonae. In addition, open and desert grasslands are richer in chloridoids and woodlands are richer in panicoid species, but there is a wide area of overlap that also includes wooded grasslands. Thus, tropical grasses of the Andropogonae can be considered broadly ruderal, the Chloridoideae tolerant and the Panicanae competitive in life-history characteristics, as defined by Grime (1979).

The suprageneric mix of fossil grasses at Fort Ternan is unlike that of a fire-prone, overgrazed, or otherwise disturbed habitat. Nor is it like an open grassland. The proportion of Chloridoideae to Panicanae in the Fort Ternan assemblage is compatible with interpretation as a wooded grassland, grassy woodland, or seasonally waterlogged ("dambo" or "vlei") grassland. Especially similar to the Fort Ternan assemblage in suprageneric composition are *Eragrostis* grasslands of seasonally flooded pans in a region of Zambesian dry woodland in Zimbabwe (map unit E6 of Rattray 1960), but these differ in having also an arundinoid component (*Phragmites*). Also similar are *Eragrostis* wooded grasslands of South Africa and Mozambique (unit E1), *Aristida* wooded grasslands of west and cen-

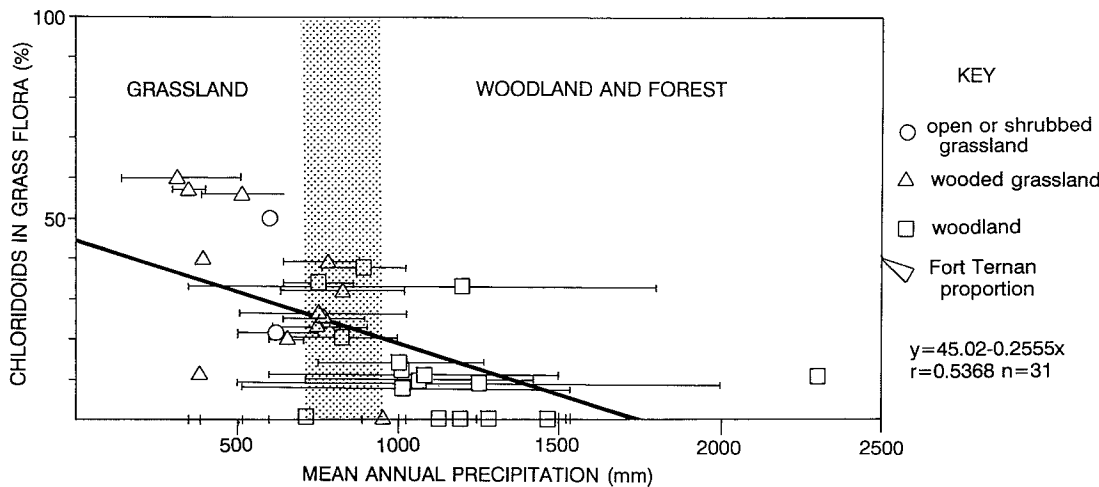


FIGURE 4. Correlation between the percentage of species within the Chloridoideae and mean annual rainfall for "natural" tropical grasslands of figure 3.

tral Africa (unit A14), *Cenchrus* wooded grasslands of Zimbabwe (unit CE1), and *Setaria* cultivated grassy woodlands of Ethiopia (unit S3).

The preference of chloridoid and panicoid grasses for tropical climates, and of chloridoids for dry climates has been known for some time (Hartley 1958; Hartley and Slater 1960). Indeed, there is an excellent relationship between the percentage of chloridoid species in grass floras and mean annual rainfall in the midwestern United States (Hartley and Slater 1960). A similar relationship can be seen in African floras (fig. 4). This analysis includes only modern floras of Rattray (1960) with at least five species of chloridoids or panicoids, and no indication of disturbed or marsh conditions. The relationship is not as highly correlated as that found in the United States (Hartley and Slater 1960), in part because of the wide ranges of precipitation given by Rattray (1960) for each of his map units. The relationship also has suffered because of taxonomic reassignments, particularly of the desert grass *Aristida* to the Arundinoideae (following Watson et al. 1985; Watson and Dallwitz 1989). Nevertheless, these results confirm that woodlands have a lower proportion of chloridoids than wooded grasslands: vegetation types separated by an ecotone at about 750–950 mm mean annual precipitation. Within the terms of this rela-

tionship, the fossil grass assemblage above the Onuria clay paleosol with 40% chloridoid species is most likely to have been a wooded grassland. The proportion of chloridoids at Fort Ternan is most like that of *Themeda* wooded grasslands of Tanzania (map unit T12 of Rattray 1960) and *Setaria* wooded grasslands of Angola (unit S2). Mean annual rainfall at Fort Ternan from comparison with these floras could have been within the range of 150–1000 mm, or less if the weakly correlated regression were used. This is compatible with more precise estimates of 250–450 mm based on compaction-corrected depth to the calcic horizon of the Onuria paleosol, and 320–590 mm for the type Chogo clay (Retallack 1991).

Functional Morphology of Fort Ternan Fossil Plants

Fossil plants from Fort Ternan can also be considered in terms of morphological features that may be related to environmental variables. This approach assumes that the spectrum of adaptations to environmental conditions found in ancient plants was similar to that found today, an assumption that may not hold for very early examples of ecosystems now showing considerable evidence of coevolution, such as grasslands and their grazers.

Dicot Fruit and Seed Size.—The size of dicotyledonous angiosperm propagules is small

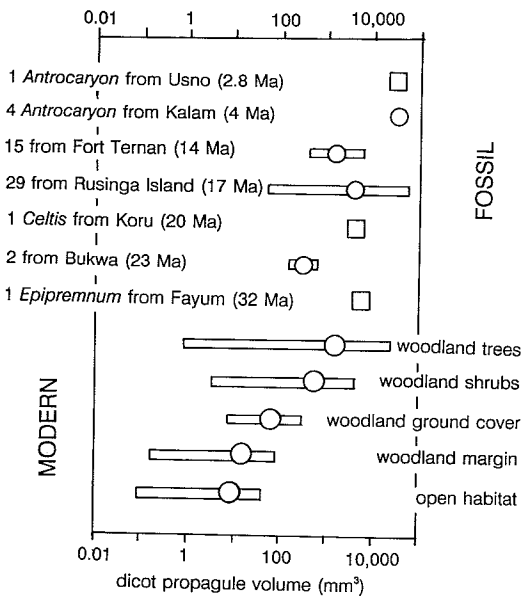


FIGURE 5. Volume of dicotyledonous propagules expected for various modern habitat types and found among fossil assemblages of fruits and seeds in East Africa (data from Hamilton 1968; Bonnefille and Letouzey 1976; Bown et al. 1982; Tiffney 1985; Retallack 1991).

in open habitats and becomes progressively larger in woodland habitats (Tiffney 1985). Within this spectrum, the small collection of 15 fruits and seeds known from the Chogo clay eroded phase paleosol matches best those of woodland (fig. 5), a conclusion that was also reached during studies of the similar fruit and seed flora of Rusinga Island, Kenya (Chesters 1957; Collinson 1983; Tiffney 1985). Prominent are woody endocarps and fleshy exocarps of the kind dispersed by animals, and large enough to sustain seedling growth under a canopy of trees. A serious shortcoming is the current paucity of these data. All published African studies lack the small seeds normally found in other collections of Tertiary forest fruits and seeds, presumably because collected by hand rather than by sieving (Tiffney 1985).

Stump and Log Size.—Natural casts in clay and calcite of root traces, stumps in growth position and loose logs have been found at Fort Ternan, but none of them are very big. Two nodular features 16 cm and 7.5 cm in diameter and 2.6 m apart, were found projecting from the surface of the Chogo clay

eroded-phase paleosol and interpreted as stumps of trees degraded by termite activity (Retallack 1991). Two better-preserved stumps with bark impressions were found in the type Dhero clay paleosol, a very weakly developed profile with abundant relict bedding between Chogo and Onuria levels. These stumps are 31 and 23 cm in diameter and distinctively fluted, with three or four boles of lesser diameter joining in a common root base. Fluted trunks with striated bark impressions are found in the thick bouldery lahars dividing paleosols. Logs seen embedded in the lahars are 8.8 and 7.4 cm in diameter, and a similar specimen found loose in the quarry is 13.2 cm in diameter (Retallack 1991: fig. 2.6). Earlier excavators at Fort Ternan have reported logs up to 50 cm diameter in the lahars (Shipman 1977).

Trunks of African wooded grassland trees have been measured in ecological studies to average about 10 cm in diameter, with some individuals up to 30 cm in diameter, whereas an average of 20 cm with some trunks up to 60 cm is found in woodland and an average of 20 cm with some up to 90 cm in dry and riparian forest (Hopkins 1962; Ward and Cleghorn 1964; Lawton 1967; Lawson et al. 1968; Malaisse et al. 1975; Rutherford and Kelly 1978). Comparable values and a general decline in tree stature from humid to dry climates are found in woody vegetation worldwide (Murphy 1975; Whittaker and Marks 1975). Striated bark, fluting, and multiple boles are common features of a variety of dry woodland and wooded grassland trees, such as *Cassia*, *Combretum*, *Terminalia*, and *Commiphora*. The fossil stumps and logs at Fort Ternan are larger than would be expected in desert vegetation, and lack the size, buttresses, and smooth bark found in stumps of woodlands and forests.

Stout-root traces were found in the Chogo clay ferruginized-nodule variant paleosol as well as in those paleosols with fossil stumps, but not in the type Onuria clay or type Chogo clay. The mix of stout-root traces and abundant fine-root traces of herbaceous plants is similar to that found under grassy vegetation in Africa today (Rutherford 1982). From these observations, a mosaic of wooded grassland,

grassy woodland, and early successional woodland was present in the various paleosols at Fort Ternan.

Grass Size.—The size of grasses has long been known to be related to mean annual rainfall, as strikingly shown by the transition from the sparse short grassland of the eastern Serengeti Plain of Tanzania to the tall grasslands in more humid regions to the west (Anderson and Talbot 1965). Similar relationships can be seen in other great grassland tracts, such as the Argentine pampas, the Russian steppe, and the North American prairie. In a detailed study of the widths of grass leaves, Redmann (1985) found that leaves of drought-resistant grasses of dry regions were generally less than 4 mm wide. Leaf widths of greater than 10 mm distinguish many kinds of forest grasses and bamboos (Watson et al. 1985). From this perspective, the Middle Miocene fossil grasses of Fort Ternan are neither like wire-grasses with their enrolled narrow leaves in arid regions, nor like broad-leaved and woody bamboos and canes in humid regions. All the fossil grasses are stout and mesophytic in appearance (fig. 6). *Stereochlaena miocenica* is represented by an incomplete specimen 23 cm long. In size and texture, the Fort Ternan grasses were most like those of grasslands intermediate between long and short types, such as the *Cynodon-Sporobolus* and *Pennisetum-Andropogon* grasslands of the Serengeti Plain (Anderson and Talbot 1965), which receive about 550 to 750 mm mean annual rainfall, only about 100 to 150 mm of which falls in the dry season from July to October (de Wit 1978).

Rooting Density and Depth.—Both Chogo and Onuria paleosols are riddled with fine-root traces forming a rhizogenous mull humus, dark-brown color, and granular structure at the surface (mollic epipedon). The density of the fossil grasses in the sandstone overlying the Onuria clay is also an indication of a lush grassy cover. The orientation of these grasses is evidence that they were pushed down in place of growth by flow from the north (Retallack et al. 1990). From the basal 17 cm of this sandstone, a block of matrix 30 × 15 × 6 cm in size was excavated grain by grain in the laboratory and yielded 50 grass fragments

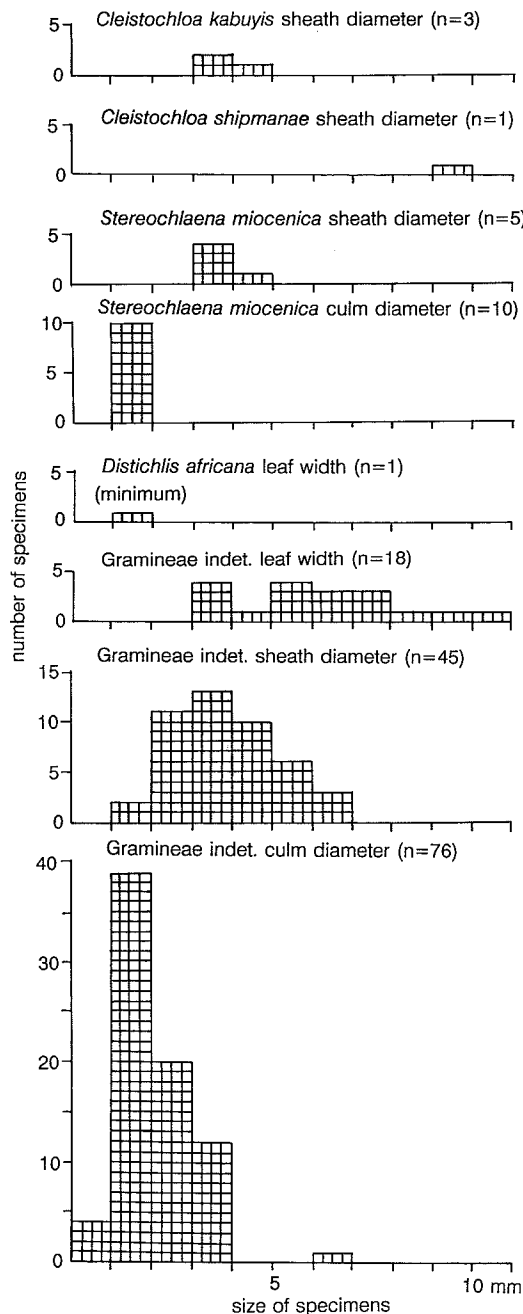


FIGURE 6. Size-frequency histograms for identified and unidentified Middle Miocene fossil grasses from the sandstone above the type Onuria clay paleosol, Fort Ternan, Kenya.

and 2 dicot fragments: a density of 19,259 grass fragments per m³ or 1155 per m² for a layer 6 cm thick.

The depth of the densely rooted zone is consistent laterally for up to 7 m within each

of the paleosols in this large quarry, and is 18 cm in the type Chogo clay paleosol, 24 cm in the Chogo clay eroded phase, 32 cm in the Chogo clay ferruginized-nodule variant and, 16 cm for the type Onuria clay. Compaction of this clayey granular upper portion of the paleosols may have been significant considering a likely volcanic overburden of 625 m, which could compact the soils to 74% of their former thickness, judging from standard compaction curves (Retallack 1991). Reconstructed depths of the rooting zone for the various paleosols mentioned are 24, 32, 43, and 22 cm, respectively. These depths are comparable to those for the *Sporobolus-Kyllinga* and *Cynodon-Sporobolus* grasslands (for Onuria and type Chogo) and for the *Pennisetum-Andropogon* grasslands (other Chogo) of Serengeti Plain (Anderson and Talbot 1965).

The pattern of rooting, lack of relict bedding or charcoal, low ratios of ferrous to ferric iron, and depletion of soda in these surface horizons, together with the well-developed calcareous nodules in the subsurface horizons of these paleosols are evidence that these were well-established grasslands of soils that had developed under such vegetation for at least thousands of years, rather than saline balds, marshes ("dambo" or "vlei"), or disturbed ground with grassy cover early in ecological succession (Retallack 1991).

Grass Silica Body and Stomatal Density.—Two features of grass epidermis that are readily measured on scanning electron microscopy (SEM) photomicrographs available of fossil and modern African grasses are the density of stomates and silica bodies, and these can be converted to a stomatal index and phytolith index in order to factor out varying cell size (Kerp 1990). Both stomates and phytoliths vary greatly in their abundance on grass cuticles, even on the same species and individual. Silica bodies are most abundant on the most heavily grazed species, as a natural defense to deter grazing (McNaughton and Tarrant 1983; Thomasson 1985). Silica bodies with complex shapes and sharp angles also may deter grazing more effectively than equidimensional round silica bodies (Herrera 1985). Stomates on the other hand are abundant in grasses of shady forest floors, but be-

come increasingly sparse, sunken, and overhung by papillae in grasses of dry habitats (Redmann 1985). These two variables are not independent, because it is grasses of open semiarid to subhumid habitats that are the most heavily grazed. The open vegetation is maintained by animal disturbance (Bell 1982). This theoretical optimum of phytolith index is seen in the data assembled here, especially in *Pogoneura biflora* (point 20 of fig. 7), which has phytoliths so closely spaced that they form a network. Fitting of a second-order polynomial curve to these data showed that this is more of a trend than a statistically tight relationship (the correlation coefficient is only 0.4).

The spectrum of these variables in living East African grasses can be better used to define broad fields of grasses of grassland and forest, with no clear distinction between grasses of open and wooded grassland or those of early successional, seasonally waterlogged, or well-drained grasslands (fig. 7). The fossil grasses of Fort Ternan group with grasses of open and wooded grasslands. *Distichlis africana* is notable for its exceptionally low density of stomates, which also are confined to stomatal grooves more deeply recessed than in the other fossil species. *Cleistochloa kabuyis* and *C. shipmanae*, on the other hand, have typical values for these epidermal features, and the latter species is marginal to the zone of overlap between forest and grassland grasses. All the fossil grasses were well defended against grazing from at least one species of common antelope at Fort Ternan, judging from the striated microwear on its teeth (Shipman et al. 1981).

Evolutionary Status of Fort Ternan Fossil Plants

Both taxonomic and functional conclusions concerning these fossil plants from Fort Ternan need to be evaluated in the context of their evolutionary status. Can these fossil plants really be compared in such detail with modern plants, or were they phyletically or adaptively distinct in ways that might compromise some of the conclusions presented here?

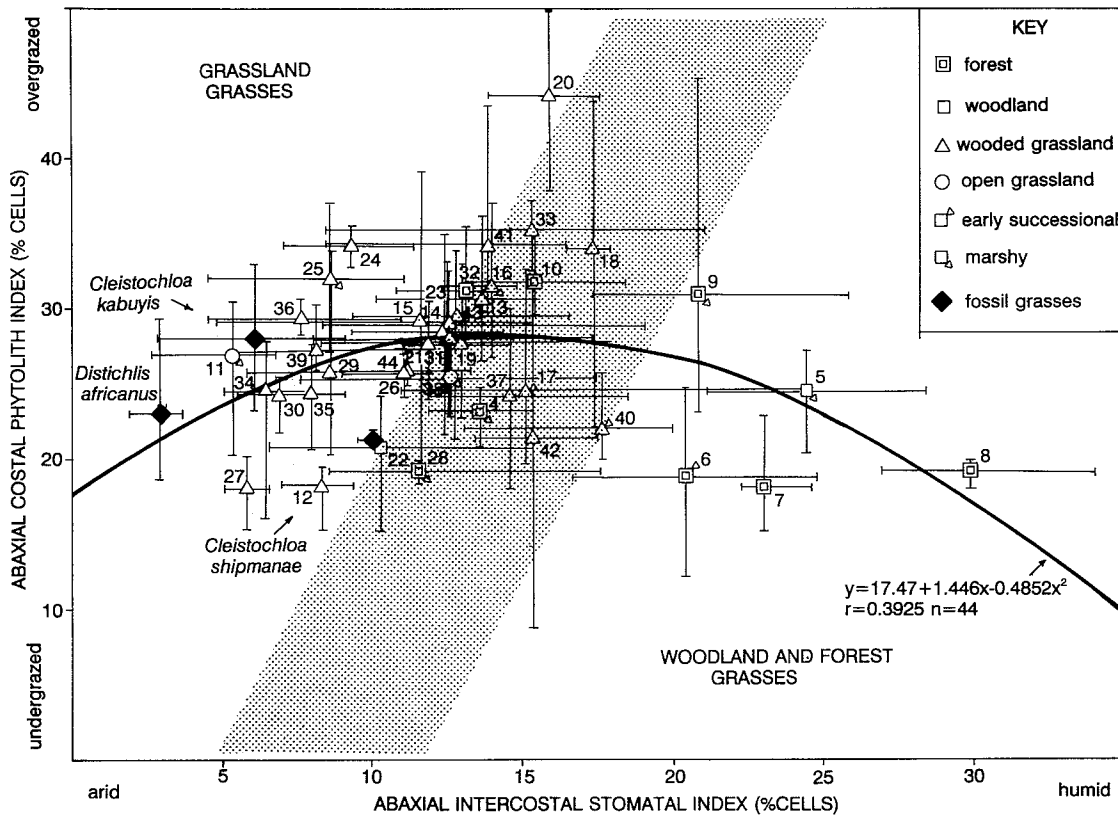


FIGURE 7. The mean and range for intercostal stomatal index and costal silica body index on abaxial leaf epidermes only, for three Middle Miocene fossil grasses from Fort Ternan, and for a variety of living East African grasses of known habitat (data from Clayton 1970; Clayton et al. 1974; Palmer and Tucker 1981, 1983; Clayton and Renvoize 1982; Palmer et al. 1985; Palmer and Gerbeth-Jones 1986, 1988; Dugas and Retallack 1993). The stippled zone includes both forest and grassland grasses. Living species: 4, *Oreobambos buchwaldii*; 5, *Oxytenanthera abyssinica*; 6, *Olyra latifolia*; 7, *Streptogyna crinita*; 8, *Maltebrunia leersioides*; 9, *Oryza punctata*; 10, *Humbertochloa greenwayi*; 11, *Aspithatherum glaucum*; 12, *Triraphis shinzi*; 13, *Stipagrostis uniplumis*; 14, *Schmidtia pappophoroides*; 15, *Acrachne racemosa*; 16, *Dinebra retroflexa*; 17, *Leptochloa obtusiflora*; 18, *Lintonia nutans*; 19, *Pogonarthria squarrosa*; 20, *Pogoneura biflora*; 21, *Trichoneura ciliata*; 22, *Chrysochloa orientalis*; 23, *Microchloa kunthii*; 24, *Oropetium capense*; 25, *Rendlia altera*; 26, *Sporobolus africanus*; 27, *Gilgichloa indurata*; 28, *Acroceras zizanoides*; 29, *Cenchrus ciliaris*; 30, *Eccoctocarpa obconiciventris*; 31, *Holcolemma inaequale*; 32, *Hylebates chlorochloae*; 33, *Capillipedium parvifolium*; 34, *Diheteropogon amplexens* var. *catangensis*; 35, *Elymandra glauca*; 36, *Heteropholis glauca*; 37, *Homozeugos eylesii*; 38, *Ischaemum afrum*; 39, *Phacelurus huillensis*; 40, *Sehima nervosa*; 41, *Sorghastrum bipennatum*; 42, *Themeda triandra*; 43, *Trachypogon spicatus*; 44, *Urelytrum digitatum*.

Dicot Fruits, Seeds, and Pollen.—The fossil flora of dicotyledonous angiosperm fruits and seeds from the Chogo clay eroded-phase paleosol have been assigned mostly to extinct species of genera with long geological histories (Chesters 1957; Collinson 1983). Only two extinct genera, *icacinocarya* (Icacinaceae) and *Leakeyia* (Apocynaceae) were recognized at Fort Ternan. The fossil pollen and spores from the type Chogo clay however have been compared only to modern genera and families (Bonfille 1984).

Fossil floras that may represent Guineo-Congolian rain forest, Guineo-Congolian dry forest, early successional dry forest, Sudanian dry woodland, and Zambezian riparian and miombo woodland are known as ancient as Early Miocene (Axelrod and Raven 1978; Retallack 1991). In contrast, the Middle Miocene fossil grasses and soils at Fort Ternan are evidence for the most geologically ancient grassland-woodland mosaic yet documented in Africa (Retallack et al. 1990), so that close correspondence in taxonomic composition

with modern grasslands would not be expected.

Comparison of the sizes of fossil propagules of dicots with those of modern woodlands is on a firmer footing, because these size ranges can be traced back in the fossil record of fruits and seeds to Early Eocene time (Tiffney 1985). Sizes of stumps and logs are an even more direct method of estimating vegetation stature. In all cases, estimates may be larger than the original actual sizes because of transport of fruits, seeds, and logs from forests higher on a volcano.

Grass Leaves and Stems.—Cladistic analyses of cuticular features of the fossil grasses and a selection of modern grasses, using herbaceous bambusoids as an outgroup, showed that the fossils group within separate clades within both Panicoideae and Chloridoideae (Dugas and Retallack 1993). The cladograms were limited to only 23 epidermal features observable on the fossils. Such problems do not affect the DIST statistic, a measure of similarity to other grass genera based on a large set of morphological and biochemical features (Watson and Dallwitz 1989). DIST values for genera most similar to the fossils range from 0.0692 to 0.0308 (table 3). The entire range of DIST values found in grasses is from 0.0032 for the New Zealand montane bambusoid *Petriella* to 0.0990 for the phyletically isolated South and Central American bambusoid *Steyermarkochloa*. The cladograms together with the DIST statistic indicate that these fossils belong to phyletically distinctive genera that arose neither during the most ancient adaptive radiation of grasses during Late Cretaceous to early Tertiary time, nor during adaptive radiations of the Neogene.

Distichlis may predate the tectonic disruption of Gondwana, although there are several salt-tolerant coastal species in this genus for which limited oceanic dispersal is conceivable (Crocker 1944; Christensen 1988). The living grasses *Amphibromus* and *Leptoloma* also show a New World-Australasian disjunct distribution (Hartley 1964). *Distichlis* does grow in open grasslands, but its evolutionary radiation in the New World has been mainly into highly alkaline and salty soils of desert grasslands (MacMahon 1988). Such dry in-

terior grasslands were widespread in South America by Eocene and in North America by Oligocene time, judging from evidence of fossil mammals and soils (Spalletti and Mazzoni 1978; Retallack 1983).

Cleistochloa and *Stereochlaena* may have been derived from ancient Gondwanan panicoid stocks of temperate forests. By Miocene time, lateritic soils low in fertility were widespread, and the forests had been thinned by northward drift of Africa and Australia through the dry subtropics. Many plants were extinguished by these environmental changes, but some genera more characteristic of wet forests prevailed in the drier impoverished soils (Beadle 1966; Hill 1990). By Middle Miocene time, *Cleistochloa* and *Stereochlaena* may have been adapted to low-nutrient lateritic soils which were then widespread on Precambrian and Mesozoic rocks in East Africa (McFarlane 1976).

At the generic level, the Fort Ternan grass flora is unusual for Africa, but at the subfamilial level it is not. Both Chloridoideae and Panicoideae are most diverse and have more endemic genera in Africa than other parts of the world, which could be taken as evidence for an evolutionary origin in East Africa-Madagascar before they separated (Hartley 1958; Hartley and Slater 1960). Andropogonae on the other hand have a distribution that can be interpreted as originally South Asian (Hartley 1964). Chloridoideae, Paniceae, and Andropogonae are proving to be robust monophyletic groups in cladistic analyses of grasses, in contrast to the paraphyletic nature of other subdivisions of grasses such as Arundoideae (Kellogg and Campbell 1987). The use of these three suprageneric groups for comparison with the Middle Miocene Fort Ternan grass flora is thus reasonable, although Andropogonae are not yet known to be that ancient in Africa.

Grass size and rooting depth and density are sound indicators of former vegetation. Less reasonable is the use of silica body and stomate density of modern African grasses for comparison with the Fort Ternan fossils. Although the Chogo paleosols have yielded one of the oldest antelope-dominated fossil faunas in Africa, as well as very ancient giraffes,

and such tree-destroyers as rhinos, gomphotheres, and deinotheres (Shipman et al. 1981; Shipman 1986), the limb proportions, tooth hypsodonty, and other adaptive features of the fauna are all more typical of woodland than of grassland faunas today (Evans et al. 1981; Kappelman 1991). This fauna would not have been as destructive of vegetation as a modern hard-hooved, hypsodont grassland fauna, so that the ecotone between grassland and woodland may well have been under drier climatic conditions (closer to 400 mm) than now (about 750 or more mm; Retallack 1991). Even today in Africa, it has been widely observed that vegetation structure in regions receiving 400–1000 mm rainfall is more clearly related to ungulate stocking density than to rainfall or other climatic variables (Norton-Griffiths 1979; Bell 1982). The animals of East African grasslands, like the vegetation, have probably evolved since Middle Miocene time when increased soil fertility and drier climate were first clearly established as primary selective pressures.

A Scenario for Evolution of East African Grasslands

During Middle Miocene time, Zambezian grassy woodlands were already widespread on extensive lateritic soils on Precambrian and Mesozoic basement rocks (Axelrod and Raven 1978), as a source for propagules for volcanic soils of carbonatite-nephelinite volcanoes, such as the one active near Fort Ternan 14 Ma (Retallack 1991). Carbonatite ash is salty for several hundred years and remains unusually calcareous after thousands of years (Hay 1989), so that phosphate procurement in such soils may have been as difficult as it is in modern highly calcareous soils (Stevenson 1986). These soils (calcareous Inceptisols, Mollisols) may not initially have been much more fertile for plants than the lateritic soils nearby (Oxisols, Ultisols). Derivation from "sour" grasses of open woodlands on dry, low-nutrient, and lateritic soils may be a part of the reason for the distinctive composition of the fossil grass flora from Fort Ternan.

Another reason for the distinctive nature of the Fort Ternan grass flora is evolution since Middle Miocene time. The less petro-

logically alkaline phonolites and trachytes, such as the voluminous Middle Miocene Kericho Phonolites, presented new opportunities for plants. Compared with laterites, carbonatites and nephelinites, they weather to more fertile soils of a kind (Mollisols and Vertisols) that now support the most productive wooded grasslands. The evolution of "sweetgrass" (or "dry eutrophic savanna" of Bell 1982) ecosystems may have been initiated during Middle Miocene climatic drying and spread of fertile volcanic soils.

The antelope- and giraffe-dominated Fort Ternan mammal assemblage that appears so abruptly in East Africa about 15 Ma (Pickford 1985) had already coevolved to a limited extent with grasses, though clearly not to the extent of modern grassland mammals of the Old World tropics (Evans et al. 1981; Kappelman 1991). The antelope had hooves, slender limbs, and moderately high crowned teeth, and the grasses were dense and liberally studded with silica bodies, perhaps because of limited coevolution in dry areas elsewhere in Africa (Bernor 1983). Although grasslands appeared in Africa during a period of climatic drying and cooling recorded in sequences of paleosols (Retallack 1991) and deep-ocean cores around the world (Kennett 1982), some of their success during Middle Miocene time may have been due to initial coevolution in directions that culminated in ecosystems of modern East African game parks.

The entry of hipparionine horses into Africa some 9 Ma heralded the appearance of a much more obviously grassland-adapted mammal fauna (Van Couvering 1980). It could be that grasses of the supertribe Andropogonae, such as *Themeda* and *Hyparrhenia*, tolerant of fire, heavy grazing, and harsh monsoonal seasonality, also spread through Africa at that time. Andropogonae are thought to have originated in South Asia (Hartley 1964), and have been encouraged in African grasslands, including such "natural" grasslands as those of the Serengeti Plain, by human disturbance (Norton-Griffiths 1979). Cuticular remains of Andropogonae are common in Pleistocene lake beds (Palmer 1976), but are not yet known earlier as fossils.

A common motivation for the reconstruction of East African Neogene vegetation has been an assumption that the earliest grasslands somehow played a role in the transition from ape to human (Hill and Ward 1988). However, the appearance of grassland 15 Ma was not at all encouraging to human evolution. Ape fossils are abundant in Early Miocene rocks of East Africa with their forested paleosols, but are very rare in Middle and Late Miocene rocks with grassland paleosols. Apes, such as *Kenyapithecus wickeri* at Fort Ternan, have been found in place only in wooded parts of the mosaic (Chogo clay eroded-phase paleosol: Retallack et al. 1990; Retallack 1991). Vervets, baboons, and other monkeys have a respectable and improving Middle and Late Miocene fossil record, at least in part within what have been interpreted as grasslands (Andrews 1981). In contrast, our remote apelike ancestors may have avoided these new grasslands, if consistently negative evidence can be trusted. The most ancient fossils of our australopithecine ancestors yet known in both woodland and grassland paleosols are only 4 m.y. old (Retallack 1990, 1991; Radosevich et al. 1992). Perhaps such basic human adaptations as erect stance evolved in forests and woodlands (Lovejoy 1981), where bone was not preserved (Retallack 1984). Grasslands may have been less significant for the ape-australopithecine transition than is widely thought.

Acknowledgments

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Literature Cited

- Anderson, G. D., and L. W. Talbot. 1965. Soil factors affecting the distribution of grassland types and their utilization by wild animals on the Serengeti Plains, Tanzania. *Journal of Ecology* 53:33-56.
- Andrews, P. 1981. Species diversity and diet in monkeys and apes during the Miocene. Pp. 25-61 in C. B. Stringer, ed. *Aspects of human evolution*. Taylor and Francis, London.
- Andrews, P., and A. Walker. 1976. The primate and other fauna from Fort Ternan, Kenya. Pp. 279-304 in G. L. Isaac and E. R. McCown, eds. *Human origins: Louis Leakey and the East African evidence*. Benjamin, Menlo Park, Calif.
- Axelrod, D. I., and P. H. Raven. 1978. Late Cretaceous and Tertiary vegetation history. Pp. 77-130 in M.J.A. Werger and A. C. Van Bruggen eds. *Biogeography and ecology in Southern Africa*. Junk, The Hague.
- Beadle, N.C.W. 1966. Soil phosphate and its role in molding segments of the Australian flora, with special reference to xeromorphy and sclerophylly. *Ecology* 47:991-1007.
- Bell, R.H.V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. Pp. 193-216 in B. J. Huntley and B. H. Walker eds. *Ecology of tropical savannas*. Springer, Berlin.
- Bernor, R. L. 1983. Geochronology and zoogeographic relationships of Miocene Hominoidea. Pp. 21-64 in R. L. Ciochon and R. S. Corruccini, eds. *New interpretations of ape and human ancestry*. Plenum, New York.
- Bonnefille, R. 1984. Cenozoic vegetation and environments of early hominoids in East Africa. Pp. 579-612 in R. O. Whyte, ed. *The evolution of the East Asian environment*. Vol. II. Palaeobotany, palaeozoology and palaeoanthropology. Centre of Asian Studies, University of Hong Kong.
- Bonnefille, R., and R. Letouzey. 1976. Fruits fossile d'*Antrocarylon* dans la Vallée de l'Omo (Éthiopie). *Adansonia* 16:65-82.
- Bonnefille, R., A. Vincens, and G. Buchet. 1987. Palynology, stratigraphy and paleoenvironment of a Pliocene hominid site (2.9-3.3 M.Y.) at Hadar, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 60:249-281.
- Bown, T. M., M. J. Kraus, S. L. Wing, J. G. Fleagle, B. H. Tiffney, E. L. Simons, and C. F. Vondra. 1982. The Fayum primate forest revisited. *Journal of Human Evolution* 11:603-632.
- Cerling, T. E., J. Quade, S. R. Ambrose, and N. E. Sikes. 1991. Fossil soils, grasses and carbon isotopes from Fort Ternan, Kenya: grassland or woodland? *Journal of Human Evolution* 21: 295-306.
- Chesters, K.I.M. 1957. The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica* B101:30-71.
- Christensen, N. L. 1988. Vegetation of the southeastern coastal plain. Pp. 317-363 in M. G. Barbour and W. D. Billings, eds. *North American terrestrial vegetation*. Cambridge University Press, Cambridge.
- Clayton, W. D. 1970. Gramineae (part 1). Pp. 1-176 in E. Milne-Redhead and R. M. Polhill, eds. *Flora of tropical East Africa*. Crown Agents for Oversea Governments and Administrations, London.
- . 1978. The genus *Stereochlaena*. *Kew Bulletin* 33:295-298.
- Clayton, W. D., and S. A. Renvoize. 1982. Gramineae (part 3). Pp. 451-898 in R. M. Polhill, ed. *Flora of tropical East Africa*. Balkema, Rotterdam.
- Clayton, W. D., S. M. Phillips, and S. A. Renvoize. 1974. Gramineae (part 2). Pp. 177-450 in E. Milne-Redhead and R. M. Polhill, eds. *Flora of tropical East Africa*. Crown Agents for Oversea Governments and Administrations, London.
- Collinson, M. E. 1983. Revision of East African Miocene floras: a preliminary report. *Newsletter of the International Association for Angiosperm Paleobotany* 8(1):4-10.
- Crepet, W. L., and G. D. Feldmann. 1991. The earliest remains of grasses in the fossil record. *American Journal of Botany* 78: 1010-1014.
- Crocker, R. L. 1944. Soil and vegetation relationships in the lower southeast of South Australia 68:144-172.
- Dalrymple, G. B. 1979. Critical tables for conversion of K-Ar ages from old to new constants. *Geology* 7:558-560.
- Davis, J. C. 1973. *Statistics and data analysis in geology*. Wiley, New York.
- de Wit, H. A. 1978. *Soils and grassland types of the Serengeti Plain (Tanzania)*. Center for Agricultural Publishing and Documentation, Wageningen, Netherlands.

- Dugas, D. P., and G. J. Retallack. 1993. Middle Miocene fossil grasses and wooded grassland at Fort Ternan, Kenya. *Journal of Paleontology* 67(1).
- Evans, E.M.N., J.A.H. Van Couvering, and P. Andrews. 1981. Palaeoecology of Miocene sites in western Kenya. *Journal of Human Evolution* 10:343-384.
- Furon, R. 1968. *Geologie de l'Afrique*. Payot, Paris.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Wiley, New York.
- Hamilton, A. C. 1968. Some plant fossils from Bukwa, Uganda. *Journal* 32:157-164.
- . 1982. *Environmental history of East Africa*. Academic Press, New York.
- Hartley, W. 1958. Studies on the origin, evolution and distribution of the Gramineae. II. The tribe Paniceae. *Australian Journal of Botany* 6:343-357.
- . 1964. The distribution of grasses. Pp. 29-46 in C. Barnard, ed. *Grasses and grasslands*. Macmillan, London.
- Hartley, W., and C. Slater. 1960. Studies on the origin, evolution and distribution of the Gramineae. III. The tribes of the subfamily Eragrostoideae. *Australian Journal of Botany* 8:256-276.
- Hay, R. L. 1989. Holocene carbonatite-nephelinite tephra deposits of Oldoinyo-Lengai, Tanzania. *Journal of Volcanology and Geothermal Research* 37:77-91.
- Herrera, C. M. 1985. Grass/grazer radiations: an interpretation of silica body diversity. *Oikos* 45:446-447.
- Heywood, V. H., ed. 1978. *Flowering plants of the World*. Oxford University Press, Oxford.
- Hill, A., and S. Ward. 1988. Origin of the Hominidae: the record of African large hominid evolution between 14 My and 4 My. *Yearbook of Physical Anthropology* 31:49-83.
- Hill, R. S. 1990. Evolution of the modern high latitude southern hemisphere flora: evidence from the Australian macrofossil record. Pp. 31-42 in J. G. Douglas, ed. *Proceedings of the Third International Organization for Paleobotany Conference*, Melbourne. University of Melbourne.
- Hopkins, B. 1962. Vegetation of the Olokmeji Forest Reserve, Nigeria. *Journal of Ecology* 50:559-598.
- Jacobs, B. F., and C.H.S. Kabuye. 1987. A middle Miocene (12.2 m.y. old) forest in the East African Rift Valley. *Journal of Human Evolution* 16:147-155.
- Kappelman, J. 1991. The paleoenvironment of *Kenyapithecus* at Fort Ternan. *Journal of Human Evolution* 20:95-129.
- Kedves, M. 1971. Présence de sporomorphes importants dans les sédiments préquaternaires Egyptiens. *Acta Botanica Hungarica* 17:371-378.
- Kellog, E. A., and C. S. Campbell. 1987. Phylogenetic analysis of the Gramineae. Pp. 310-322 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth, eds. *Grass systematics and evolution*. Smithsonian Institution Press, Washington, D.C.
- Kennett, J. P. 1982. *Marine geology*. Prentice-Hall, Engelwood Cliffs, N. J.
- Kerp, H. 1990. The study of fossil gymnosperms by means of cuticular analysis. *Palaiois* 5:548-569.
- Lawson, G. W., J. Jenik, and K. O. Armstrong-Mensah. 1968. A study of a vegetation catena in Guinea savanna at Mole Game Reserve (Ghana). *Journal of Ecology* 56:505-522.
- Lawton, R. M. 1967. The conservation and management of the riparian evergreen forests of Zambia. *Commonwealth Forestry Review* 46:223-232.
- Lovejoy, C. O. 1981. The origin of man. *Science* (Washington, D. C.) 211:341-350.
- MacMahon, J. A. 1988. Warm deserts. Pp. 231-264 in M. G. Barbour and W. D. Billings, eds. *North American terrestrial vegetation*. Cambridge University Press, Cambridge.
- Malaisse, F., R. Freson, G. Goffinet, and M. Malaisse-Mousset. 1975. Litter fall and litter breakdown in miombo. Pp. 137-152 in F. B. Golley and E. Medina, eds. *Tropical ecological systems*. Springer, New York.
- McFarlane, M. J. 1976. *Laterite and landscape*. Academic Press, New York.
- McNaughton, S. J., and J. L. Tarrants. 1983. Grass leaf silicification: natural selection for an inducible defense against herbivores. *Proceedings of the National Academy of Sciences, USA*. 80:790-791.
- Murphy, P. G. 1975. Net primary productivity in tropical terrestrial ecosystems. Pp. 217-231 in H. Lieth and R. H. Whittaker, eds. *Primary productivity of the biosphere*. Springer, New York.
- Norton-Griffiths, M. 1979. The influence of grazing, browsing and fire on the vegetation dynamics of Serengeti. Pp. 310-352 in A.R.E. Sinclair and M. Norton-Griffiths, eds. *Serengeti, dynamics of an ecosystem*. University of Chicago Press, Chicago.
- Palmer, P. G. 1976. Grass cuticles: a new paleoecological tool for East African lake sediments. *Canadian Journal of Botany* 45:1725-1735.
- Palmer, P. G., and S. Gerbeth-Jones. 1986. A scanning electron microscope survey of the epidermis of East African grasses. IV. *Smithsonian Contributions to Botany* 62:1-120.
- . 1988. A scanning electron microscope survey of the epidermis of East African grasses, V, and West African Supplement. *Smithsonian Contributions to Botany* 67:1-157.
- Palmer, P. G., and A. E. Tucker. 1981. A scanning electron microscope survey of the epidermis of East African grasses. I. *Smithsonian Contributions to Botany* 49:1-84.
- . 1983. A scanning electron microscope survey of the epidermis of East African grasses. II. *Smithsonian Contributions to Botany* 49:1-72.
- Palmer, P. G., S. Gerbeth-Jones, and S. Hutchinson. 1985. A scanning electron microscope survey of the epidermis of East African grasses. III. *Smithsonian Contributions to Botany* 55:1-136.
- Pickford, M. 1982. The tectonics, volcanics and sediments of the Nyanza Rift Valley, Kenya. *SupplementBand, Zeitschrift für Geomorphologie* 42:1-33.
- . 1985. A new look at *Kenyapithecus* based on recent discoveries in western Kenya. *Journal of Human Evolution* 14:113-143.
- . 1986. Cenozoic paleontological sites in western Kenya. *Münchener Geowissenschaftliche Abhandlungen. Reihe A, Geologie und Paläontologie* 8:1-151.
- . 1987. Fort Ternan (Kenya) paleoecology. *Journal of Human Evolution* 16:305-309.
- Radosevich, S. C., G. J. Retallack, and M. C. Taieb. 1992. A reassessment of the ecology and preservation of hominid fossils from Hadar, Ethiopia. *American Journal of Physical Anthropology*. 87:15-27.
- Rattray, J. M. 1960. The grass cover of Africa. *FAO Agricultural Studies* 49:1-168.
- Redmann, R. E. 1985. Adaptation of grasses to water stress—leaf rolling and stomate distribution. *Annals of the Missouri Botanical Garden* 72:833-842.
- Retallack, G. J. 1983. Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota. *Special Publication of the Geological Society of America* 193:1-82.
- . 1984. Completeness of the rock and fossil record: some estimates using fossil soils. *Paleobiology* 10:59-78.
- . 1990. *Soils of the past: an introduction to paleopedology*. Unwin-Hyman, London.
- . 1991. *Miocene paleosols and ape habitats in Pakistan and Kenya*. Oxford University Press, New York.
- . In press. Comment on the paleoenvironment of *Kenyapithecus* at Fort Ternan. *Journal of Human Evolution*.
- Retallack, G. J., D. P. Dugas, and E. A. Bestland. 1990. Fossil soils and grasses of middle Miocene East African grassland. *Science* (Washington, D.C.) 247:1325-1328.
- Rutherford, M. C. 1982. Woody plant biomass distribution in *Burkea africana* savannas. Pp. 120-141 in B. J. Hartley and B. H. Walker, eds. *Ecology of tropical savannas*. Springer, Berlin.

- Rutherford, M. C., and R. D. Kelly. 1978. Woody plant basal area and stem increment in *Burkea africana*-*Ochna pulchra* woodland. South African Journal of Science 74:307-308.
- Salard-Cheboldaef, M. 1979. Palynologie maestrichtienne et tertiaire du Cameroun. Étude qualitative et repartition verticale des principales espèces. Reviews of Palaeobotany and Palynology 28:365-388.
- Shipman, P. 1977. Paleoeology, taphonomic history and population dynamics of the vertebrate assemblage from the middle Miocene of Fort Ternan, Kenya. Unpublished Ph.D. thesis, Department of Anthropology, New York University, New York.
- . 1986. Paleoeology of Fort Ternan reconsidered. Journal of Human Evolution 15:193-204.
- Shipman, P., A. Walker, J. A. Van Couvering, P. J. Hooker, and J. A. Miller. 1981. The Fort Ternan hominoid site, Kenya: geology, age, taphonomy and paleoeology. Journal of Human Evolution 10:49-72.
- Spalletti, L. A., and M. M. Mazzoni. 1978. Sedimentologia del Grupo Sarmiento en el perfil ubicado al sudeste de Lago Colhue Huapi, Provincia de Chubut. Obras del Centenario del Museo de La Plata 4:261-283.
- Stevenson, F. J. 1986. Cycles of soil: carbon, nitrogen, phosphorus, sulfur and micronutrients. Wiley, New York.
- Thackray, G. D. 1989. Paleoenvironmental analysis of paleosols and associated fossils in Miocene volcanoclastic deposits, Rusinga Island, western Kenya. Unpublished M.Sc. thesis. Department of Geological Sciences, University of Oregon, Eugene.
- Thomasson, J. R. 1979. Late Cenozoic grasses and other angiosperms from Kansas, Nebraska and Colorado: biostratigraphy and relationships to living taxa. Bulletin of the Geological Survey of Kansas 218:1-68.
- . 1985. Miocene fossil grasses: possible adaptation in reproductive bracts (lemma and palea). Annals of the Missouri Botanical Garden 72:843-851.
- . 1987. Fossil grasses: 1820-1986 and beyond. Pp. 159-167 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth, eds. Grass systematics and evolution. Smithsonian Institution Press, Washington, D.C.
- Tieszen, L. L., M. M. Senyima, S. K. Imbamba, and J. H. Troughton. 1979. The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia Berlin 37:337-350.
- Tiffney, B. H. 1985. Seed size, dispersal syndromes and the rise of the angiosperms: evidence and hypothesis. Annals of the Missouri Botanical Garden 71:551-576.
- Van Couvering, J.A.H. 1980. Community evolution in East Africa during the Late Cenozoic. Pp. 272-298 in A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the making. University of Chicago Press, Chicago.
- Ward, H. K., and W. B. Cleghorn. 1964. The effects of ring-barking trees in *Brachystegia* woodland on the yield of veld grasses. Rhodesia Agricultural Journal 61:98-105.
- Watson, L., and M. J. Dallwitz. 1989. Grass genera of the world: illustrations of characters, descriptions, classification, interactive identification, information retrieval. Booklet, microfiche and computer program, privately distributed, L. Watson, Canberra, Australia.
- Watson, L., H. T. Clifford, and M. J. Dallwitz. 1985. The classification of the Poaceae: subfamilies and supertribes. Australian Journal of Botany 33:433-484.
- Webb, S. D. 1977. A history of savanna vertebrates in the New World. Part I. North America. Annual Reviews of Ecology and Systematics 8:355-380.
- . 1978. A history of savanna vertebrates in the New World. Part II. South America and the Great Interchange. Annual Reviews of Ecology and Systematics 9:393-426.
- White, F. 1983. The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris.
- Whittaker, R. H., and P. L. Marks. 1975. Methods of assessing primary productivity. Pp. 55-118 in H. Lieth and R. H. Whittaker, eds. Primary productivity of the biosphere. Springer, New York.