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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 found. Two of the fossil species are assigned to *Cleistochloa kabuyis* sp. nov. and *C. shipmanae* 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 miocenica* 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 *Polevansia*. 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-Cheboldaeff, 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 Hiwegi 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 *Leptaspis* sp. cf. *L. zeylanica* and *Humbertochloa* sp. among a diverse assemblage of angiosperm leaves some 12 million
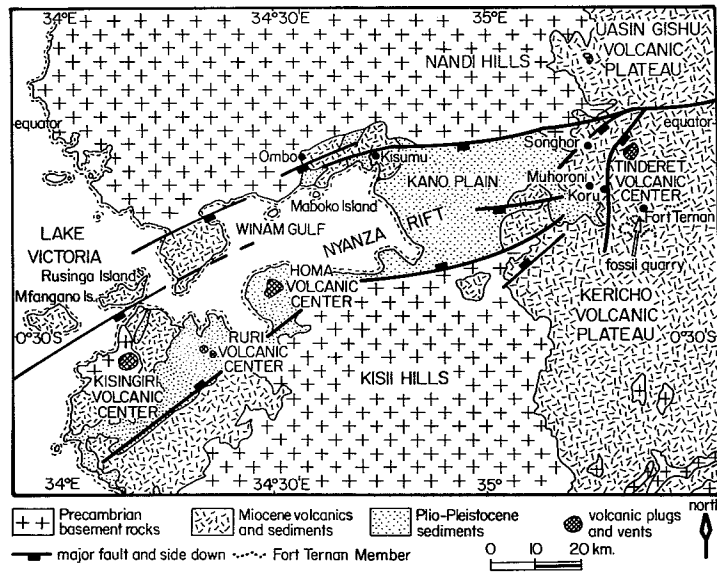
FIGURE *1*—Simplified geological map of the Nyanza Rift and the Fort Ternan fossil quarry, southwestern Kenya.
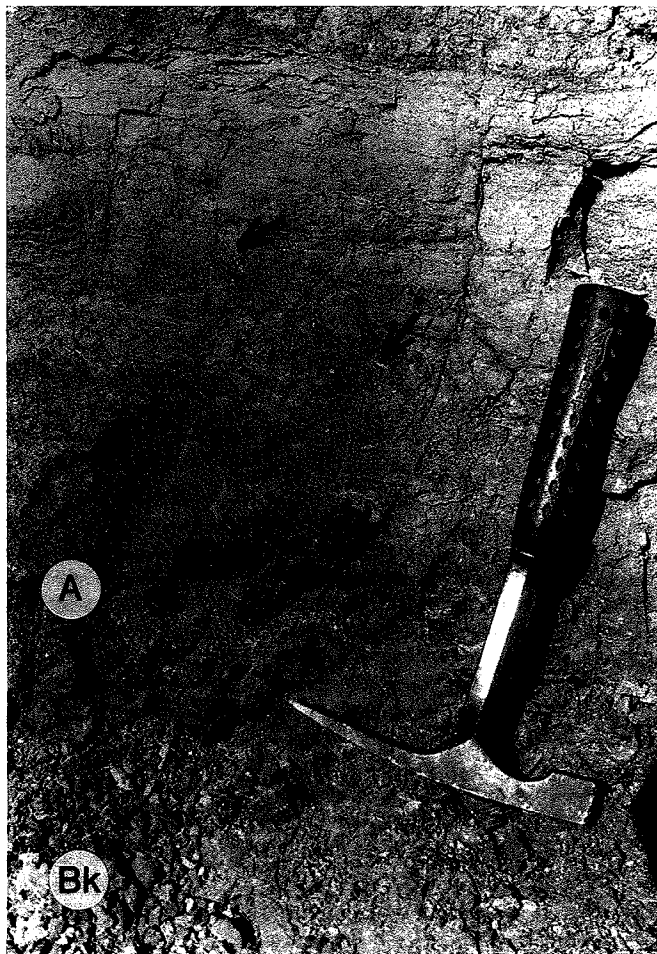

FIGURE *2*—The type Onuria paleosol at Fort Ternan National Monument, showing soil horizons (A and Bk) and some prominent grasses (at arrows) in overlying nephelinitic sandstone.

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 $^{39}Ar/^{40}Ar$ 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 $^{39}Ar/^{40}Ar$ 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 m³ 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 peds, 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 lahar. 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 (Leys, 1983), and lahars (Fisher and Schminke, 1984, p. 303). Sudden burial probably played a role in preservation of the Fort Ternan grasses, and the nephelinites 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. cf. *B. serrata, Cymbopogon caesius, Eragrostis racemosa, Hyparrhenia filipendula, H. hirta, Hyperthelia 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
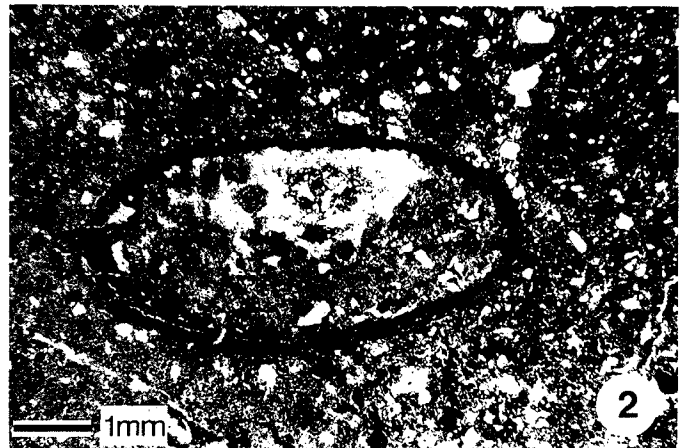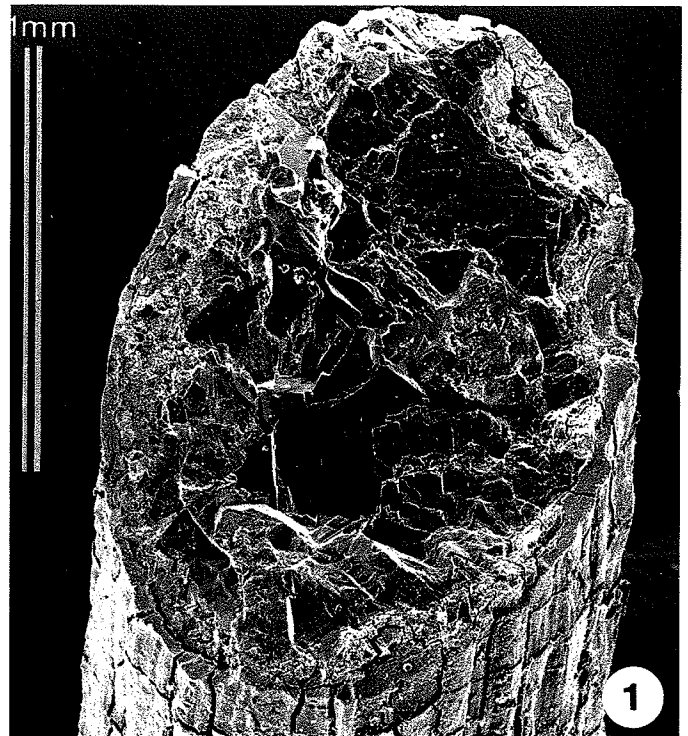

FIGURE *3*—Scanning electron micrograph (*1*) and petrographic thin section under crossed nicols (*2*) of fossil grasses from above the type Onuria paleosol, showing fill of clay and calcite within sheathing leaves. SEM is Kenyan National Museum FT-F22654: thin section is FT-R74.

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 (*Stereochlaena 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").
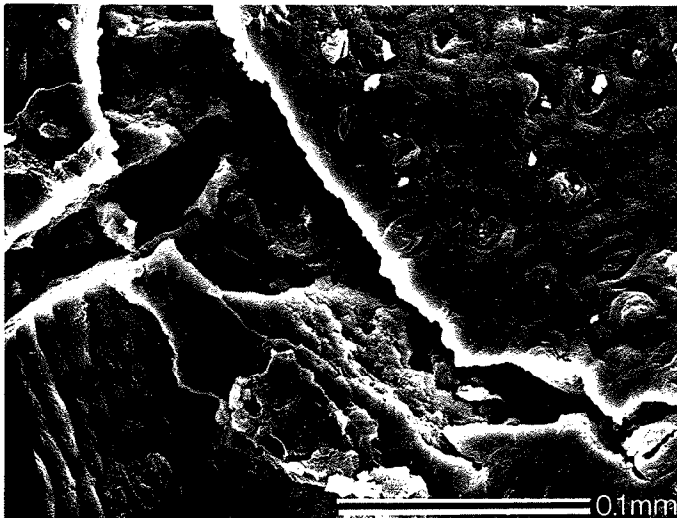
FIGURE 4—Fossil epidermis of unidentified woody dicot, showing stomates in areolar fields (KNMP-FT-F13130).

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 undulose walls. Areolar 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 cyclocytic 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 Cellareatea, Turma Anomorimatae, Subturma Lacanomorae, Form Genus Claibornicutis. The amount of material available is inadequate for determining the botanical affinities 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; Bonnefille, 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 CLEISTOCHLOA Hubbard, 1933
CLEISTOCHLOA KABUYIS sp. nov.
Figure 5

Diagnosis.—Cleistochloa fossil leaves, sheath diameter 3–4 mm, abaxial epidermis glabrous, with common costal, dumbbell, long-shank phytoliths, 19–22 μm by 8–11 μm in size, and some intercostal trilobate phytoliths, 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 Cleistochloa 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 Gerbeth-Jones (1986, 1988) of the following East African species: Acroceras zizanoides, Brachiaria brizantha, Hylebates chlorochloe, Eccoptocarpha obconiciventris (Panicanae), Rhytachne latifolia (Andropogonae), Stipagrostis uniplumis, Pentaschistis borussica (Arundinoidae), and Schmidtia pappophoroides (Chloridoidae). 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 Panicanae such as Acroceras zizanoides and Eccoptocarpha obconiciventris. Similar forms of silica bodies were described by Metcalfe (1960, p. xlii) as "intermediates between cross and dumb-bell shaped," and included by Twiss et al. (1969, p. 111) with more symmetrical phytoliths 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, Pyranthera, Rytidosperma (Arundinoidae), Eriochloa, Ottochloa, Paspalum, Thyridolepis (Panicanae), and Lophacme (Chloridoidae). 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.

Middle Miocene fossil panicoids from Fort Ternan compared with selected living grasses. Data from Watson and Dallwitz (1989) PARAM NOTU = 20 NCHAR = 23 MISSING = 0; Data (A6, A1, 1X, 23I1);	Middle Miocene fossil chloridoids from Fort Ternan compared with selected living grasses. Data from Watson and Dallwitz (1989) PARAM NOTU = 20 NCHAR = 23 MISSING = 0; Data (A6, A1, 1X, 23I1);
tetra 21222222220121111111121	tetra 21222222220121111111121
phyll 21012122202121011111021	phyll 21012122202121011111021
monoc 21222222222211120021121	parap 02020221211020110101122
penta 21222222221121120011121	arund 20220220222121111121021
stipa 22212221222121111131221	dista 22222221212121111130010
ckabu 21222222221221111111120	chloi 22212222200001111111220
smioc 00000000022211100001020	acrac 21212222220121120011121
cship 21222222221221111111121	brach 22212222222121112211011
brach 21222222222121101111011	cyclo 22212222222121111111221
cleis 21222222221021111111121	cypho 22212222222121111111221
isach 20222212200010020011201	disti 22002221200121110031101
penni 21222222220121111101121	eragr 20010220220121110001121
stere 21222222222011120011021	lepto 20200022222121110001111
zygoc 21222222222211110011121	pogoa 20202222222121111001020
schmi 21222222222111112211121	pogoe 22212222221101111111221
arist 01000022020121101001121	polev 22212222222111111101221
pipta 21020220211121110111122	sporo 22111221222121110021121
danth 21222222222121111111121	tragu 22210222220121000011000
spart 21222222222121111111021	poali 02020221011220000000102
hymen 21222222222121010011121	stipa 20000220000121111000000

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 "pooid-type" horizontally elongated, sinuous or elongate-crenate silica bodies, or 288-2 without them; 289-1 with "panicoid-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 saddle-shaped silica bodies, or 291-2 without them; 292-1 with crescentic silica bodies, or 292-2 without them; 293-1 with "oryzoid-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 interstomatals; 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 conspicuously 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 μm) narrowed the choice to *Aristida, Danthoniopsis,* and *Hymenachne* for the unlikely interpretation that the fossil has triangular stomatal subsidiary cells, and *Aristida* and *Cleistochloa* for the interpretation that they are intermediate between parallel and triangular. The epidermes of *Aristida ciliata, A. longiflora, A. scabrivalvis,* and *A. setacea* are very different from the fossil, with markedly triangular subsidiary cells to stomates recessed within narrow furrows flanked by costal prickles and macrohairs (Metcalfe, 1960; Palmer et al., 1985). Unlike the fossil, *Danthoniopsis chevalieri* has prickles, and dumbbell-shaped silica bodies are uncommon compared to round and saddle-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 *Cleistochloa.*

The only published information on the epidermis of *Cleistochloa* 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 *Cleistochloa subjuncea* (Tothill and Hacker, 1983) are characterized by a slightly shorter connecting bar than seen in the fossil phytoliths. *Cleistochloa sclerachne* (Reeder, 1948) has dumbbell phytoliths with an hourglass-shaped connective, rather than the barlike central portion seen in *C. kabuyis* sp. nov. These living species have a few phytoliths with one end of the dumbbell larger than the other, but no trilobate phytoliths were seen like those of the fossil. Both species also have pubescent leaf sheaths, whereas no microhairs or macrohairs were seen on these fossils. This is unlikely to be due to poor preservation because the bases of both microhairs and macrohairs were seen on fossil *Cleistochloa shipmanae* sp. nov. from Fort Ternan. In addition, the fossil fragments of *Cleistochloa kabuyis* sp. nov. are wider than usual for *C. subjuncea,* more like the other living species, *C. sclerachne.*

Cleistochloa 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; Tothill and Hacker, 1983). *Cleistochloa sclerachne* is a perennial on "raw clay soils" (Tropofluvents of Bleeker, 1983) of disturbed forest 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.
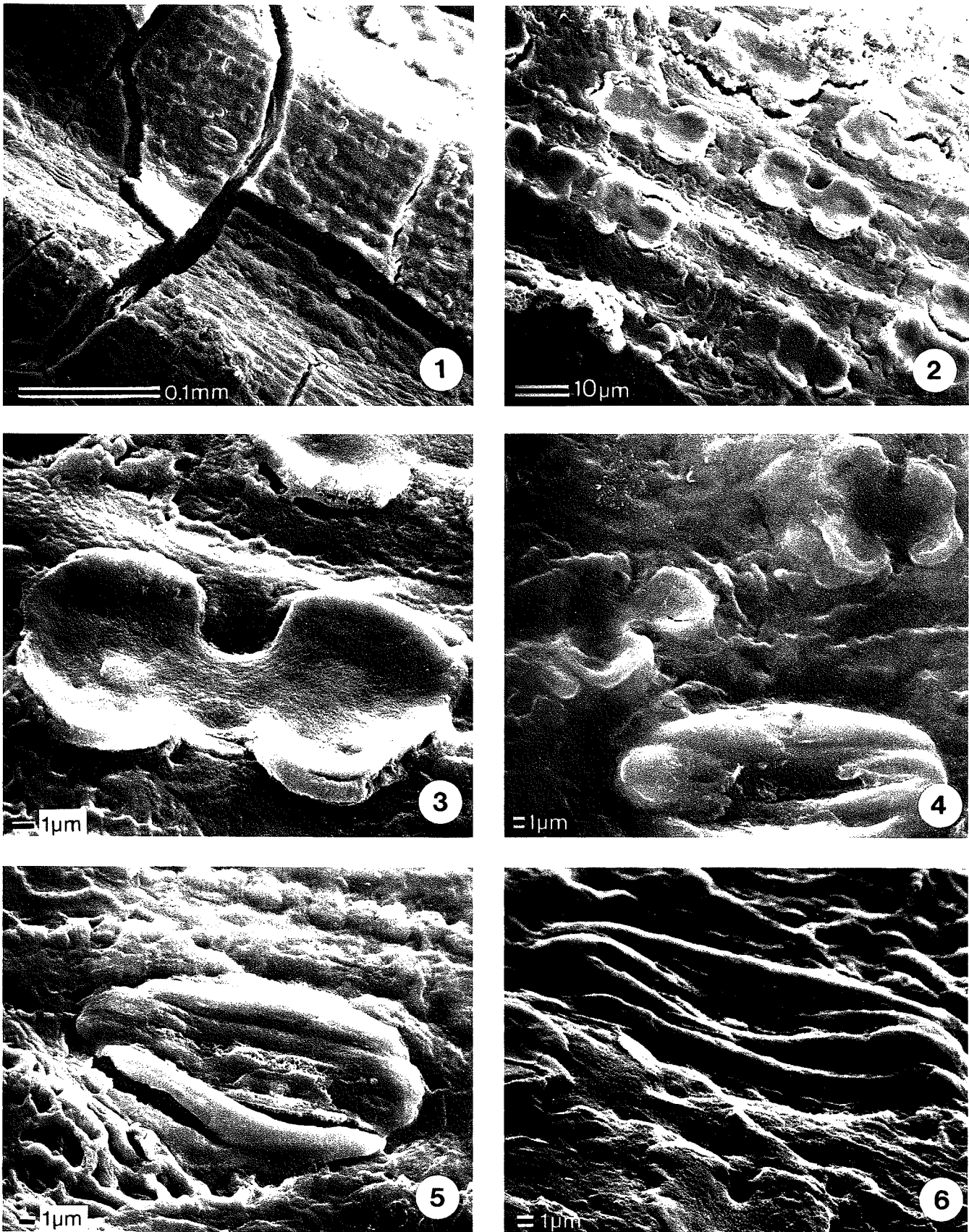
FIGURE 5—*Cleistochloa kabuyis* sp. nov., holotype, fossil grass epidermis (FT-F13120). *1,* overview of costal and intercostal zones with stomates and silica bodies. *2, 3,* costal dumbbell-shaped silica bodies. *4,* intercostal trilobate silica bodies and stomate. *5, 6,* intercostal stomates.
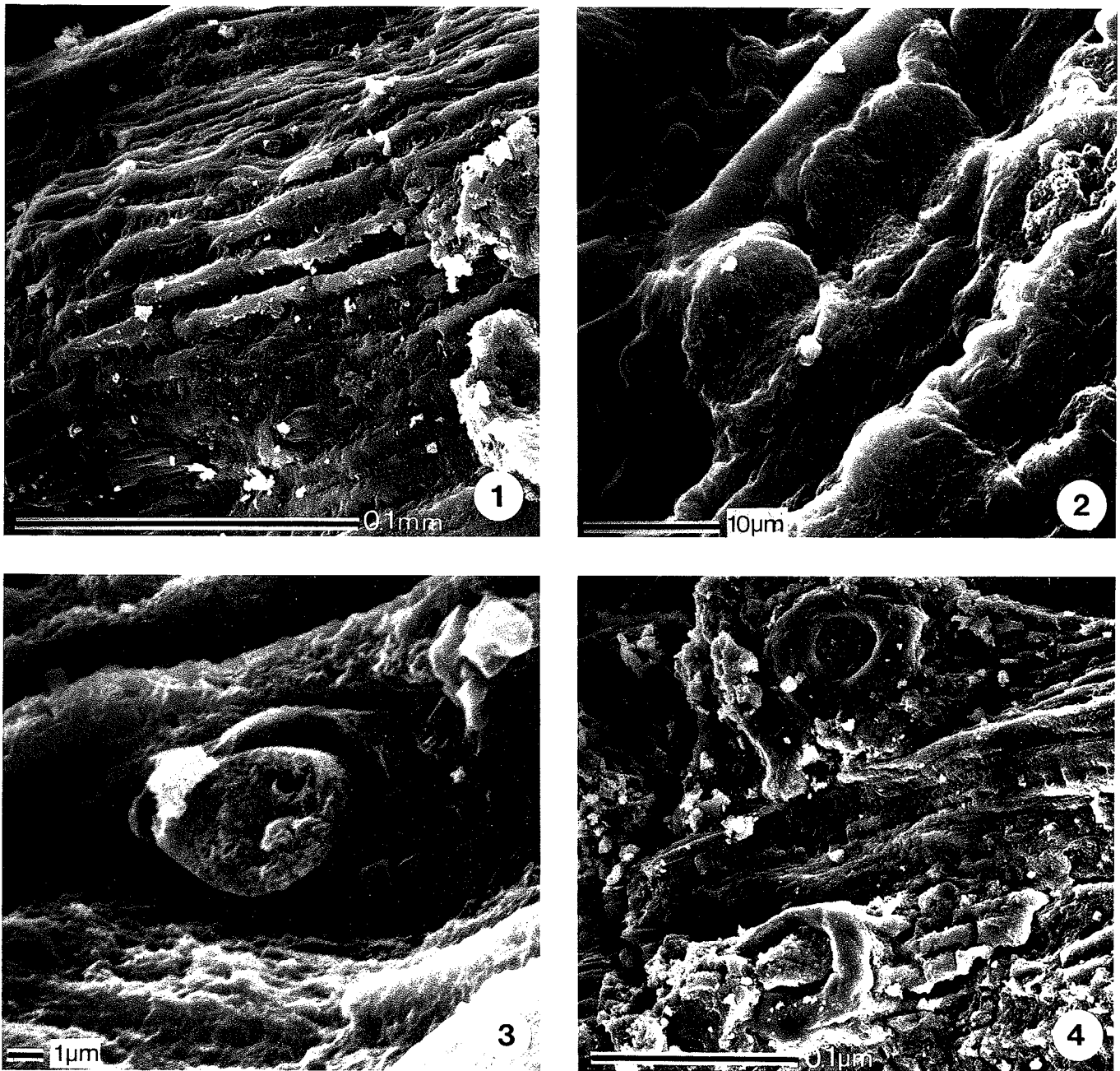
FIGURE 6—*Cleistochloa shipmanae* sp. nov., holotype, fossil grass epidermis (FT-F13123). *1*, intercostal zone with stomates (below) and costal zone (above) with internal molds of long-cells, which have exfoliated their cuticular cover. *2*, dumbbell-shaped silica body and associated cork cell. *3*, base of broken microhair. *4*, circular basal cells of two macrohairs.

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).

CLEISTOCHLOA SHIPMANAE sp. nov.
Figure 6

Diagnosis.—*Cleistochloa* fossil leaves, sheath 10 mm diameter, abaxial epidermis with common costal, dumbbell, short-shank 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-
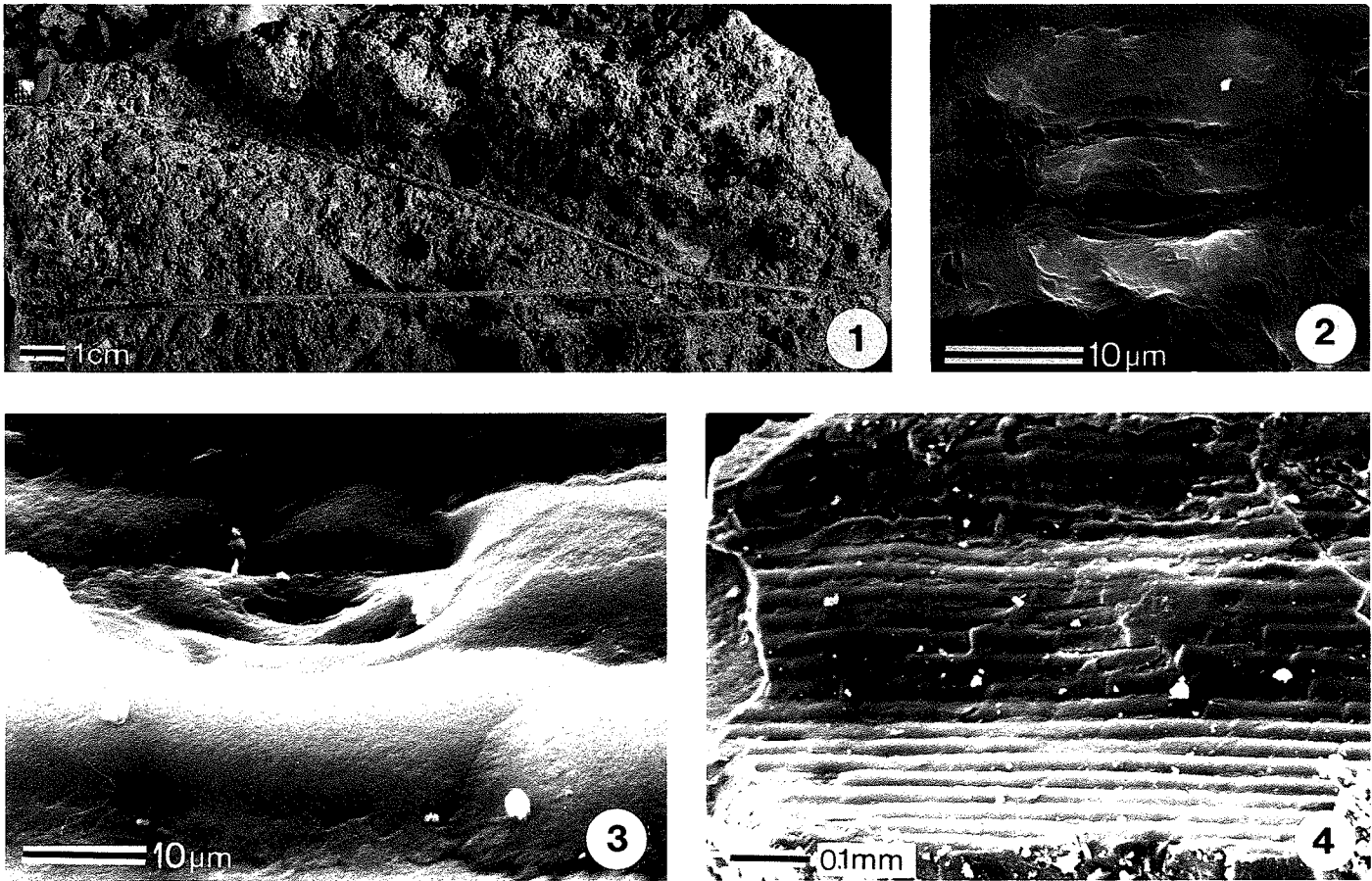
FIGURE 7—*Stereochlaena miocenica* sp. nov., holotype, grass fossil (*1*) and epidermis (all FT-F13126). *1*, branching grass plant with attached leaf sheaths. *2*, stomate with parallel sided subsidiary cells from culm. *3*, intercostal zone with stomate from leaf sheath. *4*, stomate with triangular subsidiary cells from leaf sheath.

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 *Cleistochloa* and to the subfamily Panicoideae for much the same reasons as outlined for *Cleistochloa 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 "Panicoideae 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).

Among SEM photomicrographs of modern East African grass epidermis by Palmer and Tucker (1981, 1983), Palmer et al. (1985), and Palmer and Gerbeth-Jones (1986, 1988), this fossil shows some similarity to six species, all panicoids of the supertribe Panicanae: *Urochloa mosambicensis, Gilgiochloa indurata, Zonotriche inamoena, Entolasia imbricata, Pennisetum purpureum,* and *Brachiaria brizantha.*

The dumbbell silica bodies of *Cleistochloa 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. Cleistochloa shipmanae* sp. nov. is broader leaved than either of the living species of *Cleistochloa* (Reeder, 1948; Tothill and Hacker, 1983), but like these living species and unlike *C. kabuyis* sp. nov., *C. shipmanae* has hairs.

Holotype.—SEM stub FT-F13123.

Other material.—SEM stub FT-F13125.

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

cell length 16–31 μm (mean 26 μm of five) and width 4–5 μm (mean 5 μm of five).

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 7.1, 8), with four connected culm internodes, previously described as "a branching panicoid grass" (Retallack et al., 1990) and "Panicoideae 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 epidermes of living East African grasses: *Cyrtococcum chaetophoron, Chaetopoa taylori* (Panicanae), and *Phyllorhachis sagittata* (Bambusanae). 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, Thyridolepis, Zygochloa* (Panicanae), and *Triraphis* (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): *Australopyrum, Dissanthelium* (Pooideae), *Rytidosperma, Spartochloa* (Arundinoideae), *Coelachne, Isachne, Leptoloma, Reynaudia* (Panicanae), *Buchlominus, Entoplocamia,* and *Lopholepis* (Chloridoideae). All of these differed from the fossil in such diagnostic features as microhairs, stomatal guard cells overlapped by subsidiaries, 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 epidermes with common prickles and hair bases (Palmer and Gerbeth-Jones, 1986; photomicrographs provided by Leslie Watson). In vegetative form, *Sterochlaena 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.
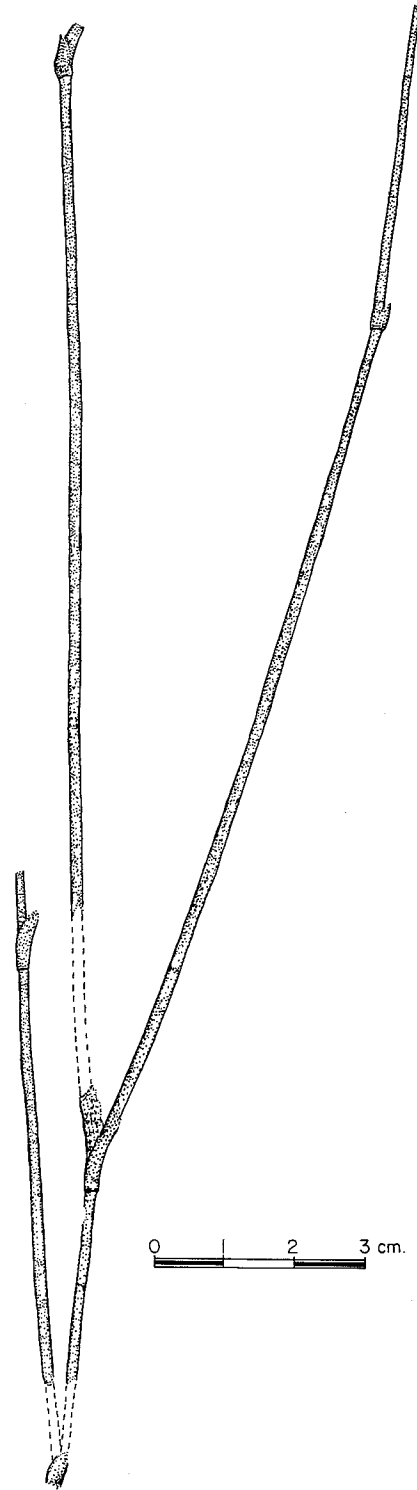

FIGURE 8—*Stereochlaena miocenica* sp. nov., holotype, interpretative sketch of branching fossil grass (FT-F13126).

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
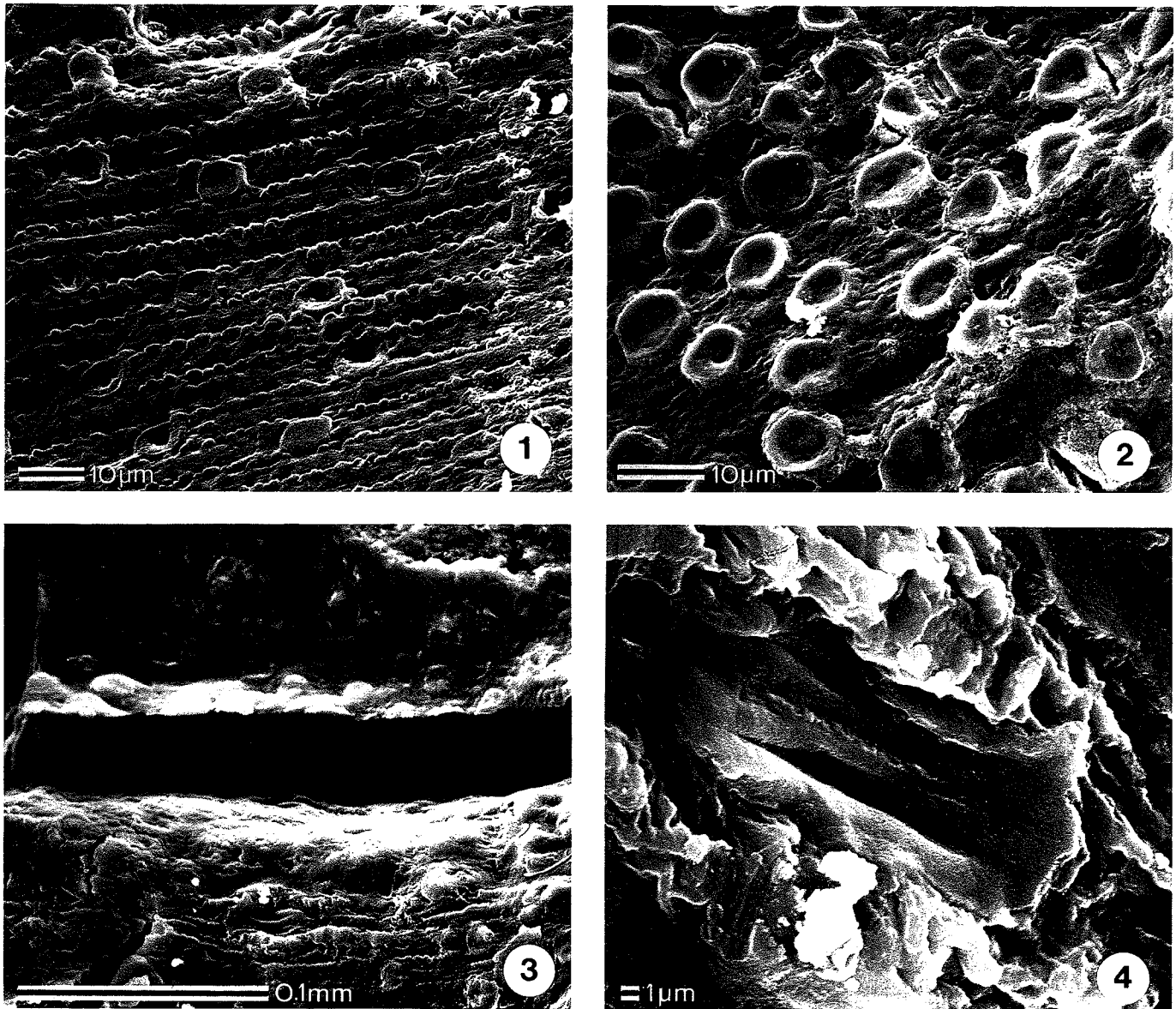
FIGURE 9—*Distichlis africana* sp. nov., holotype, fossil grass epidermes (FT-F13127). *1*, intercostal cells with undulose walls and round silica bodies arranged in crude circlets. *2*, densely aggregated circlets of round silica bodies. *3*, fractured furrow with a row of stomates (below) and papillae (above). *4*, stomate with triangular subsidiary cells partially overlapped by epidermal cells.

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 DISTICHLIS Rafinesque, 1819
DISTICHLIS AFRICANA sp. nov.
Figure 9

Diagnosis.—Distichlis 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 circlets 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, subsid-

iaries 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 africanus, Tragus berteronianus* (Chloridoideae), and *Arundinella nepalensis* (Panicanae). 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* (Pooideae), *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, macrohairs, and microhairs. Hairs are likely to have been preserved, judging from those seen on *Stereochlaena miocenica* 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).

Chloridoideae gen. et sp. indet.
Figure 10

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-
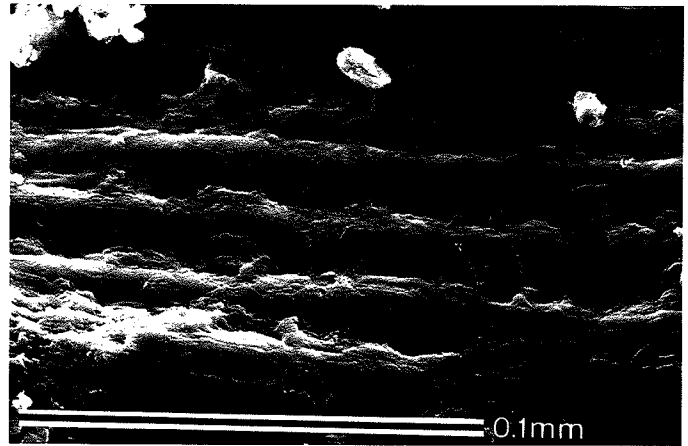

FIGURE 10—Chloridoideae gen. et sp. indet., fossil grass epidermis (FT-F13128), showing saddle-shaped silica bodies.

hairs, or papillae were seen on the small area of cuticle that showed epidermal detail.

Comparison.—Saddle-shaped silica bodies are found in the grass subfamilies Arundinoideae and Bambusoideae, as well as Chloridoidae, such as the East African species *Acrachne racemosa, Eragrostis macilenta, Cypholepis yemenica,* and *Brachyachne fulva* (Palmer et al., 1985). This fragment was identified in our preliminary studies using the table provided by Ellis (1987) as "Chloridoidae sp. indet. B" (Dugas, 1989; Retallack, 1991). Use of the computer key (Watson and Dallwitz, 1989) confirmed this identification, but, without information on stomata, could not choose among *Cyclostachya, Pogoneura,* and *Polevansia.* More precise identification of this fragment is deferred until the discovery of more informative material.

The epidermis of *Pogoneura biflora* (Palmer et al., 1985) has abundant saddle-shaped costal silica bodies almost in contact at each of four corners to produce a more striking latticelike 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 *Polevansia 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 *Polevansia rigida* and the deep stomatal grooves and less curved, almost square silica bodies of *Cyclostachya stolonifera.*

Pogoneura is represented by only *P. biflora,* which is found in wooded grassland on heavy clay soils in Uganda and Tanzania (Clayton et al., 1974). *Polevansia* and *Cyclostachya* are also monospecific genera: *Polevansia* 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).

EVOLUTIONARY 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-
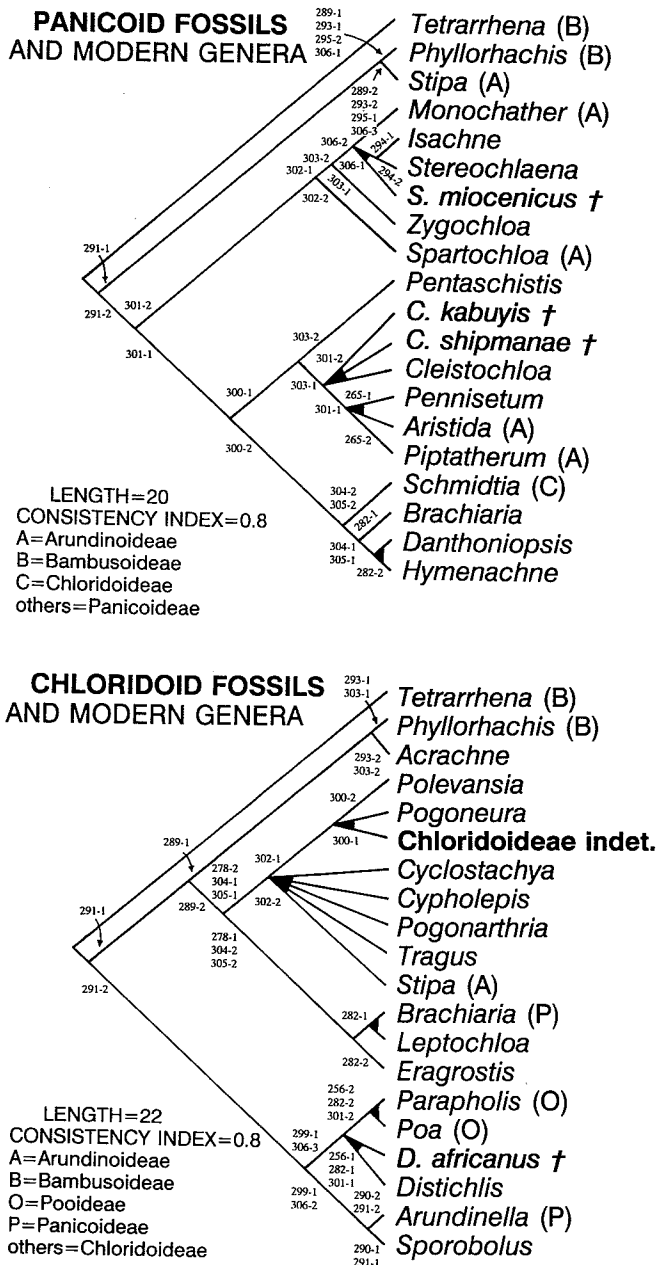
**PANICOID FOSSILS
AND MODERN GENERA**

289-1
293-1
295-2
306-1

Tetrarrhena (B)
Phyllorhachis (B)
Stipa (A)
Monochather (A)
Isachne
Stereochlaena
S. miocenicus †
Zygochloa
Spartochloa (A)
Pentaschistis
C. kabuyis †
C. shipmanae †
Cleistochloa
Pennisetum
Aristida (A)
Piptatherum (A)
Schmidtia (C)
Brachiaria
Danthoniopsis
Hymenachne

LENGTH=20
CONSISTENCY INDEX=0.8
A=Arundinoideae
B=Bambusoideae
C=Chloridoideae
others=Panicoideae

**CHLORIDOID FOSSILS
AND MODERN GENERA**

293-1
303-1

Tetrarrhena (B)
Phyllorhachis (B)
Acrachne
Polevansia
Pogoneura
Chloridoideae indet.
Cyclostachya
Cypholepis
Pogonarthria
Tragus
Stipa (A)
Brachiaria (P)
Leptochloa
Eragrostis
Parapholis (O)
Poa (O)
D. africanus †
Distichlis
Arundinella (P)
Sporobolus

LENGTH=22
CONSISTENCY INDEX=0.8
A=Arundinoideae
B=Bambusoideae
O=Pooideae
P=Panicoideae
others=Chloridoideae

FIGURE 11—Cladograms of panicoid and chloridoid grasses similar to Fort Ternan fossil grasses.

fossils together with living grasses found to be similar during computer identification (Figure 11). The cladograms were constructed using the PAUP computer program (Swofford, 1985) and data matrices (Table 1) derived from the large database of Watson and Dallwitz (1989). Bambusoids (here *Tetrarrhena* and *Phyllorhachis*) 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 pooid *Parapholis* to the chloridoid *Distichlis* is due to such features as abundant papillae 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 chloridoids 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 (*Distichlis*), 0.0455 (*Cleistochloa*), 0.0457 (*Pogoneura*), and 0.0517 (*Polevansia*). DIST values for grasses as a whole range from 0.0032 for the New Zealand montane bambusoid *Petriella* 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 Panicanae such as *Pennisetum* (0.0229) and Andropogonae such as *Andropogon* (0.0225). The chloridoid 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 *Cleistochloa* and *Stereochlaena* have few species, and are neither widespread nor abundant in Australasia or southeastern Africa, respectively (Clayton, 1978; Clayton and Renvoize, 1982; Beadle, 1981; Tothill and Hacker, 1983). The monospecific genera *Pogoneura, Polevansia,* and *Cyclostachya* also are restricted to small populations within limited geographic areas. Australian *Distichlis* also appears to be a relict rather than an introduction (Beadle, 1981), but the New World species of *Distichlis* are widespread (MacMahon, 1988; Christensen, 1988). Australia–Americas disjunct distributions also are found in the grasses *Amphibroma* and *Leptoloma* (Hartley, 1964). *Distichlis* includes some salt-tolerant littoral species (Christensen, 1988) so that limited transoceanic distribution is conceivable.

portant for the taxonomy of grasses than other 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 grasslands were modern in all respects (Retallack, 1991). Were these Miocene grass fossils extinct and archaic forms better referred to new genera or to a form-genus such as *Graminophyllum*? Or were they extinct species of archaic genera still living?

These questions can be addressed by cladistic analysis of the

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-nephelinite 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-nephelinite 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 floras (Axelrod and Raven, 1978) as they were to Australian floras (Beadle, 1966; Hill, 1990). Panicoid 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, arundinoid 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 alkaline 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 overarching papillae as in grasses of very dry climates (Metcalfe, 1960). *Distichlis africana* sp. nov. does have broad furrows with abundant papillae 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-melilitite 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 C_4 photosynthetic pathway, which is now found in *Stereochlaena, Distichlis, Cyclostachya, Pogoneura,* and *Polevansia*. However, the C_3 pathway found in most plants, and presumably primitive in grasses, is still found in *Cleistochloa* (Watson and Dallwitz, 1989). The presumed proportion of C_3 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 C_4 (Tieszen et al., 1979). The presence of C_3 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 ecosystem 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; Radosevich 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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