fields makes it difficult to draw any definitive conclusions about the global effects of Amazon deforestation from this study.

The most significant result of this study is the simulated reduction in precipitation over Amazonia, which is larger than the corresponding regional reduction in evapotranspiration, implying that the dynamical convergence of moisture flux also decreased as a result of deforestation. The spatial and temporal coherence of the decrease in precipitation implies that the deforested case is associated with a longer dry season. The lack of an extended dry season apparently sustains the current tropical forests, and therefore a lengthening of the dry season could have serious ecological implications (*26–28*). Among other effects, the frequency and intensity of forest fires could increase significantly (*29, 30*) and the life cycles of pollination vectors could be perturbed.

These results suggest that a complete and rapid destruction of the Amazon tropical forest could be irreversible. Changes in the region's hydrological cycle and the disruption of complex plant-animal relations could be so profound that, once the tropical forests were destroyed, they might not be able to reestablish themselves.

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Fossil Soils and Grasses of a Middle Miocene East African Grassland

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Fossil soils and grasses from the well-known Miocene mammal locality of Fort Ternan, southwestern Kenya, are evidence of a mosaic of grassy woodland and wooded grassland some 14 million years ago. This most ancient wooded grassland yet known on the African continent supported more abundant and diverse antelopes than known earlier in Africa. Ape fossils at Fort Ternan, including *Kenyapithecus wickeri*, were associated with woodland parts of the vegetation mosaic revealed by paleosols. Grassland habitats were available in East Africa long before the evolutionary divergence of apes and humans some 5 to 10 million years ago.

SAVANNA ECOSYSTEMS HAVE LONG been linked with early human evolution, and the antiquity of savannas in Africa has been a source of debate (*1*). Part of the problem is the loose use of the term "savanna" to include any kind of tropical grassland. We prefer the term "wooded grassland" for well-drained grassy vegetation with 10 to 40% cover by trees (*2*). Unlike wooded and open grassland, grassy woodland and marsh are at least as old as 23 million years and remained widespread 17 million years ago in East Africa, judging from evidence of paleosols (*3*), of fossil sedges and grasses (*4*), of fossil dicots (*5*), and of fossil birds allied to modern forms now found widely in grassy vegetation (*6*). Of more interest from the point of view of the evolution of African mammals is the origin of wooded grassland and open grassland among more ancient kinds of woodland and forest vegetation.

Paleosols can be useful in deciphering ancient vegetation mosaics, because, unlike fossils, they are by definition in the place they formed. They are also abundant and have been widely recognized in southwest Kenya (*3, 7–9*). The thin, brown, nodular, calcareous paleosols found throughout the 9.6-km outcrop of the middle Miocene Fort Ternan Beds are distinct from geologically older paleosols in Kenya (*3, 10*). The Fort Ternan beds are a sequence of carbonatite-nephelinite tuffs, lahars, colluvium, and alluvium. They have been dated by the K/Ar method at 14.4 ± 0.2 million years old by the use of biotite (*7, 11*). This account details only paleosols in the 8-m-thick sequence exposed in the large (*12*) quarry for fossils at Fort Ternan National Monument. Three distinct kinds of paleosols were recognized and named informally from the local Dholuo language: Chogo ("bone"), Onuria ("yellow"), and Dhero ("thin") paleosol series. The paleosols were characterized in the field, petrographically, and chemically (*13*). From these data (Fig. 1), some aspects of the original soils and their environment can be reconstructed.

One approach to interpreting paleosols is to identify them within a soil classification and compare them to modern soils, with allowance for possible alteration after burial. The distinctive surface horizons of both Onuria and Chogo paleosols are critical to their identification: they have the granular structure, thickness, dark color, and large proportion of bases that define a mollic epipedon and Mollisols (*14*). Organic mat-

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ter is not sufficiently abundant to meet mollic criteria, but it is known that organic matter is lost by about an order of magnitude from well-drained paleosols soon after burial (*15*). A mollic interpretation is not compromised either by an early burial cement of un-recrystallized sparry calcite in sandy layers or compaction of clayey parts of the profiles to an estimated 74% of their former thickness (*16*). The Chogo clays can be identified as Haplustolls and the Onuria clay as a Calciustoll (*14*). Both Chogo and Onuria paleosols are similar in profile form and in chemical and petrographic depth functions to modern soils formed on carbonatite-nephelinite ash under mid-length grassland and wooded grassland in mid-slope positions in the central Serengeti Plains of Tanzania (*17, 18*). They are neither so clayey, deeply weathered, or red as African volcanic soils under lowland or montane woodland or forest (*18, 19*) or geologically older paleosols in Kenya (*3, 9, 10*), nor are they so thin, zeolitic, or calcareous as East African desert soils on carbonatite-nephelinite ash (*20*).

A second approach for interpreting these paleosols is to assess soil features under the familiar headings of climate, organisms, topographic relief, parent material, and time for formation. The length of time represented by calcareous paleosols can be assessed from the morphology of their subsurface calcareous (Bk, Fig. 1) horizons (*21, 22*). Both Chogo and Onuria paleosols have distinct nodules with replacive and displacive microfabrics. In contrast, Dhero paleosols show little discernible pedogenic reorganization of carbonate. Like similar surface soils of known age in the Serengeti Plains of Tanzania (*21*), Chogo and Onuria paleosols may represent 2000 to 9000 years of soil formation; and Dhero paleosols, a few hundred years or less.

Topographic setting and parent materials for the paleosols are known from geological context to be on the lowest slopes of a carbonatite-nephelinite volcano (*7, 8*). Onuria and Dhero series paleosols formed on lahars; and Chogo paleosols on colluvium. These indications of good drainage and base-rich parent materials are compatible with the lack of petrographic or chemical evidence for salinization, gleization, or leaching in all the paleosols (Fig. 1). Thus, these paleosols were not restricted to salt licks, seasonally waterlogged depressions (dambos), or marshes.

Indications of grassy vegetation are provided by abundant fine root traces in all the paleosols. Fossil stumps are rooted in Dhero paleosols. These paleosols may have supported early successional vegetation, unlike Chogo and Onuria paleosols with little relict bedding. Two small stump casts 7.5 and 16 cm in diameter and 2 m apart were seen in the Chogo clay eroded-phase paleosol 5 m west along strike from the type Chogo clay. This paleosol with fossil stumps and large root traces also has an incipient subsurface clayey horizon and diffuse boundaries between horizons, as in the Chogo clay ferru-

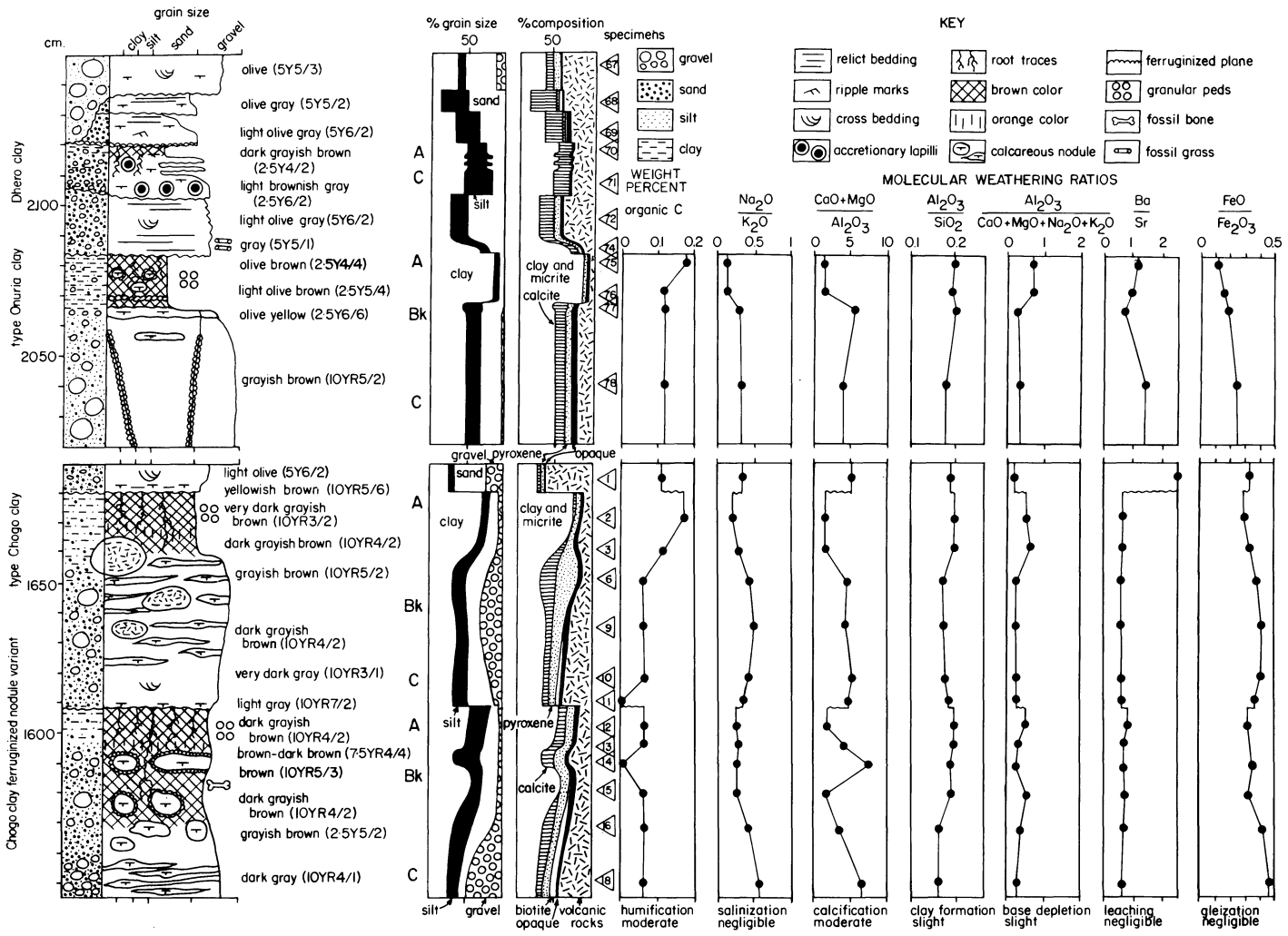

Fig. 1. Detailed sections of the four different kinds of paleosols recognized within the 8-m sequence exposed in the main fossil excavation at Fort Ternan National Monument, Kenya (*13*). Heights in centimeters are calibrated to a longer section in which the top of the underlying Baraget Phonolite is at 780 cm.

ginized nodule variant (Fig. 1) and modern soils of grassy woodland (*18*). Paleosols lacking stumps, such as the Onuria and type Chogo clay paleosols, have an abrupt and planar lower boundary to the dark surface (A, Fig. 1) horizon, as in modern soils of tall to intermediate grassland and wooded grassland (*17*). This evidence for a local vegetation mosaic in a 7-m lateral exposure of Chogo paleosols is not apparent from scattered fossil fruits and seeds of woodland trees and vines or leaves and pollen of grasses, recovered from Chogo paleosols (*23*). Abundant bones were fossilized in place as an attritional assemblage in Chogo paleosols (*7*). The most common large mammals were antelope (*Oioceros* and *Kipsigicerus*), giraffoid (*Palaeotragus*), rhinoceros (*Paradiceros*), and proboscidean (*Choerolophodon*). Rhinos and proboscideans had a prior evolutionary history in East Africa (*24*), but the antelopes were newly immigrant to this area. In tooth and limb morphology, the antelopes were better suited to open country than were early Miocene African mammals but in these adaptations were most like modern woodland antelope (*25*). Fossil snails from Chogo paleosols reflect the wooded part of the mosaic (*26*).

Mean annual rainfall at Fort Ternan was probably in the semiarid range, because the paleosols would have had a calcareous horizon at 33 cm below the surface before burial compaction (*16*), as in moderately developed soils of the central Serengeti Plains receiving 320 to 590 mm of rainfall (*17*). Similar estimates of former rainfall are gained by comparison with moderately developed soils in the United States and India (*27*).

Additional indications of tropical grassland at Fort Ternan are fossil grasses found in several of the paleosols, but best preserved in calcareous nephelinitic sandstone covering the Onuria paleosol (*28*). The grasses are strongly oriented as if pushed over in place of growth by flow from the north (*29*). In the 7-m length of the grass bed exposed in the quarry, grasses are confined to its basal 17 cm with little clumping. Many of the grasses were stout and long: some were seen up to 8 mm in diameter and 24 cm long. From these observations, the grass bed has preserved a sod-forming, mid-length to tall grassy sward.

With the scanning electron microscope (SEM), a few small areas of some fossil grasses showed well preserved stomates and phytoliths (Fig. 2). The best results were obtained with specimens mounted on stubs and coated immediately after extraction from the matrix. Cuticular details of the grasses were compared with those from SEM studies of living East African grasses (*30*) and were classified to subfamily level by reference to recent compilations of grass epidermal features (*31*). Five distinctly different morphologies and arrangements of stomates, phytoliths, and hair bases were found among the fossil grasses. Three of them are identified as different grass species of the subfamily Panicoidae and two as separate species of the subfamily Chloridoidae (*28*). Modern chloridoid species most like the fossils in cuticular morphology are found mostly in open areas prone to grazing and other disturbance. Modern panicoids most like the fossils live in grasslands and grassy woodlands. There were no bambusoid or arundinoid grasses, common in seasonally wet grasslands (dambos), woodlands, or forests (*2, 32*), nor were there pooid grasses that now dominate Afromontane and temperate vegetation (*2, 31*).

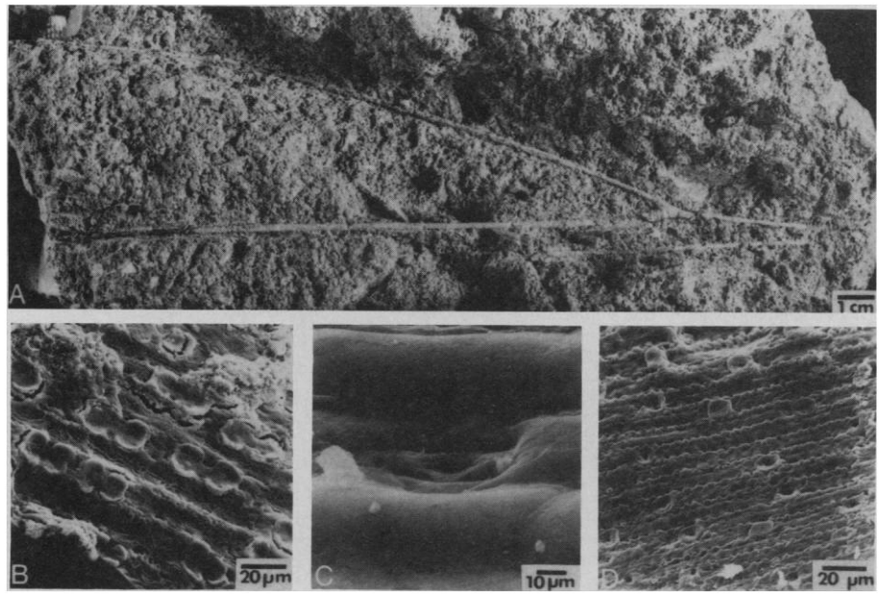

Fig. 2. Miocene fossil grasses from Fort Ternan (*28*): including a branching panicoid grass (**A**) and one of its immature stomates with domed subsidiary cells from a basal leaf blade (**C**); a second species of panicoid grass with abundant dumbbell-shaped and common three-lobed silica bodies (**B**), and a chloridoid grass with circular silica bodies (**D**). Specimens and SEM stubs are from the Kenyan National Museum, Nairobi, numbers FT-13126 (A and C), FT-13120 (B), and FT-13127 (D).

These paleoenvironmental inferences are confirmed by the functional morphology of the fossil cuticles. These were not arid or perarid grasslands, because the fossil stomates are not deeply sunken or hidden within stomatal grooves (*33*). Indications of high grazing pressure on the grasses are provided by the abundance of phytoliths on the fossil cuticles, including highly abrasive dumbbell and three-lobed forms (*34*). In both subfamilial taxonomic affinities and in their functional morphology, the fossil grasses compare well with those of intermediate to tall grasslands and wooded grasslands of the modern Serengeti Plains of Tanzania (*2, 17*).

Fossil apes from Fort Ternan, including *Kenyapithecus wickeri* (*8, 26*), have been recorded in attritional assemblages in place (*7*) only in the Chogo clay eroded-phase paleosol, here interpreted to have formed under grassy woodland at an ecotone to wooded grassland on the adjacent type Chogo clay. Such a habitat for *K. wickeri* is compatible with what little is known about its limb structure (*35*). The evidence presented here brings into clearer focus the array of potential environments for human evolution from apes, which may have occurred in East Africa 5 to 10 million years ago (*1*). Forests and woodlands certainly were present during middle and late Miocene time (*3, 32*) and have persisted to this day in well-watered areas. However, grasses and soils structurally and taxonomically similar to those of mosaics of grassy woodland and open wooded grassland also have been present for at least the past 14 million years in East Africa.

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11. Date corrected to new constants by the procedure of G. B. Dalrymple [*Geology (Boulder)* 7, 558 (1979)].
12. Floor area 132 m^2, wall length 46 m, and wall area about 165 m^2.
13. Colors compared with a Munsell chart; grain size distribution and petrographic composition determined from 500 points in thin section with a Swift automatic point counter; G. S. Smith counted Onuria and Dhero paleosols of Fig. 1, and G.J.R. confirmed Onuria and counted Chogo paleosols; organic carbon by D. A. Horneck, Soil Testing Laboratory of Oregon State University, with the Walkley-Black technique; chemical analyses from Atomic Absorption by C. McBirney, University of Oregon.
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Requirement for Activin A and Transforming Growth Factor–β1 Pro-Regions in Homodimer Assembly

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Many proteins are initially synthesized as part of a large precursor. The role of the pro-region in the biosynthesis of transforming growth factor–β1 (TGF-β1) and activin A, two structurally related disulfide-linked homodimers synthesized as large precursors, was studied. Vectors that expressed either the pro-region or the mature regions of these molecules were used in complementation experiments, only when the pro-region was coexpressed with the mature region did intracellular dimerization and secretion of biologically active homodimers occur. The pro-regions of activin A and TGF-β1, therefore, aid the folding, disulfide bond formation, and export of their respective homodimers.

ACTIVIN A AND TGF-β1 are members of a group of structurally related proteins that are involved in differentiation and have endocrine effects (*1*). This family consists of disulfide-linked homodimers derived from a large precursor that contains a hydrophobic signal sequence. The pro-regions of 290 (activin A) and 250 amino acids (TGF-β1) are linked by basic cleavage sites to the mature regions of 116 (activin A) and 112 amino acids (TGF-β1) (*2, 3*). We investigated the potential role of the pro-regions in the biosynthesis of both of these molecules.

Human 293S cells transfected with the expression plasmid pActA, which encodes the complete activin A precursor, secrete both a 25-kD disulfide-linked homodimer that comprises the COOH-terminal 116 amino acids of the activin A precursor and a protein of between 39.5 and 43.5 kD that corresponds to the activin A pro-region (*4*) (Fig. 1A and lanes 1 on Fig. 2, A and B). To independently express the pro-region and mature regions of the activin A precursor, we constructed the vectors pPTH-A and pProA (Fig. 1A). The vector pPTH-A, which contains the DNA sequence of the mature region of activin A fused in frame with a synthetic DNA sequence encoding the 31–amino acid prepro-region of human parathyroid hormone (PTH) (*5*) (Fig. 1B), was designed to determine whether the mature activin A sequences can fold correctly when expressed with a heterologous prepro-region. The prepro-PTH sequence has a well-characterized signal sequence and the six–amino acid basic pro-region is similar to

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Table 1. Bioactivity of activin A and TGF-β1 secreted from 293S cells. Serum-free conditioned medium (2.5 ml) was collected after 48 hours from confluent 60-mm dishes of transfected 293S cells. Bioactive activin A was measured in vitro by the induction of release of the pituitary hormone FSH from monolayers of rat pituitary cells (*9*). Conditioned media were assayed for FSH content by ELISA. Activin A was measured directly in conditioned media by a MAb-based ELISA. Data are averages of three experiments. Bioactive TGF-β1 was determined in a mink lung cell growth inhibition assay (*10*) after heat-activation of samples for 5 min at 75°C. TGF-β1 was measured by ELISA of conditioned medium after heat activation. UD, undetectable.

Plasmid	Activin A (ng/48 hours)		Plasmid	TGF-β1 (ng/48 hours)	
	Bioactive	ELISA		Bioactive	ELISA
Act A	950	730	TBF-β (SBβ)	1069	1190
PTH-A	UD	UD	PTH-TGF	2	UD
ProA	UD	UD	ProTGF	1	UD
PTH-A + ProA	83	65	PTH-TGF + ProTGF	25	26
Vector	UD	UD	Vector	3	UD