MIDDLE MIOCENE FOSSIL GRASSES FROM FORT TERNAN, KENYA

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ABSTRACT—At the well-known fossil mammal locality of Fort Ternan in southwestern Kenya, radiometrically dated at about 14 million years old (middle Miocene), fossil grasses have been preserved by nephelinitic sandstone in place of growth above a brown paleosol (type Onuria clay). Large portions of grass plants as well as fragments of leaves have revealed details of silica bodies, stomates, and other taxonomically important features under the scanning electron microscope. The computer database for grass identification compiled by Leslie Watson and colleagues was used to determine the most similar living grass genera to the five distinct kinds of fossil grass. Two of the fossil species are assigned to Cleistochloa kabuyis sp. nov. and C. shimpmax sp. nov. This genus includes one species from low fertility dry woodland soils of New South Wales and Queensland and a second species from "raw clay soils" in western New Guinea. A third fossil species, represented by a large portion of a branching culm, is assigned to Stereochlaena micocica sp. nov. This genus includes five species of low-fertility woodland soils in southeastern Africa. Both Cleistochloa and Stereochlaena are in the supertribe Panicanae of the subfamily Panicoideae. A fourth species is assigned to Distichlis africana sp. nov. and provides a biogeographic link between the single species of this genus now living in coastal grasslands in southeastern Australia and the 12 species of dunes and deserts found throughout the Americas from Patagonia and the West Indies to the United States and Canada. A fifth species is, like D. africana, in the subfamily Chloridoideae, but its stomata were not seen and it could belong to Cyclostachya, Pogoneura, or Povenista. This earliest known wooded grassland flora in Africa is taxonomically unlike the modern grass flora of fertile volcanic African landscapes, and may have been recruited from an archaic grass flora of Gondwanan desert and lateritic soils.

INTRODUCTION

Tropical Africa has long been suspected as an important area of grass evolution. Not only does this region now include some of the best known natural grassland ecosystems (Vesey-Fitzgerald, 1973; Bell, 1982), but it also appears to have been an important evolutionary center for grasses (Clayton, 1975, 1981; Cross, 1980). The evolution of African grasslands also has been considered important to the evolution of early human ancestors (Hill and Ward, 1988). It is unfortunate, then, that so little is known of the fossil record of grasses in Africa.

Grass pollen is common in rocks as old as Eocene in Cameroon (Salard-Cheboldaef, 1979), as well as in rocks of younger Tertiary age elsewhere in Africa (Kedves, 1971; Bonnefille, 1984; Bonnefille et al., 1987). Considerable antiquity for grassy woodland is also apparent from the fossil record of leaves, woods, and fruits of dicotyledonous trees now common in such vegetation in Africa (Axelrod and Raven, 1978; Dechamps, 1987). Possible grasses have been recorded from the early Miocene (about 23 million years old according to Van Couvering, 1972) fossil mammal site of Bukwa in Uganda, although fossil rhizomes from this locality were referred to Juncellus laevigatus, a living sedge of alkaline lake margins (Hamilton, 1968). Unidentified fossil grasses also have been recorded in Miocene rocks of southwestern Kenya: from Rusinga Island, in the upper Hwesi Formation (Thackray, 1989), some 17 million years old, and from Ombo and Majiwa, some 15–16 million years old (Pickford, 1984, 1986, personal commun.). The first pre-Pleistocene megafossil grasses identified from Africa were remains of Leptospis sp. cf. L. zeylanica and Humbertochloa sp. among a diverse assemblage of angiosperm leaves some 12 million.
years old near Ngorora, Kenya (Jacobs and Kabuye, 1987). Taxonomically both these fossil grasses and associated leaves are most like living forms of rain forest, and could be construed as evidence against the existence of open vegetation so far back into the Miocene. A very different conclusion can be drawn from the fossil grasses reported here from the well-known fossil mammal site, some 14 million years old, near Fort Ternan, Kenya. Along with the paleosols preserved there (Retallack et al., 1990; Retallack, 1991), these fossil grasses are evidence of the oldest wooded grassland yet known in East Africa.

FORT TERNAN PREHISTORIC SITE

All the fossil plants described in this paper came from the basal portion of a nephelinitic sandstone with calcareous cement overlying the Onuria clay paleosol, a brown clayey layer below 21 m in measured section of Retallack (1991, fig. 4.10) in the high wall of the large fossil excavation into the Fort Ternan Member of the Kericho Phonolites at Fort Ternan National Monument, southwestern Kenya (Figure 1). Biotite from Chogo paleosols, which also contain poorly preserved fossil grasses, lower in the section (16 m in section of Retallack, 1991, fig. 4.10) has been dated using the K/Ar technique at 14.4 ± 0.2 and 15.1 ± 0.7 million years old, and by the 39Ar/40Ar stepwise degassing technique at 13.9 ± 0.3 million years (Shipman et al., 1981; corrected by method of Dalrymple, 1979). The age of the fossil grasses is probably close to this, and certainly is no younger than a lava 15 m higher in the sequence: 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 39Ar/40Ar total fusion, stepwise degassing, and K/Ar techniques, respectively (Shipman et al., 1981). No fossil mammals have been found in the Onuria paleosol, but Chogo paleosols lower in the sequence contain a diverse fossil fauna that has been taken as a standard for middle Miocene faunas of East Africa (Pickford, 1981).

As we have noted elsewhere (Dugas, 1989; Retallack et al., 1990; Retallack, 1991), the fossil grasses above the Onuria paleosol appear to have been preserved in growth position when overwhelmed by the nephelinitic sand. They are most abundant nearest the Onuria paleosol in the basal 17 cm of the overlying bed, with only a few arching up into higher levels of the sandstone (Figure 2). A block of matrix 30×15×6 cm in size was
excavated grain by grain in the laboratory and yielded 52 leaf fragments, which is a density of 19,529 grasses per m² or 1,155 per m² for such a thin layer. Many of the grasses were stout and long: up to 8 mm in diameter and 23 cm long. The fossil grasses are consistently oriented as if pushed over by flow from the north.

The Onuria paleosol has the granular pedds, dark color, smectitic clays, and shallow calcareous horizon of a Calciustoll (of Soil Survey Staff, 1975), a kind of soil that supports grassland today—for example on the Serengeti Plains of Tanzania (de Wit, 1978). This soil may have been overwhelmed by outwash of a volcanic lahars. Such boulder breccias are also found in the excavation at Fort Ternan, and one of them formed the parent material of the Onuria paleosol. Grasses elsewhere have been fossilized by the sudden influx of volcanic flows (Lockwood and Lipman, 1980), tuffs (Leyes, 1983), and lahars (Fisher and Schminke, 1984, p. 303). Sudden burial probably played a role in preservation of the Fort Ternan grasses, and the nephelineites and carbonatites there are also chemically unusual. Carbonatites can form a natural Portland cement (Barker and Nixon, 1983; Hay, 1986) capable of preserving lizard tongues (Estes, 1962), insects (L. S. B. Leakey, 1952; Wilson and Taylor, 1964; Paulian, 1976), flowers (Hamilton, 1968), and footprints (M. D. Leakey and Harris, 1987).

MATERIALS AND METHODS

The fossil grasses from Fort Ternan were studied by mounting grass fragments and matrix directly on SEM stubs, coating with gold and carbon, and examining them using the JEOL-25 instrument in the Department of Geological Sciences, University of Oregon. Photomicrographic prints and negatives were made with Polaroid 55 film. The only preparations that revealed useful details were 12 that had been freshly excavated from the rock.

Most specimens, including all those excavated in the field, proved uniformly barren of cuticular detail. This observation, together with observations in petrographic thin sections and using the EDAX analytical capability of the SEM, indicates that the fossils have very little organic matter remaining, and are in large part internal casts of calcite and clay (Figure 3). Exposure to air may be enough to oxidize what little organic matter remains around stomatal complexes and silica bodies.

Although the fossil grass bed is in fresh rock of the high wall of a large excavation and 2 m below the surface soil, we were concerned with the possibility of contamination with cuticle fragments of modern grasses in and around the excavation, and identified (with the generous assistance of Christine Kabuye, as well as Bogdan, 1976; Clayton, 1970; Clayton, et al., 1974; Clayton and Renvoize, 1982) the following species of living grasses in flower on June 22, 1987, at Fort Ternan National Monument: Brachiaria sp. of B. serra, Cymbopogon caesius, Eragrostis racemosa, Hyparrhenia filipendula, H. hirta, Hypotheria dissoluta, Loudetia kagerensis, Rhynchelytrum repens, Setaria sphacelata, Sporobolus festivus, and Themeda triandra.

The modern grass flora here is very different from the fossil flora. In addition, all the grass fossils completely excavated in the field turned out to be uninformative, presumably because their organic matter decayed or flaked off during transport to the laboratory. Only specimens freshly extracted from matrix in the laboratory showed useful microscopic details. Thus, contamination of the fossil assemblage with cuticles from modern grasses was not a problem.

The computer key to modern genera of grasses by Watson and Dallwitz (1989; Watson et al., 1986, 1989) was used to identify the Miocene fossil grasses to generic level, by means of a "MATCH O" comparison to eliminate those genera in the database for which there is no epidermal information. Full "MATCH IOU" comparisons also were done, yielding additional rare arundinoid and bambusoid genera of unknown cuticular anatomy but unlikely to be related to the fossils. Only those features that could clearly be seen on the fossils were used, with emphasis on silica bodies and stomatal subsidiary cells. At least 23 characters of the fossils were compared with those of 665 living grass genera for which cuticular information is available (Table 1). Information on leaves and culms was used only for one especially large fossil (Streelochlanae miocenica sp. nov.). The robustness of the computer identifications was tested by listing genera differing by one or two characters ("SET TOLERANCE 1 or 2"), and considering how significant taxonomically those characters were ("DESCRIBE").

FIGURE 3—Scanning electron micrograph (1) and petrographic thin section under crossed nicols (2) of fossil grasses from above the type Onuria paleosol, showing fill of clay and calcite within sheathing leaves. SEM is Kenyan National Museum FT-F22654: thin section is FT-R74.
All the fossil specimens, including SEM stubs, are in the paleontological collections of The International Louis Leakey Museum for African Prehistory, Kenyan National Museums, curated by Meave Leakey.

**SYSTEMATIC PALEONTOLOGY**

Kingdom Plantae
Division Angiospermae
Subdivision DICOTYLEDONAE

Dicotyledonae fam., gen., et sp. indet.

**Figure 4**

**Material.**—A small (10 mm by 10 mm) fragment of well-preserved leaf epidermis could be from either the adaxial or, more likely, the abaxial surface of a dicotyledonous angiosperm. The illustrated fragment was too small to reveal venation, and other fragments of leaves with angiospermous venation did not show epidermal structure.

Cells above presumed veins are rectangular, linear, elongate, with surface striations, rounded ends, and slightly undulate walls. Areolae epidermal cells are rectangular, occasionally isodiametric, rounded, and randomly oriented. Randomly oriented stomata about 15–22 μm long are abundant in areolar areas. Their subsidiary cell arrangement is cycloctic and laterocytic. Their guard-cells are level with epidermis.

**Measurements.**—Stomatal length 15–22 μm (mean 19 μm of 12 measured); stomatal width across guard cells 8–25 μm (mean 11 μm of 22).

**Affinities.**—This material is illustrated to show that the fossil grass bed also includes rare (2 out of 52 in one block) remains of dicotyledonous leaves. Judging from the texture of the leaf impressions and epidermal cells and abundance of stomata, this was a woody mesophytic plant. Using the form generic classification of Roselt and Schneider (1969, as translated and augmented by Kovach and Dilcher, 1984), this material could be placed within Anteturma Cellareae, Turma Anomorimatae, Subturma Lacanomorae, Form Genus Calbrionicas. The amount of material available is inadequate for determining the botanical affiliations of this fossil, although broadly similar cuticles are found in the families Sapindaceae, Celastraceae, and probably others (Dilcher, 1965; den Hartog-van der Tholen and Baas, 1978; Upchurch, 1984). Further progress in identifying the dicotyledonous plant fossils at Fort Ternan needs to be based on additional material from above the Onuria paleosol, as well as a reassessment of fossil pollen, fruits, and seeds of a variety of dicots from the underlying Chogo paleosols (Shipman, 1977; Bonnichence, 1984; Retallack, 1991).

**Material.**—SEM stub FT-F13130.

**Subdivision MONOCOTYLEDONAE**

**Class LILIOPSIDA**

**Family GRAMINEAE Jussieu, 1789**

**Subfamily PANICOIDEA Braun, 1853**

**Supertribe PANICANAE Watson, Clifford, and Dallwitz, 1985**

**Genus CLEISTOCHELIA Hubbard, 1933**

**CLEISTOCHELIA KABUSYIS sp. nov.**

**Figure 5**

**Diagnosis.**—*Cleistochelia* fossil leaves, sheath diameter 3–4 mm, abaxial epidermis glabrous, with common costal, dumbbell, long-shank phylloths, 19–22 μm by 8–11 μm in size, and some intercostal trilobate phylloths, 12–16 μm long.

**Description.**—Abaxial leaf sheath epidermis 10–13 mm wide or 2–4 mm diameter, parallel veins, clear costal/intercostal zonation, but with similarly shaped long and short cells in costae and intercostae; silica bodies, dumbbell (19–22 μm long), with ends round to concave, and middle wide and short; intercostal trilobate silica bodies (12–16 μm long), with ends round to concave and middle wide and short; stomata common (28–38 μm long), arranged in two bands per intercostal zone and with parallel to low-domed subsidiary cells; long-cells, rectangular, long, narrow, width uniform, ends straight; cell walls markedly sinuous, interlocking, raised; costal short-cells greater than five per row; intercostal short cells solitary or paired; costal silica cells abundant; intercostal silica cells common; costal cork-cells common; no intercostal cork cells, microhairs, papillae, or macrohairs were seen.

**Discussion.**—Assignment to the genus *Cleistochelia* was based principally on the occurrence of dumbbell-shaped silica bodies and stomata with parallel to low-domed subsidiary cells (Watson and Dallwitz, 1989). Assignment to the subfamily Panicoideae also can be made on these characters, using the table provided by Ellis (1987). This was the basis for our earlier informal identification of this fossil as Panicoideae sp. indet. A (Dugas, 1989; Retallack, 1991) and “a second species of panicoid grass” (Retallack et al., 1990). Individually these characters are widespread among grasses, so that our SEM photomicrographs are generally similar to those by Palmer and Tucker (1981, 1983), Palmer et al. (1985), and Palmer and Gerbenth-Jones (1986, 1988) of the following East African species: *Acrocarpus zizanoides*, *Brachiaria brizantha*, *Hylebates chlorochoe*, *Ecciptocarpha obconicentris* (Panicaceae), *Rhytachne latifolia* (Andropogonae), *Stipagrostis uniplumis*, *Pentaschis borussica* (Arundinioideae), and *Schmitia pappophoroidei* (Chloridoideae).

A distinctive feature of the fossil is the presence of trilobate intercostal silica bodies (Figure 5.4). Among African grasses, trilobate silica bodies are seen in Panicaceae such as *Acrocarpus zizanoides* and *Ecciptocarpha obconicentris*. Similar forms of silica bodies were described by Metcalfe (1960, p. xii) as “intermediates between cross and dumb-bell shaped,” and included by Twiss et al. (1969, p. 111) with more symmetrical phylloths within the category “cross, thick shank.”

In the computer database (Watson and Dallwitz, 1989), 10 genera differ from the fossil in only one character among the characters chosen: *Tetrarrhena* (Bambusoideae), *Aristida*, *Piptatherum*, *Pyrranthera*, *Rytyospetra* (Arundinioideae), *Eriochloa*, *Ottochloa*, *Paspalum*, *Thyridolepis* (Panicaceae), and *Lophace* (Chloridoideae). Several of these genera have silica bodies in shapes other than dumbbell and trilobate, and all have differently shaped subsidiary cells. This latter feature is highly significant taxonomically (Metcalfe, 1960), but although trian-
### Table 1—Character matrices of modern and Miocene fossil grasses used in cladistic analyses.

<table>
<thead>
<tr>
<th>Character Matrices</th>
<th>Description</th>
<th>Data Source</th>
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<tr>
<td>Middle Miocene fossil panicoids from Fort Ternan compared with selected living grasses.</td>
<td>Data from Watson and Dallwitz (1989)</td>
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**Note:** Full names of the operational taxonomic units can be seen in Figure 11. Characters of abaxial leaf epidermis from left to right in both matrices from Watson and Dallwitz (1989) are: 288-1 with “poooid-type” horizontally elongated, siniuous or elongate-crate silica bodies, or 288-2 without them; 289-1 with “poooid-type” cross-shaped to dumbbell-shaped or nodular silica bodies, or 289-2 without them; 290-1 with tall-and-narrow silica bodies, or 290-2 without them; 291-1 with paddle-shaped silica bodies, or 291-2 without them; 292-1 with crescentic silica bodies, or 292-2 without them; 293-1 with “oryxoid-type” vertically oriented dumbbells or nodules, or 293-2 without them; 294-1 with sharp-pointed silica bodies, or 294-2 without them; 295-1 with round to oval silica bodies, or 295-2 without them; 296-1 with elongated smooth silica bodies, or 296-2 without them; 299-1 with stomatal guard cells overlapped by interstomatal cells, or 299-2 having guard cells overlapping to flush with interstomata; 300-1 stomata without triangular subsidiary cells, or 300-2 commonly with triangular subsidiary cells; 301-1 stomata without parallel-sided subsidiary cells, or 301-2 with parallel-sided subsidiary cells; 302-1 exhibiting on the same leaf a mixture of stomatal complexes with triangular and parallel-sided subsidiaries, or 302-2 not exhibiting a mixture of triangular and parallel-sided subsidiary cells; 281-1 mid-intercostal long cells having markedly sinuous walls, or 281-2 having straight or only gently undulating walls; 280-1 mid-intercostal long cells more or less rectangular, or 280-2 more or less fusiform; 303-1 intercostal short cells common, or 303-2 absent or rare; 304-1 intercostal short cells in cork/silica cell pairs, or 304-2 not paired; 305-1 intercostal short cells silicified, or 305-2 not silicified; 306-1 intercostal short cells conspicious in long rows of five or more cells, or 306-2 predominantly paired, or 306-3 neither grouped into long rows nor paired; 276-1 costal/intercostal zonation conspicuous, or 276-2 lacking; 278-1 long-cells similar in shape costally and intercostally, or 278-2 markedly different in shape; 282-1 papillae present, or 282-2 absent; 265-1 microhairs present, or 265-2 absent.

Gular stomatal subsidiary cells are generally distinct, there is room for interpretation of the continuum from parallel to domed subsidiary cells. The fossil epidermis was keyed out again as if its subsidiary cells were triangular (all choices but 300-2, 301 = 1 in Table 1) and neither parallel nor triangular (all but choice 301 = 1). For the first alternative 20 taxa were chosen with an additional 30 differing by only one feature, and for the second alternative 8 and 27 taxa respectively. Input of additional characters (277 = 1, 279 = 1, 284 = 2, 287 = 2, 297 = 2, 298 = 28-38 mm) narrowed the choice to *Aristida, Danthoniopsis*, and *Hymenachne* for the unlikely interpretation that the fossil has triangular stomatal subsidiary cells, and *Aristida* and *Clisetchoila* for the interpretation that they are intermediate between parallel and triangular. The epidermes of *Aristida ciliata, A. longiflora, A. scabribralis*, and *A. setacea* are very different from the fossil, with markedly triangular subsidiary cells to stomata recessed within narrow furrows flanked by costal prickles and microhairs (Metcalfe, 1960; Palmer et al., 1985). Unlike the fossil, *Danthoniopsis chevalieri* has prickles, and dumbbell-shaped silica bodies are uncommon compared to round and siliate-shaped silica bodies (Palmer and Gerbeth-Jones, 1988). *Hymenachne* differs from the fossil in having microhairs and triangular stomatal subsidiary cells (Watson and Dallwitz, 1989). The fossil epidermis may well prove to belong to a new and extinct genus when more is learned, but the most similar living genus is *Clisetchoila*.

The only published information on the epidermis of *Clisetchoila* is in the computer data bank and microfiche of Watson and Dallwitz (1989) and Watson et al. (1986). Leslie Watson generously provided light photomicrographs for comparison with the fossils, and from these the dumbbell-shaped phytoliths of *Clisetchoila subjuncea* (Toothill and Hacker, 1983) are characterized by a slightly shorter connecting bar than seen in the fossil phytoliths. *Clisetchoila scerachne* (Reeder, 1948) has dumbbell phytoliths with an hourglass-shaped connective, rather than the late-like central portion seen in C. *kabuyis* sp. nov. These living species are generally confined to the wetter end of the dumbbell larger than the other, but no triolate phytoliths were seen like those of the fossil. Both species also have pubescent leaf sheaths, whereas no microhairs or microhairs were seen on these fossils. This is unlikely to be due to poor preservation because the bases of both microhairs and microhairs were seen on fossil *Clisetchoila* sp. nov. from Fort Ternan. In addition, the fossil fragments of *Clisetchoila* kabyus sp. nov. are wider than usual for C. *subjuncea*, more like the other living species, C. *scerachne*.

*Clisetchoila subjuncea* is a perennial understory grass in woodlands dominated by spotted gum (*Eucalyptus maculata*) and by lancewood (*Acacia shirleyi*) on low-fertility podzolic and lithosolic soils of sandstone in New South Wales and Queensland (Beadle, 1981; Toothill and Hacker, 1983). *Clisetchoila scerachne* is a perennial on "raw clay soils" (Troppofluvets of Bleeker, 1983) of disturbed soils and in western New Guinea and northern Australia (Reeder, 1948). Holotype.—SEM stub FT-F13120. Other material.—SEM stub FT-F13124. Etymology.—The specific epithet is in honor of Christine Kabuye of the Kenyan National Herbarium.
FIGURE 5—*Cleistochloa kahuyis* sp. nov., holotype, fossil grass epidermis (FT-F13120). 1, overview of costal and intercostal zones with stomates and silica bodies. 2, 3, costal dumbbell-shaped silica bodies. 4, intercostal trilobate silica bodies and stomate. 5, 6, intercostal stomates.
Measurements. — Leaf sheath diameter 3.4–4.1 mm (mean 3.8 mm of three measured); dumbbell silica body length 19–22 μm (mean 21 μm of eight), lobe width 8–11 μm (mean 10 μm of 12), bar width 4–5 μm of six); trilobate silica body diameter 12–16 μm (mean 14 μm of four); stomatal length 28–38 μm (mean 32 μm of six), width across subsidiary cells 11–18 μm (mean 14 μm of six) and across guard cells 5–8 μm (mean 7 μm of seven); costal long cell length 27–42 μm (mean 36 μm of four) and width 10–15 μm (mean 13 μm of four); costal short cell length 15–19 μm (mean 17 μm of six) and width 13–15 μm (mean 14 μm of six); intercostal long cell length 31–46 μm (mean 39 μm of four) and width 12–15 μm (mean 14 μm of four); intercostal short cell length 15–23 μm (mean 18 μm of eight) and width 10–15 μm (mean 13 μm of eight).

Diagnosis. — Cleistochloa fossil leaves, sheath 10 mm diameter, abaxial epidermis with common costal, dumbbell, shortshank phytoliths, 10–16 μm by 6–10 μm in size.

Description. — Abaxial leaf sheath epidermis, 10 mm diameter, parallel veins, clear costal/intercostal zonation, with narrower costal than intercostal long cells; silica bodies (10–16 μm long), dumbbell-shaped, narrow in the middle so that lobes overlap or are touching; stomata (30–36 μm long), common, paracytic, subsidiaries parallel to low-domed; interstomatal cells, rectangular, long, narrow, width uniform, ends markedly concave; cell walls markedly sinuous, interlocking, raised; long-cells, long, narrow, width uniform, ends rounded; margins mark-
edly sinuous, interlocking, raised; short-cells (silica cells) common; cork-cells, none seen; narrow microhair bases seen but apices not preserved; macrohairs, basal cells present, circular.

Discussion.—This fossil could be assigned to the genus Cleistochoa and to the subfamily Panicoideae for much the same reasons as outlined for Cleistochoa kabuyis sp. nov. Genera differing from C. shipmanae by only one character among those chosen (Table 1) include all those listed for C. kabuyis except Piptatherum. We have earlier referred to this species as “Pani- coideae sp. indet. C” (Dugas, 1989; Retallack, 1991). The distinctive raised central areas of the long-cells in some of these specimens (Figure 6.1) are interpreted as internal casts of epidermal cells from which cuticle has exfoliated. Distinctive of this species are what appear to be bases of microhairs (Figure 6.3). These are too narrow to be bases of hook cells. They are too damaged to be useful taxonomically. Large basal cells of macrohairs, perhaps prickles, also were seen (Figure 6.4).


The dumbbell silica bodies of Cleistochoa shipmanae sp. nov. are small, with narrow central embayments, so that they look more like butterflies than dumbbells, unlike the large, open dumbbells with barlike connective in C. kabuyis sp. nov., or the open hourglass shape in living species, C. sclerachne and C. subjuncea. Although distinctive, the compact form of the fossil phytoliths, as well as microhairs and macrohairs on the fossil, are more like C. subjuncea than C. sclerachne. Cleistochoa ship- manae sp. nov. is broader leaved than either of the living species of Cleistochoa (Reeder, 1948; Tothill and Hacker, 1983), but like these living species and unlike C. kabuyis sp. nov., C. ship- manae has hairs.

Holotype.—SEM stub FT-13123.

Other material.—SEM stub FT-13125.

Etymology.—This species is named in honor of Pat Shipman, and her research on the fossils of Fort Ternan, including fossil fruits and seeds.

Measurements.—Leaf sheath diameter 9.9 mm (of one measured); dumbbell silica body length 10–16 µm (mean 13 µm of four), width of lobes 6–10 µm (mean 9 µm of eight) and width of bar 3–4 µm (mean 4 µm of four); stomatal length 30–36 µm (mean 33 µm of three), width across subsidiary cells 9–13 µm (mean 11 µm of three), and width across guard cells 5 µm (mean 5 µm of three); microhair basal diameter 5 µm (one seen) and shaft diameter 4 µm (one seen); macrohair basal cell diameter 61–64 µm (mean 63 µm of two) and shaft basal diameter 24–27 µm (mean 26 µm of two); intercostal long cell length 31–62 µm (mean 40 µm of eleven) and width 9–13 µm (mean 11 µm of eleven); intercostal short cell length 11–17 µm (mean 15 µm of six) and width 9–14 µm (mean 11 µm of five); costal long
Genus Stereochlaena Hackel, 1908

Stereochlaena miocenica sp. nov.

Figures 7, 8

Diagnosis.—Stereochlaena fossil with open branched culms 1.3–1.9 mm diameter, leaf sheaths 2.6–3.4 mm diameter, abaxial epidermis glabrous.

Description.—Culms up to 2 mm in diameter and at least 23 cm long, racemose at nodes; leaf sheaths 2.6–3.4 mm in diameter; abaxial leaf sheath epidermis, indistinct costal/intercostal zonation; stomata (24–28 μm wide), paracytic, in rows; stomatal subsidiary cells, triangular and low domed to parallel; interstomatal cells, rectangular, long, narrow, width uniform, ends concave, with sinuous walls; no silica bodies, short cells, microhairs, or papillae seen.

Discussion.—The type specimen is a large grass fossil in matrix (Figures 7, 8), with four connected culm internodes, previously described as "a branching panicoid grass" (Retallack et al., 1990) and "Panicoidae sp. indet. B" (Dugas, 1989, Retallack, 1991). The culm is branched at two nodes. Leaves arising from the two apical nodes are smaller than those lower on the plant.

Because silica bodies were not observed, it was not possible to identify this fossil on the basis of cuticular features alone. A general comparison with SEM photomicrographs by Palmer and Tucker (1981, 1983), Palmer and Gerbeth-Jones (1986, 1988), and Palmer et al. (1985) revealed the following generally similar epidermises of living East African grasses: Cyrtococcum chaetophorum, Chaetopoa taylorii (Panicaceae), and Phyllocladus sagittatus (Bambusaceae). On the incomplete cuticular information available, the computer key (Watson and Dallwitz, 1989) matched the fossil with seven living genera: Monachather (Arundinoideae), Chaetium, Stereochlaena, Thrasya, Thrydolepis, Zygochloa (Panicaceae), and Thripes (Chloridoideae). The addition to the computer key of a very conservative selection of additional features of the culm and leaves (008=2, 012=1, 024=2, 026=2) resulted in selection of the genus Stereochlaena. The vegetative features that distinguish these other genera from Stereochlaena include woodiness, lack of branching, and mostly basal leaf attachment. Eleven additional genera differ by only one character from all those chosen (Table 1): Australopryrum, Dissanthelium (Pooidaeae), Rytidosperma, Spartochloa (Arundinoideae), Coelachne, Isachne, Leptoloma, Reynauldia (Panicaceae), Buchlominus, Entoplocamia, and Lopholepis (Chloridoideae). All of these differed from the fossil in such diagnostic features as microhairs, stomatal guard cells overlapped by subsidiary, or differently shaped stomatal subsidiary cells.

There are five living species of Stereochlaena: S. annua, S. cameronii, S. caespitosa, and S. tridentata of Brachystegia woodlands on low-fertility lateritic soils on Precambrian bedrock from Tanzania southwards into South Africa (Clayton and Renvoize, 1982) and S. foliacea from Mozambique (Clayton, 1978). All the living species have pubescent leaf sheaths and blades, but no hairs were found on the fossil cuticles. Stereochlaena caespitosa and S. cameronii have very distinctive epidermises with common prickles and hair bases (Palmer and Gerbeth-Jones, 1986; photomicrographs provided by Leslie Watson). In vegetative form, Stereochlaena annua is the most similar species to S. miocenica sp. nov., the other species being larger, with wider leaves and growing in denser tufts (Clayton and Renvoize, 1982).

Holotype.—Branching grass specimen and SEM preparations from it, all labelled with number FT-F13126.

Etymology.—The specific epithet is in reference to the Miocene geological age of the fossils.

Measurements.—Preserved length 230 mm; culm internode length from basal left 77, 49, 147, and 122 mm, respectively; culm diameter 1.3–1.9 mm (mean 1.6 mm of 10 measured); leaf sheath diameter 2.6–3.4 mm (mean 2.9 of five); stomatal length 24–38 μm (mean 22 μm of three), width across subsidiary

Figure 8—Stereochlaena miocenica sp. nov., holotype, interpretative sketch of branching fossil grass (FT-F13126).
cells 12–19 μm (mean 17 μm of three) and across guard cells 6–8 μm (mean 7 μm of three); long-cell length 85–269 μm (mean 144 μm of 15) and width 15–31 μm (mean 21 μm of 15).

Subfamily CHLORIDOIDEAE Rouy, 1913
Genus DISTICHILIS Rafinesque, 1819
DISTICHILIS AFRICANA sp. nov.
Figure 9

Diagnosis.—Distichilis leaf fossils, blade 4–6 mm wide, abaxial epidermis with shallow intercostal furrows and broad costal zones; oval to round, saucer-shaped phytoliths exceptionally abundant, 5–12 μm in diameter, arranged in crude circles of 6–7 phytoliths forming up to six rows within the costal zone.

Description.—Leaf at least 4 mm wide; abaxial leaf epidermis, with shallow intercostal furrows; silica bodies (5–12 μm diameter), abundant, round to oval, centers generally concave; stomata (33–41 μm long), infrequent, in rows within intercostal furrows, paracytic, over-arched by adjacent long-cells, subsidiary triangular with outward projecting tip; interstomatal cells, rectangular, long narrow, width uniform, ends concave, with sinuous, thick, raised walls; costal long-cells, rectangular, long, narrow, width uniform, ends slightly concave to rounded, with sinuous, interlocking, raised walls; short-cells silicified, abundant, single to occasionally paired with cork cells, never adjacent between bands; papillae common at ends of long-cells, and especially dense within intercostal furrows; no microhairs, macrohairs, or salt glands seen.

Discussion.—Among published SEM photos of modern East African grass epidermes (Palmer and Tucker, 1981, 1983; Palmer et al., 1985; Palmer and Gerbeth-Jones, 1986, 1988), four species show generally similar features to these fossils: Pogonarthria squarrosa, Sporobolus africanaus, Tragus berteronianus (Chloridoideae), and Arundinella nepalensis (Panicoideae). These observations together with the diagnostic combination of round silica bodies and triangular stomatal subsidiary cells (following Ellis, 1987) were the basis for our initial assignment of these
fossils to the subfamily Chloridoideae (as “a chloridoid grass” of Retallack et al., 1990, and “Chloridoid sp. indet. A” of Dugas, 1989). This assignment was subsequently confirmed by use of the computer key of Watson and Dallwitz (1989), which narrowed the choice to the genus *Distichlis*. This was the most surprising identification provided by the computer, and yet it also proved to be the most robust. Even allowing for one mistakenly keyed character (“SET TOLERANCE=1” of Watson and Dallwitz, 1989), *Distichlis* was still the only choice. Only four genera differed by two of the characters chosen (Table 1): *Parapholis*, *Poa* (Pooidae), *Stipa* (Arundinoideae), and *Leptochloa* (Chloridoideae). These differ from the fossils by such taxonomically significant features as stomatal guard cell level, subsidiary cell shape, and silica body shape.

The epidermes of *Distichlis distichophylla* and *D. stricta* have been reported (Metcalfe, 1960; Oross and Thompson, 1982) and are very similar to the fossils in such features as the saucer-shaped silica bodies arranged in crude circlets, papillae (shrunken back in the fossil) at the ends of the long cells, and infrequent stomata within furrows. The fossils are distinct mainly in their shallower furrows and wider intercostal zone with up to six crude ranks of silica body circlets. The fossils also lack evident salt glands, microhairs, and microhairs. Hairs are likely to have been preserved, judging from those seen on *Stereochlaena micrakenica* sp. nov., but sunken salt glands are very difficult to distinguish under the SEM from papillae, even on fresh material (Oross and Thompson, 1982).

*Distichlis* includes 12 living species distributed throughout the Americas from Patagonia through central America and the West Indies to Canada (Hitchcock, 1971; Watson and Dallwitz, 1989) and a single and separate species from southeastern South Australia, through Victoria, and Tasmania to New South Wales (Beadle, 1981). It is well known as a dune-binding and salt tolerant plant of coastal salt marshes, but also is a widespread element of alkali scrub in inland deserts (Christensen, 1988; MacMahon, 1988; West, 1988). *Distichlis* also is known from habitats more like those implied by the Onuria paleosol at Fort Ternan: in Mollisols supporting prairie in Kansas (Sims, 1988) and supporting grassland lightly wooded with *Banksia* in southeastern South Australia (Crocker, 1944).

**Holotype.** —SEM stubs FT-F13127.

**Other material.** —SEM stubs FT-F13122.

**Etymology.** —The specific epithet refers to the African locality for this species.

**Measurements.** —Round silica body diameter 5–12 μm (mean 9 μm of 55 measured); stomatal length 33–41 μm (mean 36 μm of three), width across subsidiary cells 15–18 μm (mean 16 μm of three), and width across guard cells 8–10 μm (mean 9 μm of three); papillae diameter 5–8 μm (mean 6 μm of eight); intercostal long-cell length 31–51 μm (mean 45 μm of six) and width 12–15 μm (mean 14 μm of five); costal long-cell length 23–44 μm (mean 33 μm of 14) and width 4–7 μm (mean 5 μm of 14); costal short-cell length 10–14 μm (mean 12 μm of 13) and width 5–7 μm (mean 6 μm of 13).

**Discussion.** —This specimen is a fragment of leaf blade, 25 mm × 5 mm, with parallel venation. Preservation is adequate for identification in only one small area. This shows a costal zone with several rows of common, saddle-shaped silica bodies. These distinctive silica bodies are 7–10 μm long and 8–12 μm wide, convex horizontally and concave vertically. Costal long-cells are long, narrow, uniform in width and have sinuous walls. Some possible stomates were seen, but none sufficiently well preserved for positive identification. No microhairs, macro-

**Figure 10** —Chloridoideae gen. et sp. indet., fossil grass epidermis (FT-F13128), showing saddle-shaped silica bodies.

**Pogoneura biiflora** (Palmer et al., 1985) has abundant saddle-shaped costal silica bodies almost in contact at each of four corners to produce a more striking lattice-like effect than seen in the fossil. This living species also has papillae, prickles, and microhairs not seen in the fossil. Microhairs are also common on the epidermes of *Cyclostachya stolonifera* and of *Polevanisia rigida* (photomicrographs provided by Leslie Watson), which have epidermes even less similar to the fossil. Other distinguishing features of these living species include long rows of saddle-shaped and multilobed silica bodies side by side in *Polevanisia rigida* and the deep stomatal grooves and less curved, almost square silica bodies of *Cyclostachya stolonifera*.

***Pogoneura*** is represented by only *P. biiflora*, which is found in wooded grassland on heavy clay soils in Uganda and Tanzania (Clayton et al., 1974). *Polevanisia* and *Cyclostachya* are also monospecific genera: *Polevanisia* from mountain grasslands of Orange Free State, Lesotho, and Cape Province in South Africa and *Cyclostachya* from dry open hilly country in Mexico (Watson and Dallwitz, 1989).

**Material.** —SEM stub FT-F13128.

**Measurements.** —Saddle-shaped silica body length at lobes 7–10 μm (mean 9 μm of six measured), length at waist 7–8 μm (mean 8 μm of six), and width (transverse to long cells) 8–12 μm (mean 10 μm of six); costal long-cell length 38–47 μm (mean 43 μm of four) and width 8–12 μm (mean 10 μm of four); costal short-cell length 15–22 μm (mean 19 μm of four) and width 13–17 μm (mean 15 μm of four).

**Evoluotional Status of Miocene African Grasses**

The fossil grasses described here have been assigned to modern genera in large part because of the strength and scope of cuticular comparisons. Cuticular features have been more im-
PANICOID FOSSILS
AND MODERN GENERA

Tetrarrhena (B)  
Phyllorchidis (B)  
Stipa (A)  
Monochather (A)  
Isachne  
Steroechlaena  
S. miocenicus  
Zygochloa  
Spartoehloa (A)  
Pentaschistis  
C. kabylis  
C. shipmanae  
Cleitoehloa  
Pennisetum  
Aristida (A)  
Piptatherum (A)  
Schmidtnia (C)  
Brachiaaria  
Danthoniopsis  
Hymenachne

LENGTH=20
CONSISTENCY INDEX=0.8
A=Arundinoideae  
B=Bambusioideae  
C=Chloridoideae  
other=Panicoideae

CHLORIDOID FOSSILS
AND MODERN GENERA

Tetrarrhena (B)  
Phyllorchidis (B)  
Acraehne  
Polevaehia  
Pogonehia  
Chloridoideae indet.  
Cyclostachyea  
Cypheolepis  
Pogonarthria  
Tragus  
Stipa (A)  
Brachiaaria (P)  
Leptoehloa  
Eragrostis  
Parapholis (O)  
Poa (O)  
D. africanus  
Distichis  
Arundinella (P)  
Sporobolus

LENGTH=22
CONSISTENCY INDEX=0.8
A=Arundinoideae  
B=Bambusioideae  
O=Pooideae  
P=Panicoideae  
other=Chloridoideae

Figure 11—Cladograms of panicoid and chloridooid grasses similar to Fort Ternan fossil grasses.

important for the taxonomy of grasses other than plant groups (Metcalfe, 1960; Twiss et al., 1969) and are now well documented for most modern genera of grasses (Watson and Dallwitz, 1989). Miocene fossil grasses (Thomasson, 1987; Jacobs and Kabuye, 1987) and other angiosperm leaves (Axelrod and Raven, 1978) are commonly referred to extant genera. However, a few extinct Miocene plant genera have been described (Thomasson, 1979; Smiley and Huggins, 1981) and it is unlikely that mid-Miocene grassland were modern in all respects (Retallack, 1991). Were these Miocene grass extinct and archaic forms better referred to new genera or to a form-genus such as Grumitnophyllum? Or were they extinct species of archaic genera still living?

These questions can be addressed by cladistic analysis of the fossils together with living grasses found to be similar during computer identification (Figure 11). The cladograms were constructed using the PAUP computer program (Swoford, 1985) and data matrices (Table 1) derived from the large database of Watson and Dallwitz (1989). Bambusoideae (here Tetrarrhena and Phyllorchidis) were used as an outgroup, as is common in phylogenetic analyses of grasses. The cladogram for panicoids was run initially with 47 taxa mentioned in this paper, then pruned of all clades not containing fossils and rerun with edited data. The appearance of arundinoid grasses in various positions in the cladograms is a common experience in cladistic analysis of grasses, and confirms widely held suspicions that this group may be polyphyletic (Kellog and Campbell, 1987). The proximity of the poodi Parapholis to the chloridooid Distichis is due to such features as abundant papilae and round silica bodies. Both genera include salt tolerant species and these convergent features may be related to similar habitat preferences. The appearance of panicoids at two places in the cladogram of chloridooids and several cases of unresolved branch order diminish the overall phylogenetic significance of the cladograms, although these are common problems with phylogenetic analyses of grasses (Watson et al., 1985; Kellog and Campbell, 1987). For the purpose of estimating evolutionary status of the Miocene fossils, however, the cladograms display fossil taxa clustered with related taxa on deeply separated clades. This pattern indicates that the fossils belong to genera ancient within grasses, rather than archaic extinct groups or part of a recent adaptive radiation of grasses.

A comparable conclusion can be gained by considering the DIST statistic, which is a measure of similarity between grass genera based on a large set of morphological, anatomical, and chemical features (Watson and Dallwitz, 1989). DIST values for genera most like the fossils range from 0.0308 (Stereochlaena) to 0.0692 (Cyclostachya), with the others 0.0322 (Distichis), 0.0455 (Cleitoehloa), 0.0457 (Pogonehia), and 0.0517 (Polevaehia). DIST values for grasses as a whole range from 0.0032 for the New Zealand montane bambusoid Petriehля to 0.0990 for the phyletically isolated South and Central American bambusoid Steyermarkochloa. Compared with common grasses of East Africa today, the panicoid genera similar to the fossils have comparable DIST values to Andropogonae such as Themeda (0.0409) and Hyparrhenia (0.0334), but are more phyletically isolated than Panicaeae such as Pennisetum (0.0229) and Andropogonae such as Andropogon (0.0225). The chloridooid genera similar to the fossils have comparable DIST values to Sporobolus (0.0380), but are more phyletically isolated than Chloris (0.0304) and Cynodon (0.0165). These values indicate that the genera comparable with the fossils are not the most archaic, relict taxa among grasses, but then neither are they among a geologically recent adaptive radiation of grasses.

A third indication of the antiquity of grass genera comparable with the fossils is their biogeographic distribution and species richness. Both Cleitoehloa and Stereochlaena have few species, and are neither widespread nor abundant in Australasia or southeastern Africa, respectively (Clayton, 1978; Clayton and Renvoie, 1982; Beadle, 1981; Tothill and Hacker, 1983). The monospecific genera Pogonehia, Polevaehia, and Cyclostachya also are restricted to small populations within limited geographic areas. Australian Distichis also appears to be a relict rather than an introduction (Beadle, 1981), but the New World species of Distichis are widespread (MacMahon, 1988; Christensen, 1988). Australia–Americas disjunct distributions also are found in the grasses Amphibromia and Leptoloma (Hartley, 1964). Distichis includes some salt-tolerant littoral species (Christensen, 1988) so that limited transoceanic distribution is conceivable.
More likely, however, this genus predated the Neogene separation of Australia and the New World by oceans and Antarctic ice.

Although assignable to modern genera, the middle Miocene fossils from Fort Ternan are a different grass flora than found in East African wooded grasslands today, which are dominated by chloridoids such as *Sporobolus* and *Chloris* and panicoids of the supertribe Andropogonae such as *Hyparrhenia* and *Themeda* (de Wit, 1978; White, 1983). The dominance of these latter genera in some East African grasslands was established at least by 28,000 years ago (Palmer, 1976). In contrast, grasses of this middle Miocene carbonatite-nephiteline volcanic center exploited young volcanic soils within a vast area of low fertility lateritic soils developed on the stable Precambrian continental shield of Africa (Retallack, 1991). Carbonatite-nephiteline volcanic soils of the early and middle Miocene were probably not much more fertile than lateritic soils for plants. Like modern tuffaceous soils of this kind, they would have been salty and highly alkaline after eruption (Hay, 1989) and their abundant carbonate would have made phosphate procurement difficult (judging from modern studies of plant nutrition, Stevenson, 1986). From this perspective it is not surprising that a middle Miocene grass flora shows affinities with oligotrophic species of old Gondwanan lateritic soils and salt-tolerant widespread species. Dry and infertile lateritic soils were probably as important to the evolution of African florae (Axelrod and Raven, 1978) as they were to Australian florae (Beadle, 1966; Hill, 1990). Panophilic and chloridoid grasses form coherent clades that may have diversified as temperate rain forests of the Gondwanan early Tertiary evolved into warm temperate to subtropical open woodlands on relict lateritic soils in dry parts of northward-moving Australia, Africa, and South America. Late Tertiary extinctions of archaic, and probably polyphyletic, aranoid grasses of lateritic soils could be one reason why it is difficult to determine phylogenetic relationships between living grass subfamilies (Stebbins, 1982). The modern flora of East African grasslands probably began to appear with the middle to late Miocene eruption of phonolites, trachytes, and other less alcaline volcanic rocks, which weather to especially fertile soils (Bell, 1982).

Although distinct from modern wooded grasslands at the generic level, these early grasslands were similar to modern tall grasslands in some adaptive features of their epidermes. The Fort Ternan fossil grasses do not have deeply recessed stomata with overarchung papilae as in grasses of very dry climates (Metcalf, 1960). *Distichlis africana* sp. nov. does have broad furrows with abundant papilae and scattered stomata, but the subsidiary cells are not deeply sunken. Nor is it certain whether this fossil had salt glands like some living *Distichlis*. As in the Serengeti Plain, the presence of salt-tolerant chloridoids is not necessarily an indication of dry climate, but also an adaptation to dustings of highly alkaline carbonatite-meltillite volcanic ash (de Wit, 1978), for which there is petrographic evidence in the Onuria paleosol (Retallack, 1991).

Many of the species of this middle Miocene grassland were probably similar physiologically to modern East African grasses in utilizing the C₃ photosynthetic pathway, which is now found in *Streptochloaena, Distichlis, Cyclostachya, Pogoneura*, and *Pelevania*. However, the C₄ pathway found in most plants, and presumably primitive in grasses, is still found in *Cleistochloa* (Watson and Dallwitz, 1989). The presumed proportion of C₃ grasses in the fossil flora is like that of African grasslands at elevations of 2,000–3,000 m, rather than like that of modern African lowland savannas, which are almost entirely C₄ (Tieszen et al., 1979). The presence of C₄ grasses also is indicated by isotopic studies of paleosols at Fort Ternan (Cerling et al., 1991), although their values represent sparry calcite cement formed during burial rather than pedogenic calcite (Retallack, 1992).

The appearance of middle Miocene tall grassland in East Africa may have been in part due to the destructive effects of mammalian fauna, which at Fort Ternan includes rhinoceros, elephant-ancestors, and the earliest giraffe and antelope known in Africa (Shipman et al., 1981; Pickford, 1984, 1986). This is not to say that plants and animals of this early grassland eco-system were as highly co-evolved as in modern grasslands. Indeed, the abundant fossil antelope at Fort Ternan are adaptively more like Indian woodland antelope than modern African grassland species in their hypsodonty and cursoriality (Kappelman, 1991). Some of the fossil antelope teeth do however show clear surface striations of the kind formed by feeding on siliceous grasses (Shipman, et al., 1981). This is not surprising in view of the abundance and variety in shape demonstrated here among the silica bodies of fossil grasses from Fort Ternan. Grasses on the Serengeti Plains of Tanzania have been shown to have higher amounts of opaline silica in their leaves in regions that are more heavily grazed (McNaughton and Tarrants, 1983). Silica body shape has also been proposed as a defense against grazing (Herrera, 1985). In this scenario, increased morphological complexity results in an increase in the number of sharp ridges and total edge length per unit volume, creating greater abrasive potential against the teeth of grazers.

The appearance of grasslands in East Africa 15 million years ago was not immediately encouraging to human evolution. Apes were abundant and diverse in East Africa during early Miocene time, but became increasingly rare in the fossil record after middle Miocene time as vervets, baboons, and other monkeys diversified in savanna vegetation (Andrews, 1981). Early australopithecine ancestors of humans are not known in grassland paleosols older than 4 million years (Retallack, 1990, 1991; Radoshevich et al., 1992).

The antelope-dominated fauna of Fort Ternan is so different from earlier Miocene faunas of East Africa that it is thought to have immigrated into this area some 15 million years ago. Although it shares one antelope genus with Eurasia, this fauna is sufficiently distinctive that it probably evolved for some time in more or less open vegetation within the present area of the Namibian or Saharan deserts, and then extended its range into East Africa during global middle Miocene cooling and drying (Bernor, 1983). In contrast, biogeographic affinities of the Fort Ternan grass flora are not Eurasian, but rather with southern Africa, Australia, and the New World. Similarly, the fossil dicotyledon flora of Chogo paleosols at Fort Ternan includes some widely distributed genera, but matches especially Zambezian riparian forest and miombo woodland (as defined by White, 1983) of lateritic soils on Precambrian bedrock of southern Africa (Retallack, 1991). Modern relatives of the Fort Ternan grasses may be regarded as remnants of an archaic Gondwanan flora of deserts and dry woodlands on impoverished sandy and lateritic soils. This archaic Gondwanan flora has been supplanted since middle Miocene time in Africa by grassland ecosystems that co-evolved with antelope, then zebra as well, and finally with human modification of increasingly extensive, fertile, volcanic landscapes.

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DUGAS AND RETALLACK—MIOCENE GRASSES FROM AFRICA


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