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Poaceae phytoliths from the Niassa Rift, Mozambique

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ABSTRACT

The most common grass phytoliths from “Zambezi” miombos are described here for the first time. Their potential for long term preservation in sediments makes them a useful tool in the reconstruction of ancient plant communities and plant/human interactions. We processed 60 plant samples (26 identified genera and species), with an average of 300 phytoliths counted per sample to a total of 18,586. Forty-seven morphotypes were described as per the International Code for Phytolith Nomenclature, with exceptions, including forty-five discreet shapes and two articulated forms, which can be used as comparative reference materials. We conducted three forms of statistical analyses: Discriminant Analysis, Cluster Analysis, and Principal Component Analysis. The highest biomineral content was recorded among the Bambuseae and Paniceae, while the lowest silica production is detected in the Cynodonteae tribe. Typologically, the subfamily Panicoideae yielded 50% of the types reported here, 32% are from the Chloridoideae, 12% from the Bambusoideae, and 8% from the Arundinoideae sensu lato. Overall, the idealized Zambezi Poaceae phytolith spectrum is dominated by a small subset of Poaceae short cells, which include five morphotypes conventionally associated with Panicoid grasses (Bilobate concave outer margin long shaft, Bilobate concave outer margin short shaft, Bilobate convex outer margin long shaft, Bilobate convex outer margin short shaft, Cross), one morphotype commonly seen in Chloridoid taxa (saddle), and two types that appear across subfamily boundaries (tower, tower horned). The next logical step to take in regional phytolith research is the account of phytoliths deposited in soils underneath living plants, for they represent the interface between existing vegetation communities and the inevitably distorted fossil assemblages that the paleobotanist uses for environmental reconstruction.

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1. Introduction

African archaeologists are interested in phytoliths from modern, reference plants to reconstruct the landscape that served as environmental background to human evolution. Recent studies of African extracellular and intracellular silicifications from grasses have advanced our understanding of phytoliths from live plants in three phytochoria (White, 1983): the Somalia-Masai (Palmer and Tucker, 1981, 1983; Palmer et al., 1985; Palmer and Gerbeth-Jones, 1986; Ball et al., 2002; Barboni and Bremond, 2009), Sudano-Sahelian (Fahmy, 2008), and Guineo-Congolian (Runge, 1999) vegetation zones. Quantitative information on the amount and types of biogenic silica produced by African grassy plants, however, is very limited (cf. Albert and Weiner, 2001). This

scarcity is in contrast with the long-standing investigations of silica bodies among the European grasses; dating as far back as the late 19th and 20th centuries (see review of early work in Parry and Smithson, 1964). In other parts of the world, the phytoliths extracted from living Poaceae have been subjected to qualitative and quantitative analysis; for example, in South East Asia (Whang et al., 1998; Lu and Liu, 2003a), India (Krishnan et al., 2000), Western Melanesia (Boyd et al., 1998), the New Zealand grasslands (Marx et al., 2004; Thorn, 2004, 2008), the European Atlantic zone, as well as the Alpine and Mediterranean regions (Parry and Smithson, 1964; Ollendorf et al., 1988; Kaplan et al., 1992; Carnelli et al., 2004; Tsartsidou et al., 2007). Grass reference collections have also been developed in North America (Blackman, 1971; Brown, 1984; Fredlund and Tieszen, 1994; Blinnikov, 2005), the Neotropics (Piperno and Pearsall, 1998) and South America (Zucol, 1998; Iriarte, 2003; Gallego and Distel, 2004; Fernández Honaine et al., 2006).

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Biogenic silica may be preserved for long periods of time. Phytolith analysis is a valuable tool for reconstructing ancient plant communities' physiognomy and structure (Retallack, 1992; Alexandre et al., 1997; Barboni et al., 1999; Mercader et al., 2000; Albert et al., 2006; Barboni et al., 2007; Strömberg et al., 2007), especially in the field of paleoagrostology (for the most recent treatment of Poaceae phylogenetics see G.P.W.G., 2001; Bouchenak-Khelladi et al., 2008). The analysis of phytoliths from living plant tissues helps establish rates of silica production in ecosystems of known floristic composition, determines the frequency of different morphotypes in a given regional phytolith spectrum, and highlights the types that, because of prominence, indicate likely membership to a subfamily, tribe or genus. In this context, we aim to fill the existing gap in phytolith research of the most common Poaceae species in the African woodlands growing along the Niassa Rift of Mozambique. From a quantitative perspective, we verify whether specific morphotypes are solid indicators of taxonomic affiliation and environmental predictors, establish the relative composition of the overall phytolithic spectrum that a "Zambeian" grassy cover would leave behind in the geological and archaeological record, and discuss whether the lessons learned from modern local phytoliths can be of any guidance for future research in prehistoric plant landscape composition and climatic trends in the woodlands, savannas, and grasslands surrounding the Great African Rift.

In addition to being the largest phytochorion in sub-Saharan Africa, the "Zambeian" zone contains the richest and most diverse flora and vegetation in Africa (White, 1983, pp. 89). The Flora Zambesiaca contains an estimated 11,400 taxa, half of which can be found in Mozambique (Timberlake et al., 2006, pp. 751, 754). The Zambeian zone is dominated by miombo woodlands, typified by a single storey stand dominated by Fabaceae trees forming a discontinuous canopy with underlying shrubs, sedges, and heliophytic grasses (Campbell, 1996), but until recently no phytoliths from miombo plants were documented (Mercader et al., 2009). White (1983, pp. 93) has drawn a distinction between "wetter" (>1000 mm of precipitation) and "drier" (<1000 mm of precipitation) miombos. The Niassa Rift area supports both and they are interspersed with semi-evergreen forests, savannas, and hydromorphic grasslands called "dambo" or "mbungas". Grasses make up a relatively minor part of the vegetation in a mature miombo where 95–98% of the above ground biomass is made up of woody plants (Frost, 1996, pp. 22). However, the tree to grass ratio can change drastically if the miombo undergoes alteration to the point where canopy cover can be reduced to 40% in moderately modified settings (Bloesch and Mbago, 2006) and grass biomass can even exceed that of woody species in disturbed areas (Ribeiro et al., 2008).

The study area (Fig. 1) is located on the eastern escarpment of the Lake Niassa Rift at 465 m a.s.l. (Lago district) and the adjacent highlands at 1841 m a.s.l. (Sanga district). Precipitation is unimodal with a five month rainy season (January–May) followed by a severe, drought-prone dry season from June to December. Mean annual precipitation ranges from 700 mm in the lowlands to 1400 mm in the highlands (Gama, 1990, pp. 31–33). This area belongs to the "Lichinga-Cobue" geological unit (Lächelt, 2004) and is composed of a crystalline basement overlain with a Proterozoic cover of granodiorite, granosyenite, granites, and diverse gneisses and paragneisses (Lächelt, 2004). Soils in the lowlands are shallow and neutral with a silty sand texture (classified as Ferric Lixisols by FAO, 1998; Instituto Nacional de Investigaçao Agronômica, 1995). In the highlands soils are clayey, deep, and oxic with alkaline to acidic pH (also known as Rhodic Ferrasols, FAO, 1998).

2. Methodology

The botanical specimens studied in this paper include those collected by our crew from two localities; Metangula (Lago district, lowlands) and Njawala (Sanga district, highlands) in Niassa, Northern Mozambique. Our reference collection is deposited at the Tropical Archaeology Laboratory at the University of Calgary, Canada. The collection procedure was governed by 5 km-radius transects where all grasses encountered were collected, as well as all the trees and shrubs (Mercader et al., 2009). Mature specimens were taken during the dry season to ensure better phytolith build up in their tissues. Specimens from other regions and neighboring countries believed to be significant for our study were included in this paper as well. Some samples were obtained from the Pretoria Herbarium, SANBI (South Africa), while others were donated generously by Dr. E. Arnold (University of Illinois, Urbana-Champaign, USA). The primary source for grass identification was the manual by Gibbs Russell (1988) and Gibbs Russell et al. (1991). In some instances we also consulted Barkworth et al. (2007). Tribal nomenclature is from Clayton and Renvoize (1986). We follow the index of accepted names for the flowering plants of Sub-Saharan Africa (Klopper et al., 2006).

Our botanical collection represents 75% of the most common grass genera from Niassa (Gama, 1990; da Silva et al., 2004; Timberlake et al., 2004; Bloesch and Mbago, 2006; Ribeiro et al., 2008) (Table 1), and provides data on an additional 16, less prominent local genera. In total, we study the phytoliths from 60 botanical specimens (Appendix A, supplementary material online) representing 26 genera and 26 confirmed species plus a significant number of unidentified Poaceae. The description of laboratory methodologies presented here is that of Mercader et al. (2009): "Phytolith extraction from botanical samples followed the dry ashing methodology outlined by Albert and Weiner (2001) (cf. Parr et al., 2001), with minor modifications. All specimens were cleaned by immersion in 5% lab grade soap solution (Micro-90) and sonication (Fisher Scientific, FS 60) for 30 min. In situations where samples were dirt-coated the specimen was soaked in a 5% soap–sodium hexametaphosphate water-based solution overnight in order to deflocculate contaminants, followed by successive 30 min sonication cycles. Specimens were then dried at 100 °C overnight. After cooling, mass was measured on a high precision balance. The samples then went into a muffle furnace for combustion over the course of 36 h at 500 °C. The mass of the resulting ash was noted, and it then received a 10 ml 50:50 solution made of hydrochloric and nitric acids at 3 N and was boiled. Successive washing cycles removed acids from the sample by (5 min) centrifugation at 3000 r.p.m. When acid elimination was complete, and the remainder of a sample had been dried and weighed, phosphate and carbonate loss was estimated by calculating mass differential. After this, approx. 10 ml of hydrogen peroxide at 30% was added to the sample to destroy organic matter (if the matrix is rich in carbonates, sodium hypochlorite at 6% was used instead; Mikutta et al., 2005). The sample was dried at 100 °C overnight. The resulting biominerals formed the acid insoluble fraction (AIF) and it was here where phytoliths, among other biogenic precipitates, were found. An aliquot of 0.001 g was taken for mounting, after proper mixing of this extract by vortexing. The mounting medium was made up of two droplets of resin solution 'Entellan New'. The aliquot was well mixed, and the microscopic inspection and counting took place within 48 h of mounting before media were able to dry (3-D shifting of phytoliths was necessary to carry out identification: system microscope, Olympus BX51: 400 magnifications). Inspection and counting were done under polarized light, regular light microscopy and differential interference

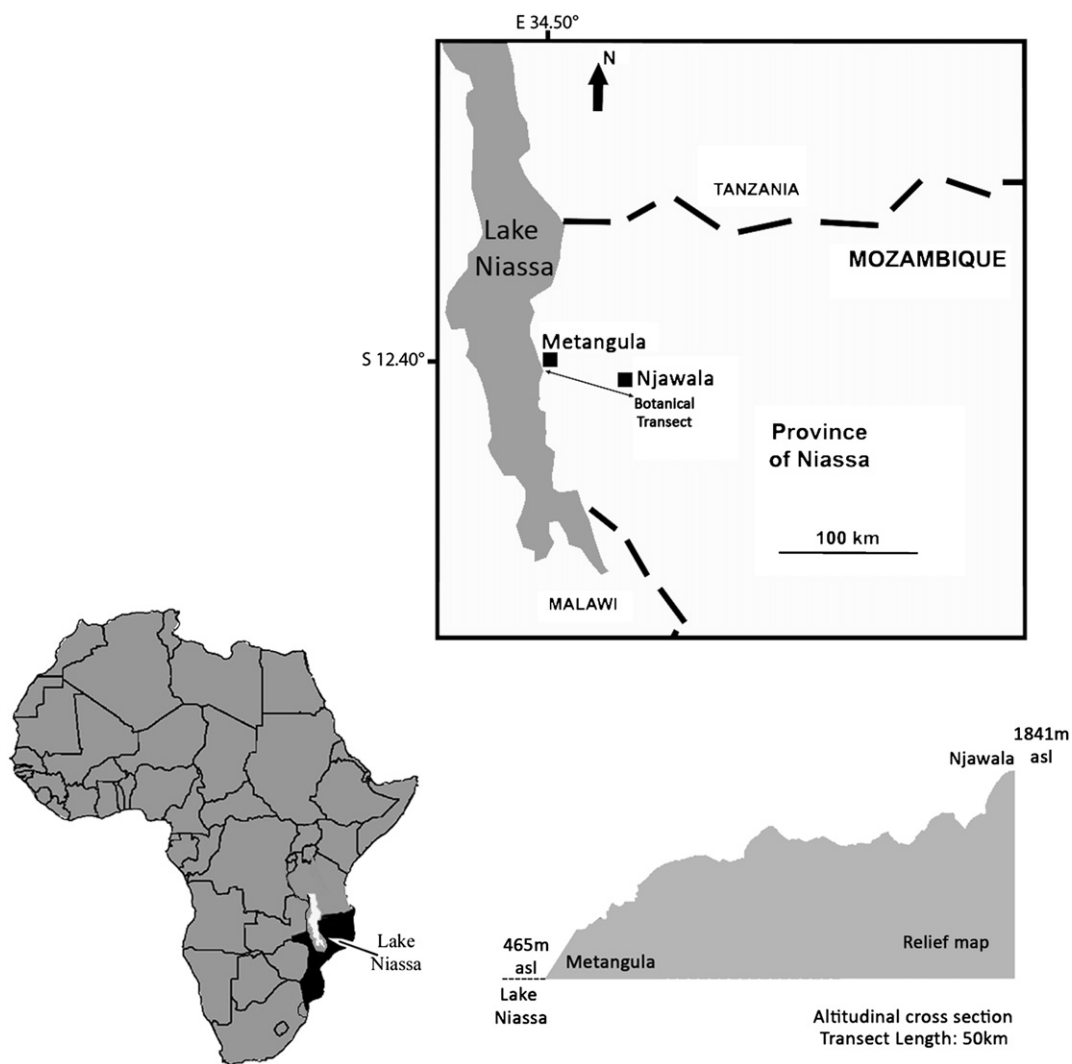


Fig. 1. Study area in Northern Mozambique, location of botanical transect carried out, and altitudinal cross-section.

contrast (DIC) which greatly enhances contrast and resolves fine structural details.”

The total number of phytoliths counted for this paper is 18586 (Appendix A, supplementary material online). Average count per sample is 300 (>200 short cell phytoliths). Specimens were inspected in adjacent but not overlapping lines across the cover slip

Table 1
List of common Poaceae genera in the province of Niassa, Northern Mozambique.

<i>Andropogon</i>	Poaceae
<i>Aristida</i>	Poaceae
<i>Eragrostis</i>	Poaceae
<i>Hyparrhenia</i>	Poaceae
<i>Hyperthelia</i>	Poaceae
<i>Loudetia</i>	Poaceae
<i>Melinis</i>	Poaceae
<i>Miscanthus</i>	Poaceae
<i>Oxytenanthera</i>	Poaceae
<i>Panicum</i>	Poaceae
<i>Pennisetum</i>	Poaceae
<i>Phragmites</i>	Poaceae
<i>Sporobulus</i>	Poaceae
<i>Themeda</i>	Poaceae
<i>Urochlaena</i>	Poaceae

(22 mm in length). We calculated the percentage of each morphotype per species (Table 2), and, mostly described types according to the descriptors from the International Code for Phytolith Nomenclature 1.0 (Madella et al., 2005), with exceptions duly noted. Phytoliths were grouped in this study because it allows for the identification of specific phytolith morphotypes that can be used as predictors of the taxonomic membership of unknown plant samples (Huberty, 1994).

To this end, we used the SYSTAT® 10 software package (SPSS Inc., 2000) to run a series of exploratory discriminant analyses and identify associations between phytolith morphotypes and specimens that determine taxonomic position. PCA and CA were employed to reduce the number of variables in our reference collection to a smaller set of principal components, reveal internal structure and group type variables, and detect covariance (Kim and Mueller, 1978; Basilevsky, 1994; Jolliffe, 2002).

Table 2
Phytolith taxonomy: code, name, descriptors, totals, and their frequency (%) in the assemblage.

Number	Morphotype	Source	Descriptors	n	%
1	Bilobate concave outer margin long shaft	Fahmy (2008: 15)	See cited source	930	5
2	Bilobate concave outer margin short shaft	Fahmy (2008: 15)	See cited source	2277	12.2
3	Bilobate convex outer margin long shaft	Fahmy (2008: 15)	See cited source	1020	5.4
4	Bilobate convex outer margin short shaft	Fahmy (2008: 15)	See cited source	1393	7.4
5	Bilobate flattened outer margin long shaft	Fahmy (2008: 15)	See cited source	165	0.8
6	Bilobate flattened outer margin short shaft	Fahmy (2008: 15)	See cited source	423	2.2
7	Bilobate nodular	Fahmy (2008: 15)	See cited source	372	2
8	Bilobate notched/flared outer margin long shaft	Fahmy (2008: 15)	See cited source	298	1.6
9	Bilobate notched/flared outer margin short shaft	Fahmy (2008: 15)	See cited source	296	1.5
10	Blocky crenate	This study	Block with psilate texture and scalloped edges	51	0.2
11	Blocky pilate	Mercader et al. (2009)	Orbicular, oblong, rectangle, polygonal or irregular block with scrobiculate texture and projections that have straight to slightly curved ends	209	1.1
12	Bulliform	Madella et al. (2005: 259)	See cited source	499	2.6
13	Carinate	This study	Phytolith shaped like a keel with psilate texture	88	0.4
14	Conical	This study	Cone shaped body with psilate texture and rounded/pointed apex	217	1.1
15	Cylindroid	Mercader et al. (2009)	Cylindroid with a psilate texture	198	1
16	Cylindroid bulbous	Mercader et al. (2009)	Cylindroid/renate with a psilate texture and irregular bulbous enlargements	77	0.4
17	Cylindroid pilate	Mercader et al. (2009)	Cylindroid body with scrobiculate texture and projections that have straight or slightly curved ends	125	0.6
18	Cylindroid reticulate	Mercader et al. (2009)	Subcylindroid psilate body partly covered by a net-like pattern	3	n/a
19	Cylindroid scrobiculate	Mercader et al. (2009)	Large cylindroid with scrobiculate texture	47	0.2
20	Elongate orthogonal section	This study	Elongate body with orthogonal cross-section, scrobiculate texture, and marked ridges	2	n/a
21	Epidermal crenate	This study	Thin epidermal cells with crenate outline and psilate texture	214	1.1
22	Epidermal polygonal	Mercader et al. (2009)	Thin epidermal polygonal cells. Variable textures	42	0.2
23	Globular psilate	Mercader et al. (2009)	Spheroid with a subsmooth texture	413	2.2
24	Ovate	This study	Sub-tabular, orbicular to ovate phytolith with psilate texture	37	0.1
25	Polylobate	Panicoid class 3i (Twiss et al., 1969: 111; Madella et al., 2005: 257)	See cited source	485	2.6
26	Quadrilobate/cross	Panicoid class 3a (Twiss et al., 1969: 111)	See cited source	832	4.4
27	Saddle	Chloridoid class 2a (Twiss et al., 1969: 111)	See cited source	1572	8.4
28	Saddle long	Piperno and Pearsall (1998: p. 5); Lu and Liu (2003b: p. 597)	See cited source	511	2.7
29	Saddle long, wavy side	Piperno and Pearsall (1998: p. 5); Lu and Liu (2003b: p. 597)	See cited source	3	n/a
30	Saddle ovate	This study	Saddle in which the abaxial view is orbicular to ovate	462	2.4
31	Saddle plateau	Lu and Liu (2003b: 591)	Saddle with a narrow base and suborbicular abaxial outline	320	1.7
32	Saddle squat	Chloridoid class 2a (Twiss et al., 1969: 111; Piperno, 2006: 33)	Saddle with side notches and a much longer axis than its tangential line	239	1.2
33	Scutiform	Madella et al. (2005: 256)	See cited source	486	2.6
34	Stomata/Hair	This study	Stomatal complex, hair bases, and hairs	741	3.9
35	Tabular crenate	Mercader et al. (2009)	Tabular body with psilate texture and scalloped edges	675	3.6
36	Tabular dendriform	Mercader et al. (2009)	Large elongate parallelepiped with psilate texture and sides covered by irregular dedritic processes	55	0.2
37	Tabular elongate	Mercader et al. (2009)	Elongate	30	0.1
38	Tabular facetate	Mercader et al. (2009)	Facetate with partly psilate and partly corniculate textures	13	n/a
39	Tabular scrobiculate	Mercader et al. (2009)	Variably wide parallelepiped with an elongate outline and scrobiculate texture	41	0.2

Table 2 (continued)

Number	Morphotype	Source	Descriptors	n	%
40	Tabular sinuate	Mercader et al. (2009)	Thick parallelepiped/subcylindroid with psilate texture. One or two sides are sinuate; sometimes, one side is sinuate and the other one is columellate	31	0.1
41	Tabular thin	Mercader et al. (2009)	Thin parallelepiped, square to rectangular shape with psilate texture	10	n/a
42	Tower	Lu and Liu (2003b: 591, 595)	Conical, tall body with tapering/flat apex. See cited source	1306	7
43	Tower beveled	This study	Spooliform in which the apex is conical, spiked, nodular or lobate	73	0.3
44	Tower horned	This study	Conical, tall body in which the apex ends in one or two outward apices	948	5.1
45	Tower wide	This study	Conical, tall body with tapering/flat apex; its base is at least three times wider than the apex	247	1.3
46	Trapezoid crenate	This study	Elongate body with a trapezoidal cross-section and wavy edges	100	0.5
47	Vessel laminate	Mercader et al. (2009)	Tabular, sub-polygonal body covered with layers	10	n/a

The dataset was not normalized and we ran the analyses on the original correlation matrix. Ward's method and the squared Euclidean distance, with the variables rescaled to 0–1, were used for the CA.

3. Results

3.1. Biomineral production

Ash and biomineral contents are expressed in Table 3 where higher ranks indicate greater silica production. Biogenic silica averages 4.598% of the plant's dry weight (range: 0.658–23.300%). Typical ash production is 6.974% of the original mass (range: 0.558–27.300%), and the Acid Insoluble Fraction (A.I.F.) % of the ash fraction averages 62.918% (range: 26.749–85.348). From 54 samples analyzed for ash and silica production, 10% emerged as prominent producers (>twice the average), another 10% made above average, 25% produced average values, but 55% of the specimens fall well below the average. The absolute highest biomineral content has been recorded among members of C₃ grasses from the Bambuseae (leaf tissue) and Paniceae, while the lowest silica production is detected in C₄ members of the Cynodonteae tribe (*Eragrostis superba* Peyr, *Eragrostis* spp.), as well as in the culm of one C₃ grass (*Oxytenanthera abyssinica* (A. Rich) Munro).

From a botanical perspective, the subfamily Panicoideae yielded about 50% of the types reported here, 32% are from the Chloridoideae, 12% from the Bambusoideae, and 8% from the Arundinoideae *sensu lato* (e.g. including the Arundineae and Aristideae; Bouchenak-Khelladi et al., 2008). Type variability is largest with the Panicoideae, which peaks at 12 morphotypes (26 specimens, range: 8–17). The Arundinoideae (5 specimens, range: 6–10) and Bambusoideae (6 specimens, range: 4–15) average 7 morphotypes, while the Chloridoideae is last with only 6 (16 specimens, range: 2–12). Nine types are major contributors with levels twice the average or higher, including morphotypes 2, 27, 4, 42, 3, 44, 1, 26, and 35. This subset of phytoliths accounts for 56% of the total. Types that contribute slightly above average are 25, 28, 12, 33, 30, 6, and 23 and these represent 24% of the whole spectrum. These two subsets combined comprise >80% of all phytoliths studied. From this sub-assembly, 2/3 consists of grass short cell phytoliths.

3.2. Common morphotypes

More than half of the variability documented in our collection is accounted for by a subset of eight short cell phytoliths that, in a typical assemblage, may occur at levels twice the average or higher. From higher to lower rank these are:

- Bilobate concave outer margin short shaft* (morphotype 2, $n = 2277$, ~12% of the total assemblage, Fig. 2 (1–4)). Average production per sample is 53 (range: 1–202). The highest absolute production is documented in a C₄ member of the Paniceae tribe: *Melinis repens* (Willd.) C.E. Hubb subsp. *repens*. Very prominent contributors (at least twice the average) are C₄ members of the Andropogoneae such as *Hyparrhenia* spp., *Schizachyrium jeffreysii* (Hack.) Stapf, and *Themeda* spp. Qualitative microscopy of the specimens on one slide suggests that most bodies measure 5–10 μm in maximum length. The concavity seen in the lobate's edges is very tenuous and the mesial strangulation that creates the shaft reaches about 5 μm.
- Saddle* (morphotype 27, $n = 1572$, ~8% of the total count, Fig. 2 (5–7)). Average number is 131 (range 8–273). The maximum production is seen in three C₄ members of the Cynodonteae (*Cynodon* spp., *Eragrostis* spp., and an unidentified sample). Qualitative microscopy of the specimens on one slide suggests that a typical saddle measures between 5 and 18 μm in maximum length.
- Bilobate convex outer margin short shaft* (morphotype 4, $n = 1393$, ~7% of the assemblage, Figs. 2 (8–10) and 3 (1–2)). The average number is 36 (range: 1–143). Our highest values are from C₄ species from the Andropogoneae (*Andropogon amethystina* Steud and *Themeda triandra* Forssk), although high counts were made in *Leptaspis cochleata* Nees ex Steud (Phareae). Qualitative microscopy of the specimens on one slide suggests that the longest axis averages 10–20 μm.
- Tower* (morphotype 42, $n = 1306$, ~7% of the total, Figs. 2 (11–13) and 5 (13–16)). This type refers to a tall spool body (Lu and Liu, 2003a,b: Plate 2b,c) and we intentionally separate it from the shorter "rondel" (Lu and Liu, 2003a,b: Plate 2a). The average number observed per sample is 48 (range: 1–235). The most prominent producers are all C₄ members of the Cynodonteae tribe (*Eragrostis superba* Peyr, *Eragrostis* spp.). Yet, some C₃ grasses from the Bambuseae (e.g. *Oreobambos buchwaldii* K. Schum) yield comparably high numbers. Qualitative microscopy of the specimens on one slide suggests that the tower's maximum height ranges 10–15 μm, and its plateau is often psilate.
- Bilobate convex outer margin long shaft* (morphotype 3, $n = 1020$, ~5% of the assemblage, Fig. 2 (14–16)). Average count per sample is 36 (range: 1–210). Two taxonomically unrelated variants must be distinguished. In the first one, the bilobate is large (18 to >60 μm) and its shank is very slim (<3 μm wide). The highest contribution for this subtype is coming from the Arundinoideae (tribes Aristideae and Arundineae), in which we find an average of 138 phytoliths per slide.

Table 3
Rank of ash and silica producers.

Specimen	Plant Part	Dry weight (g)	Ash (g)	Ash %	Post-acid (g)	A.I.F. (g)	Ash – A.I.F. %	Dry weight – A.I.F. %	Rank
<i>Oxytenanthera abyssinica</i> (A. Rich) Munro	Leaf (culm >4 cm diam.)	1.000	0.273	27.300	0.236	0.233	85.348	23.300	1
Unidentified Poaceae	Culm/Leaf/Inflorescence	0.100	0.025	25.000	0.017	0.015	60.000	15.000	2
Unidentified Poaceae	Culm/Leaf/Inflorescence	2.500	0.336	13.440	0.298	0.292	86.905	11.680	3
<i>Oplismenus</i> spp.	Culm/Leaf/Inflorescence	0.100	0.017	17.000	0.013	0.011	64.706	11.000	4
Unidentified Poaceae	Culm/Leaf/Inflorescence	0.200	0.030	15.000	0.023	0.021	70.000	10.500	5
Unidentified Poaceae	Culm/Leaf/Inflorescence	1.900	0.209	11.000	0.178	0.175	83.732	9.211	6
<i>Panicum maximum</i> Jacq.	Culm/Leaf/Inflorescence	1.700	0.169	9.941	0.138	0.135	79.882	7.941	7
<i>Rottboellia</i> spp.	Culm/Leaf/Inflorescence	0.400	0.043	10.750	0.033	0.031	72.093	7.750	8
<i>Themeda</i> spp.	Culm/Leaf/Inflorescence	0.400	0.039	9.750	0.032	0.030	76.923	7.500	9
<i>Cynodon</i> spp.	Culm/Leaf/Inflorescence	0.100	0.014	14.000	0.007	0.006	42.857	6.000	10
Unidentified Poaceae	Culm/Leaf/Inflorescence	1.300	0.088	6.769	0.074	0.072	81.818	5.538	11
<i>Themeda triandra</i> Forssk	Culm/Leaf/Inflorescence	0.900	0.101	11.222	0.051	0.049	48.515	5.444	12
<i>Themeda</i> spp.	Culm/Leaf/Inflorescence	3.300	0.225	6.818	0.183	0.178	79.111	5.394	13
<i>Hyparrhenia</i> spp.	Culm/Leaf/Inflorescence	2.400	0.164	6.833	0.133	0.128	78.049	5.333	14
<i>Pennisetum purpureum</i> Schumach	Culm/Leaf/Inflorescence	4.300	0.332	7.721	0.226	0.223	67.169	5.186	15
Unidentified Poaceae	Culm/Leaf/Inflorescence	1.100	0.071	6.455	0.052	0.052	73.239	4.727	16
<i>Urochloa</i> spp.	Culm/Leaf/Inflorescence	0.500	0.032	6.400	0.024	0.022	68.750	4.400	17
Cynodonteae	Culm/Leaf/Inflorescence	2.600	0.230	8.846	0.120	0.109	47.391	4.192	18
<i>Pennisetum polystachion</i> (L.) Schult. subsp. <i>polystachion</i>	Culm/Leaf/Inflorescence	2.700	0.185	6.852	0.110	0.105	56.757	3.889	19
<i>Panicum</i> spp.	Culm/Leaf/Inflorescence	1.500	0.078	5.200	0.061	0.058	74.359	3.867	20
<i>Melinis repens</i> (Willd.) C.E. Hubb subsp. <i>repens</i>	Culm/Leaf/Inflorescence	1.500	0.088	5.867	0.060	0.057	64.773	3.800	21
<i>Eragrostis plana</i> Nees	Culm/Leaf/Inflorescence	1.400	0.064	4.571	0.056	0.053	82.813	3.786	22
<i>Andropogon amethystina</i> Steud	Culm/Leaf/Inflorescence	5.900	0.033	0.558	0.224	0.222	67.772	3.763	23
<i>Hyparrhenia</i> spp.	Culm/Leaf/Inflorescence	5.100	0.254	4.980	0.193	0.189	74.409	3.706	24
<i>Brachyachne</i> spp.	Culm/Leaf/Inflorescence	2.700	0.140	5.185	0.101	0.098	70.000	3.630	25
<i>Cymbopogon</i> spp.	Culm/Leaf/Inflorescence	2.700	0.140	5.185	0.101	0.098	70.000	3.630	26
<i>Melinis</i> spp.	Culm/Leaf/Inflorescence	1.800	0.109	6.056	0.070	0.065	59.633	3.611	27
<i>Coelorachis</i> spp.	Culm/Leaf/Inflorescence	1.700	0.077	4.529	0.063	0.059	76.623	3.471	28
Andropogoneae	Culm/Leaf/Inflorescence	1.300	0.067	5.154	0.047	0.045	67.164	3.462	29
<i>Hyparrhenia hirta</i> (L.) Stapf	Culm/Leaf/Inflorescence	2.600	0.108	4.154	0.094	0.090	83.333	3.462	30
<i>Arundinella</i> spp.	Culm/Leaf/Inflorescence	1.600	0.103	6.438	0.053	0.051	49.515	3.188	31
<i>Phragmites australis</i> (Cav.) Steud	Culm/Leaf/Inflorescence	2.800	0.134	4.786	0.091	0.087	64.925	3.107	32
<i>Bewisia biflora</i> (Hack.) Goossens	Culm/Leaf/Inflorescence	1.600	0.074	4.625	0.052	0.049	66.216	3.063	33
<i>Aristida</i> spp.	Culm/Leaf/Inflorescence	0.700	0.027	3.857	0.022	0.021	77.778	3.000	34
<i>Eragrostis</i> spp.	Culm/Leaf/Inflorescence	1.400	0.076	5.429	0.048	0.042	55.263	3.000	35
Unidentified Poaceae	Culm/Leaf/Inflorescence	0.400	0.020	5.000	0.012	0.012	60.000	3.000	36
<i>Ischaemum</i> spp.	Culm/Leaf/Inflorescence	0.300	0.014	4.667	0.011	0.008	57.143	2.667	37
Chlorideae	Culm/Leaf/Inflorescence	1.100	0.057	5.182	0.030	0.028	49.123	2.545	38
<i>Eragrostis hierniana</i> Rendle	Culm/Leaf/Inflorescence	0.200	0.017	8.500	0.008	0.005	29.412	2.500	39
<i>Pennisetum polystachion</i> (L.) Schult. subsp. <i>polystachion</i>	Culm/Leaf/Inflorescence	1.600	0.099	6.188	0.045	0.040	40.404	2.500	40
Unidentified Poaceae	Culm/Leaf/Inflorescence	2.000	0.082	4.100	0.051	0.047	57.317	2.350	41
<i>Schizachyrium jeffreysii</i> (Hack.) Stapf	Culm/Leaf/Inflorescence	1.900	0.077	4.053	0.052	0.044	57.143	2.316	42
<i>Melinis nerviglumis</i> (Franch.) Zizka	Culm/Leaf/Inflorescence	1.200	0.058	4.833	0.029	0.027	46.552	2.250	43
<i>Aristida congesta</i> (Trin & Rupr.) De Winter	Culm/Leaf/Inflorescence	0.600	0.018	3.000	0.014	0.013	72.222	2.167	44
<i>Melinis ambigua</i> Hack.	Culm/Leaf/Inflorescence	1.000	0.046	4.600	0.026	0.021	45.652	2.100	45
Unidentified Poaceae	Culm/Leaf/Inflorescence	1.300	0.061	4.692	0.027	0.027	44.262	2.077	46
<i>Oxytenanthera abyssinica</i> (A. Rich) Munro	Culm <4 cm diameter	11.500	0.462	4.017	0.227	0.225	48.701	1.957	47
<i>Eragrostis</i> spp.	Culm/Leaf/Inflorescence	2.800	0.086	3.071	0.054	0.053	61.628	1.893	48
<i>Eleocharis</i> spp.	Culm/Leaf/Inflorescence	0.900	0.024	2.667	0.018	0.016	66.667	1.778	49
<i>Eragrostis</i> spp.	Culm/Leaf/Inflorescence	0.400	0.020	5.000	0.012	0.007	35.000	1.750	50
Unidentified Poaceae	Culm/Leaf/Inflorescence	0.700	0.023	3.286	0.014	0.012	52.174	1.714	51
<i>Eragrostis superba</i> Peyr	Culm/Leaf/Inflorescence	0.900	0.018	2.000	0.015	0.014	77.778	1.556	52
<i>Eragrostis</i> spp. spp.	Culm/Leaf/Inflorescence	1.000	0.023	2.300	0.012	0.010	43.478	1.000	53
<i>Oxytenanthera abyssinica</i> (A. Rich) Munro	Culm >4 cm diameter	58.500	1.025	1.752	0.396	0.385	37.561	0.658	54

The second variant comes from a bilobate with a length around 20 µm and a shaft 3–5 µm wide. This stockier type is common in the Panicoideae (tribes Andropogoneae and Paniceae).

(f) *Tower horned* (morphotype 44, $n = 948$, ~5% of the total, Fig. 5 (17–19)). Average representation per slide is 68 (range: 2–238). The most prominent producer is a C₄ member of the Cynodonteae (*Brachyachne* spp.). Other high producers include *Sporobolus consimilis* Fresen (Clorideae), *Pennisetum purpureum* Schumach (Paniceae), and *Hyparrhenia* spp. (Andropogoneae). Qualitative microscopy of the specimens on one slide suggests that horned towers are small to medium bodies with heights

5–15 µm. The apex' endings are either thick (e.g. *Hyparrhenia* spp.) or just a slender outward apex (e.g. *Brachyachne* spp.)

(g) *Bilobate concave outer margin long shaft* (morphotype 1, $n = 930$, ~5% of the total collection, Fig. 2 (21, 22)). Average number per slide is 32 (range: 1–103). All top producers are C₄ grasses that belong in the Andropogoneae (e.g. *Cymbopogon* spp., *Ischaemum* spp., and *Hyparrhenia hirta* (L.) Stapf). Qualitative microscopy of the specimens on one slide suggests that the maximum length is 25–35 µm, and the edge's concavities are variably deep. The shaft's length ranges from 4 to 8 µm.

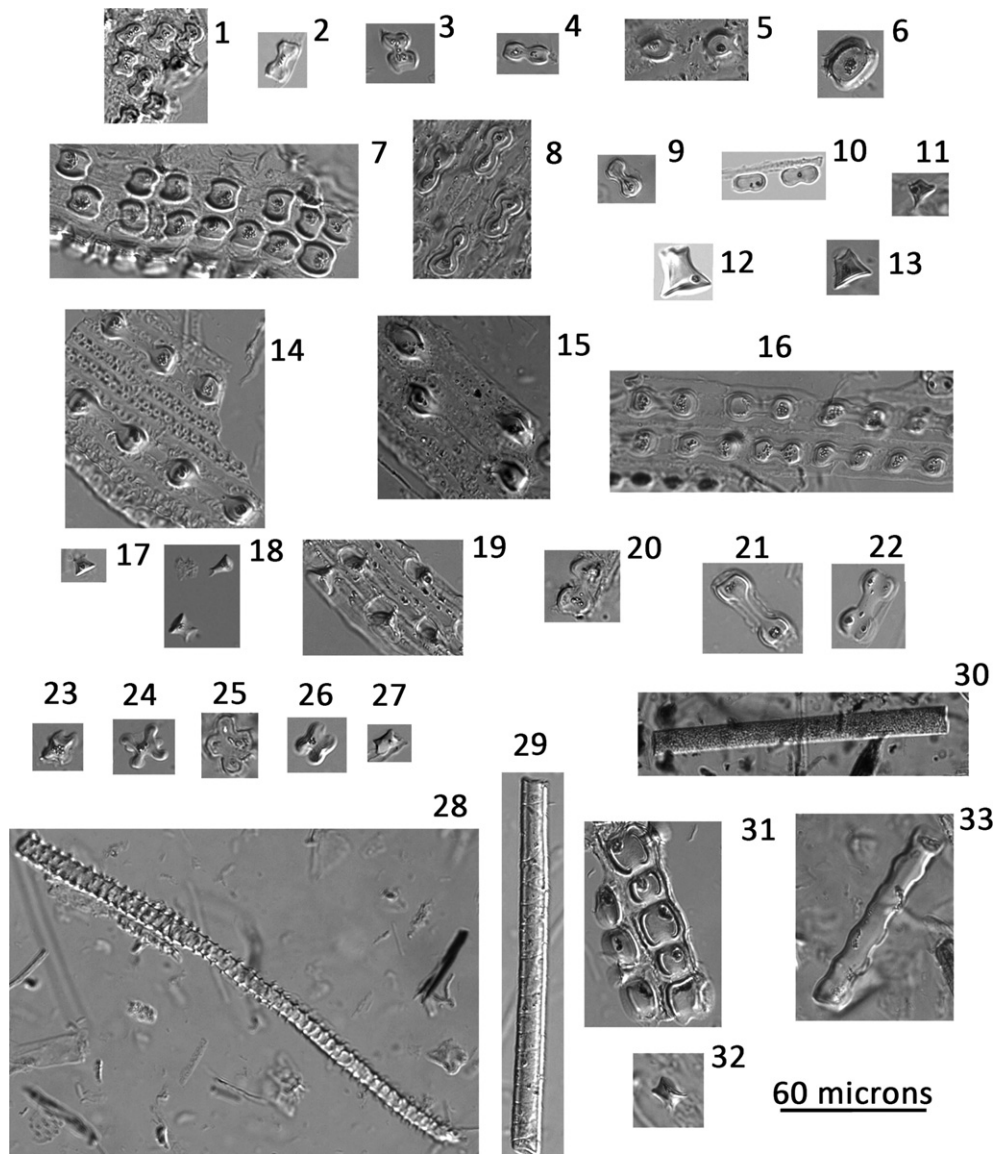


Fig. 2. (1) Bilobate concave outer margin short shaft, *Melinis repens* (Willd.) C.E. Hubb subsp. *repens*. (Culm/Leaf/Inflorescence). (2) Bilobate concave outer margin short shaft, *Hyparrhenia* spp. (Culm/Leaf/Inflorescence). (3) Bilobate concave outer margin short shaft, *Schizachyrium jeffreysii* (Hack.) Stapf. (Culm/Leaf/Inflorescence). (4) Bilobate concave outer margin short shaft, *Themeda* spp. (Culm/Leaf/Inflorescence). (5) Saddle, *Eragrostis* spp. (Culm/Leaf/Inflorescence). (6) Saddle, *Cynodontae*. (Culm/Leaf/Inflorescence). (7) Saddle, *Cynodon* spp. (Culm/Leaf/Inflorescence). (8) Bilobate convex outer margin short shaft, *Andropogon amethystina* Steud. (Culm/Leaf/Inflorescence). (9) Bilobate convex outer margin short shaft, *Themeda triandra* Forssk. (Culm/Leaf/Inflorescence). (10) Bilobate convex outer margin short shaft, *Leptaspis cochleata* Nees ex Steud. (Culm/Leaf/Inflorescence). (11) Tower, *Eragrostis superba* Peyr. (Culm/Leaf/Inflorescence). (12) Tower, *Eragrostis* spp. (Culm/Leaf/Inflorescence). (13) Tower, *Eragrostis* spp. (Culm/Leaf/Inflorescence). (14) Bilobate convex outer margin long shaft, *Aristida* spp. (Culm/Leaf/Inflorescence). (15) Bilobate convex outer margin long shaft, unidentified Arundinoid species. (Culm/Leaf/Inflorescence). (16) Bilobate convex outer margin long shaft, unidentified Panicoid species. (Culm/Leaf/Inflorescence). (17) Tower horned, *Brachyachne* spp. (Culm/Leaf/Inflorescence). (18) Tower horned, *Sporobolus consimilis* Fresen. (Culm/Leaf/Inflorescence). (19) Tower horned, *Pennisetum purpureum* Schumach. (Culm/Leaf/Inflorescence). (20) Bilobate concave outer margin long shaft, *Hyparrhenia hirta* (L.) Stapf. (Culm/Leaf/Inflorescence). (21) Bilobate concave outer margin long shaft, *Ischaemum* spp. (Culm/Leaf/Inflorescence). (22) Bilobate concave outer margin long shaft, *Hyparrhenia hirta* (L.) Stapf. (Culm/Leaf/Inflorescence). (23) Cross, *Urochloa* spp. (Culm/Leaf/Inflorescence). (24) Cross, *Oplismenus* spp. (Culm/Leaf/Inflorescence). (25) Cross, *Melinis nervigulumis* (Franch.) Zizka. (Culm/Leaf/Inflorescence). (26) Cross, *Coelorachis* spp. (Culm/Leaf/Inflorescence). (27) Carinate, *Leptaspis cochleata* Nees ex Steud. (Culm/Leaf/Inflorescence). (28) Cylindroid pilate, *Oxytenanthera abyssinica* (A. Rich) Munro. (Culm/Leaf/Inflorescence). (29) Cylindroid reticulate, *Oxytenanthera abyssinica* (A. Rich) Munro. (Culm/Leaf/Inflorescence). (30) Cylindroid scrobiculate, *Oxytenanthera abyssinica* (A. Rich) Munro. (Culm/Leaf/Inflorescence). (31) Saddle plateau, *Phragmites mauritanus* Kunth. (Culm/Leaf/Inflorescence). (32) Saddle plateau, *Phragmites australis* (Cav.) Steud. (Culm/Leaf/Inflorescence). (33) Trapezoid crenate, *Bewisia biflora* (Hack.) Goossens. (Culm/Leaf/Inflorescence). (34) Tower horned, *Hyparrhenia hirta* (L.) Stapf. (Culm/Leaf/Inflorescence).

(h) *Quadralobate*/Cross (morphotype 26, $n = 832$, ~4% of the entire collection, Fig. 2 (23–26)). The average number per slide is 24 (range: 1–148). The highest cross producers always are C₃/C₄ grasses of the Paniceae (*Urochloa* spp., *Oplismenus* spp., *Melinis nervigulumis* (Franch.) Zizka), and to a lesser extent some C₄ species from the Andropogoneae (*Coelorachis* spp.). Some Chloridoids make crosses in low numbers (e.g. *Sporobolus africanus* (Poir.) Robyns & Tournay). Qualitative microscopy of the specimens on one slide suggests that the longest axis

ranges 15 to >20 μm . The cross's outline varies from curved to markedly sinuous lines, and its texture may yield irregular bulbous enlargements (e.g. *Oplismenus* spp.)

3.3. Uncommon and rare morphotypes

About 25% of our phytolith collection is made up of the addition of many types that, although produced at slightly above average rates, one on one, still are relatively uncommon: just 2–4% of the

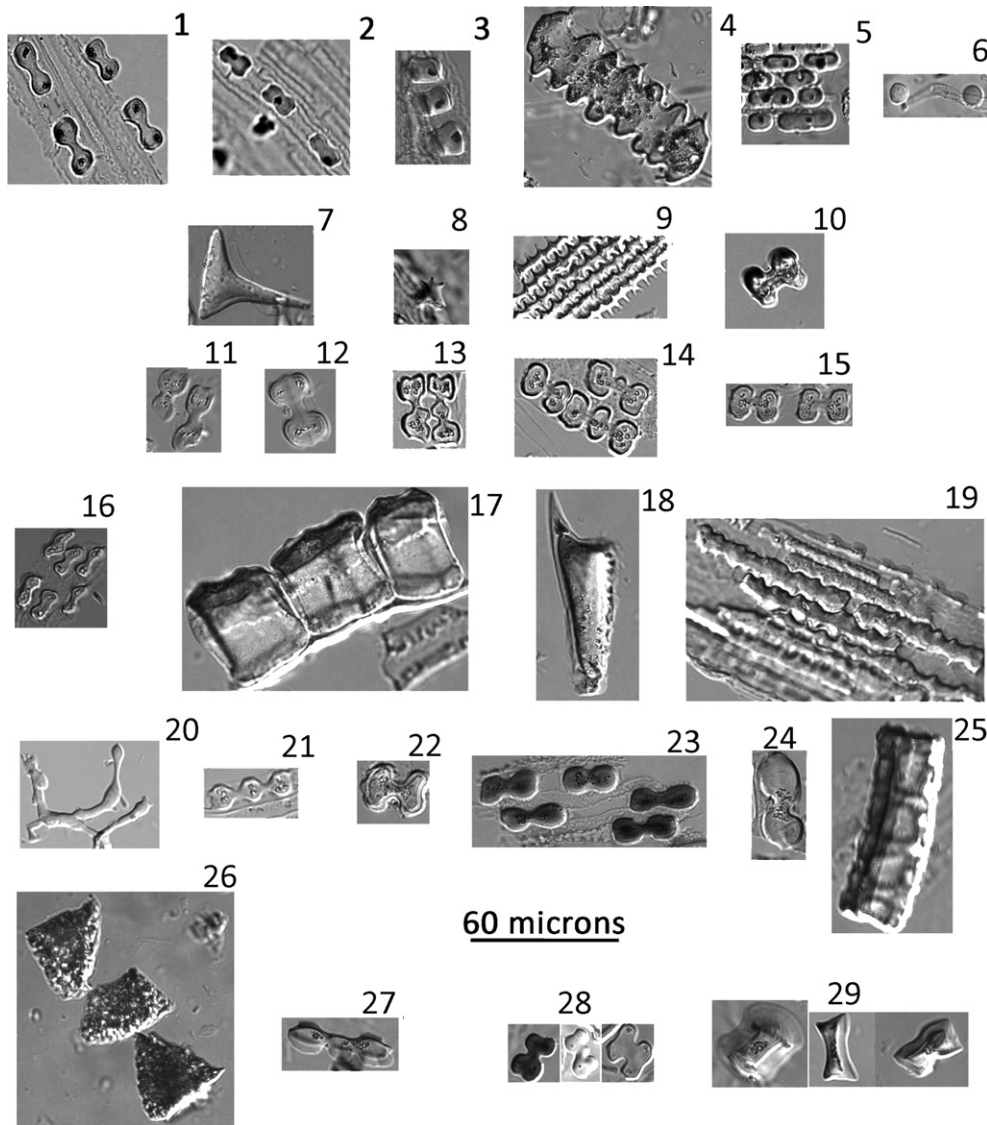


Fig. 3. (1) Bilobate convex outer margin short shaft, *Aristida junciformis* (Stapf) De Winter. (Culm/Leaf/Inflorescence). (2) Bilobate convex outer margin short shaft, *Arundinaria alpina*. (Culm/Leaf/Inflorescence). (3) Saddle long, *Arundinaria alpina*. (Culm/Leaf/Inflorescence). (4) Tabular crenate, *Leptaspis cochleata* Nees ex Steud. (Culm/Leaf/Inflorescence). (5) Ovate, *Leptaspis cochleata* Nees ex Steud. (Culm/Leaf/Inflorescence). (6) Globular psilate, *Melinis nervigulumis* (Franch.) Zizka. (Culm/Leaf/Inflorescence). (7) Bulliform, *Aristida congesta* (Trin & Rupr.) De Winter. (Culm/Leaf/Inflorescence). (8) Tower beveled *Phragmites australis* (Cav.) Steud. (Culm/Leaf/Inflorescence). (9) Glum, long cell crenate phytoliths, *Hyparrhenia* spp. (Culm/Leaf/Inflorescence). (10) Bilobate flattened outer margin long shaft, *Hyparrhenia* spp. (Culm/Leaf/Inflorescence). (11) Bilobate notched/flared outer margin short shaft, *Schizachyrium jeffreysii* (Hack.) Stapf. (Culm/Leaf/Inflorescence). (12) Bilobate convex outer margin long shaft, Unidentified Poaceae. (Culm/Leaf/Inflorescence). (13) Bilobate notched/flared outer margin short shaft, *Melinis ambigua* Hack. (Culm/Leaf/Inflorescence). (14) Bilobate nodular, *Melinis ambigua* Hack. (Culm/Leaf/Inflorescence). (15) Bilobate flattened outer margin short shaft, *Melinis ambigua* Hack. (Culm/Leaf/Inflorescence). (16) Bilobate convex outer margin short shaft, *Melinis ambigua* Hack. (Culm/Leaf/Inflorescence). (17) Bulliform, *Melinis ambigua* Hack. (Culm/Leaf/Inflorescence). (18) Scutiform, *Pennisetum unisetum* (Nees) Benth. (Culm/Leaf/Inflorescence). (19) Tabular crenate, *Pennisetum unisetum* (Nees) Benth. (Culm/Leaf/Inflorescence). (20) Cylindroid bulbous, *Melinis* spp. (Culm/Leaf/Inflorescence). (21) Polylobate, *Melinis* spp. (Culm/Leaf/Inflorescence). (22) Bilobate flattened outer margin short shaft, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (23) Bilobate convex outer margin short shaft, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (24) Bilobate convex outer margin short shaft, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (25) Elongate orthogonal section, Poaceae from the Cynodonteae tribe. (Culm/Leaf/Inflorescence). (26) Bulliform, *Themeda* spp. (Culm/Leaf/Inflorescence). (27) Bilobate notched/flared outer margin long shaft, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (28) Unidentified Poaceae. (Culm/Leaf/Inflorescence). (29) Saddle long, *Brachyachne* spp. (Culm/Leaf/Inflorescence).

total collection per type. In order of higher frequency these types are the tabular crenate (no. 35: Fig. 3 (4, 19)), polylobate (no. 25: Fig. 3 (21)), long saddle (no. 28: Fig. 3 (3, 29); Fig. 4 (17–19)), bulliform (no. 12: Fig. 3 (7, 17, 26); Fig. 4 (12, 20)), scutiform (no. 33: Fig. 3 (18); Fig. 5 (2)), saddle ovate (no. 30: Fig. 5 (1)), bilobate flattened outer margin short shaft (no. 6: Fig. 3 (6)), and globular psilate (no. 23: Fig. 3 (6)). Of these nine morphotypes only four are short cells (polylobate, long saddle, saddle ovate and bilobate with flattened outer margin and short shaft). We note that tabular

crenates represent 3.61% of the assemblage and are documented throughout the collection. Bulliform cells and scutiforms amount to a mere 2.44–2.38% of the total respectively. Lastly, globular psilates rank no. 17 in the collection and represent 2.05%.

3.4. Restricted types

Within the study area, and in our limited sample, there are 12 morphotypes that signal specific subfamilies and/or tribes and/or

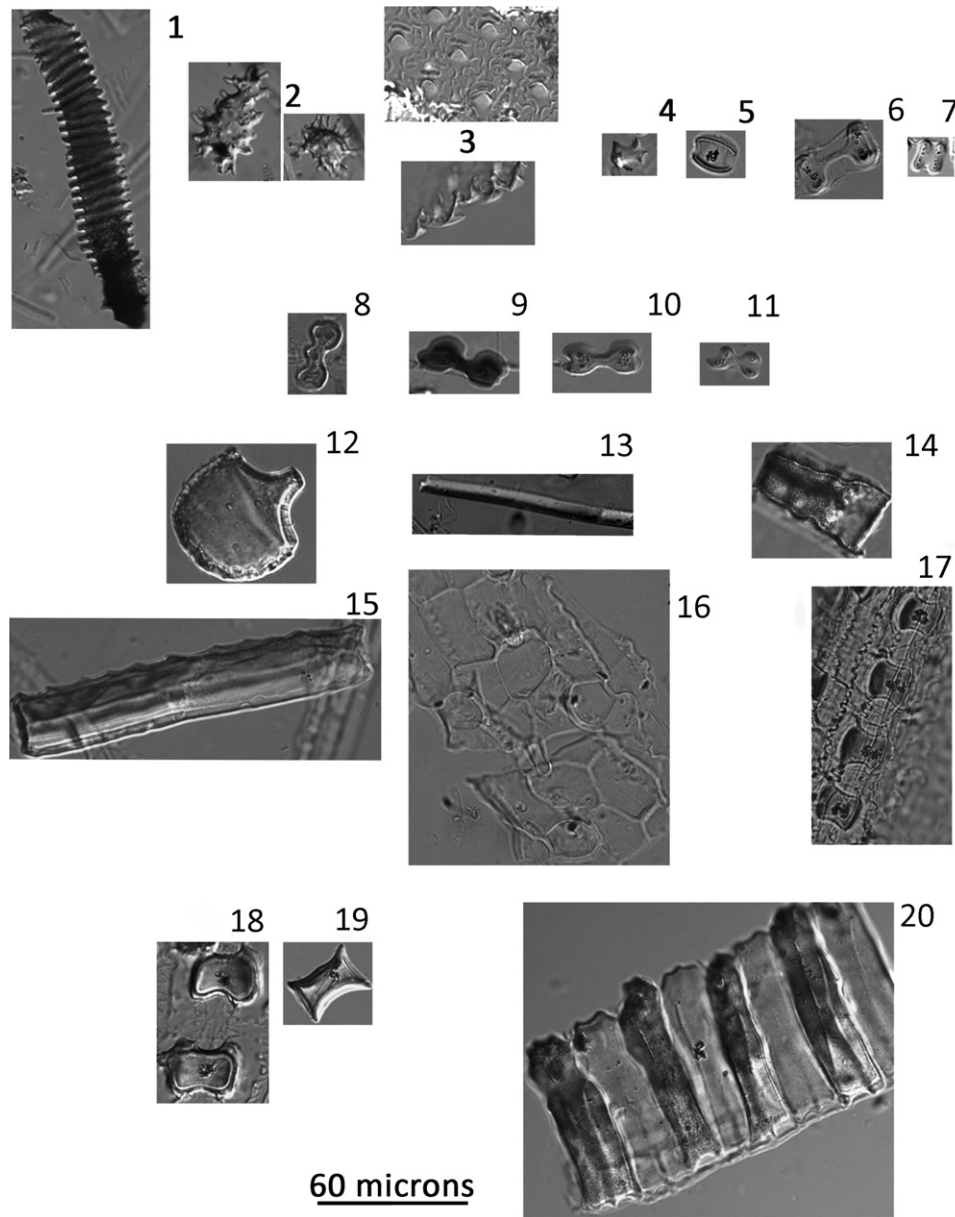


Fig. 4. (1) Vessel laminate, *Oxytenanthera abyssinica* (A. Rich) Munro. (Culm/Leaf/Inflorescence). (2) Blocky pilate, *Oxytenanthera abyssinica* (A. Rich) Munro (culm). (3) Conical, abaxial and side views, *Chloris virgata* Swartz. (Culm/Leaf/Inflorescence). (4) Saddle long, wavy side, *Oxytenanthera abyssinica* (A. Rich) Munro. (Culm/Leaf/Inflorescence). (5) Saddle squat, *Eragrostis racemosa* (Thunb.) Steud. (Culm/Leaf/Inflorescence). (6) Bilobate flattened outer margin long shaft, *Ischaemum* spp. (Culm/Leaf/Inflorescence). (7) Bilobate flattened outer margin short shaft, *Schizachyrium jeffreysii* (Hack.) Stapf. (Culm/Leaf/Inflorescence). (8) Bilobate nodular, Unidentified Poaceae. (Culm/Leaf/Inflorescence). (9) Bilobate notched/flared outer margin long shaft, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (10) Bilobate notched/flared outer margin long shaft, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (11) Bilobate notched/flared outer margin short shaft, *Schizachyrium jeffreysii* (Hack.) Stapf. (Culm/Leaf/Inflorescence). (12) Bulliform, *Eragrostis hierniana* Rendle. (Culm/Leaf/Inflorescence). (13) Cylindroid, *Bewisia biflora* (Hack.) Goossens. (Culm/Leaf/Inflorescence). (14) Elongate orthogonal section, *Oxytenanthera abyssinica* (A. Rich) Munro (culm). (15) Tabular facetate, *Oplismenus* spp. (Culm/Leaf/Inflorescence). (16) Epidermal polygonal, *Pennisetum purpureum* Schumach. (Culm/Leaf/Inflorescence). (17) Saddle long, *Oxytenanthera abyssinica* (A. Rich) Munro (leaf). (18) Saddle long, *Oxytenanthera abyssinica* (A. Rich) Munro (leaf). (19) Saddle long, side view, *Oxytenanthera abyssinica* (A. Rich) Munro. (leaf). (20) Bulliform, *Oxytenanthera abyssinica* (A. Rich) Munro (leaf).

genera. Because we did not include two or more specimens per species analyzed we cannot ascertain the natural variability inherent to each taxon, and therefore the reader is asked to exert caution when interpreting these results. A phytolith type that appears in members of the Chloridoideae sample is the saddle *sensu stricto* (morphotype 27, $n = 1572$, Fig. 2 (5–7)). A distinctive identifier of the Cynodonteae is the conical shape (morphotype 14, $n = 217$, Fig. 4 (3)). The long saddle with wavy sides suggests both subfamily and tribe: Bambusoideae, Bambuseae (morphotype 29, $n = 3$, Fig. 4 (4)). Subfamily and genus are represented by vessel

laminates (morphotype 47, $n = 10$, Bambusoideae, *Oxytenanthera* Fig. 4 (1)) and squat saddles (morphotype 32, $n = 239$, Chloridoideae, *Eragrostis*, Fig. 4 (5)). Tribe and genus are implied in blocky pilates (morphotype 11, $n = 209$, Bambuseae, *Oxytenanthera*, Fig. 4 (2)), carinates (morphotype 13, $n = 88$, *Leptaspis cochleata* Nees ex Steud, Fig. 2 (27)), and cylindroid pilates (morphotype 17, $n = 125$, *Oxytenanthera abyssinica* (A. Rich) Munro, Fig. 2 (28)). Lastly; subfamily, tribe, and genus are signified by cylindroid reticulates (morphotype 18, $n = 3$, *Oxytenanthera abyssinica* (A. Rich) Munro, Fig. 2 (29)), cylindroid scrobiculates (morphotype

19, $n = 47$, *Oxytenanthera abyssinica* (A. Rich) Munro, Fig. 2 (30)), plateau saddles (morphotype 31, $n = 320$, *Phragmites* spp., Fig. 2 (31)), and trapezoid crenates (morphotype 46, $n = 100$, *Bewisia biflora* (Hack.) Goossens, Fig. 2 (33)).

4. Statistical classification, taxonomy, and grouping

Discriminant function analysis (DA) using the SYSTAT[®]10 interactive stepping procedure (SYSTAT[®]10 Statistics 1) was carried out to discover if phytolith assemblages could distinguish grass subfamilies. Both complete and jackknifed classification matrices were used to cross-validate results (SYSTAT[®]10 Statistics 1). Fifty-four specimens from four subfamilies were used. This procedure established a best classification solution using five collapsed, generic phytolith classes defined in Table 4 and represented by Bilobates, Carinates, Cross, Long Saddles, and Plateau Saddles (Appendix B, supplementary material online). The full sample and jackknifed classification produced identical results with an overall correct classification of 78% (Table 5). Panicoids

were most accurately classified with an 89% success rate, while 11% were classed as Chloridoids. The second most successful classification is that of the Chloridoids; at 81% success rate (13% classified as Panicoids; 6% as Bambusoids). Bambusoids were classified with only a 50% success (the rest of the Bambusoid assemblage is classed as Chloridoid). Arundinoid specimens were least successful (40%) as shown by the fact that 60% of Arundinoids were classified as Panicoids.

Importantly, while part of the wide-encompassing “saddle” class (saddle *sensu stricto*, saddle long; saddle long, wavy edge; saddle plateau; saddle ovate; saddle squat) is very common in the Chloridoideae, some of its variants are present amongst the Arundinoideae and, in lower frequencies, amongst the Bambusoideae. The addition of the saddle class to the DA introduced differences in the results between the complete sample and jackknifed results, reducing the overall correct classification to 74%. The greatest negative impact on correct classification was, ironically, amongst the Chloridoideae. Correct classification in that group dropped to 69% from 81% in the best-solution DA result with three

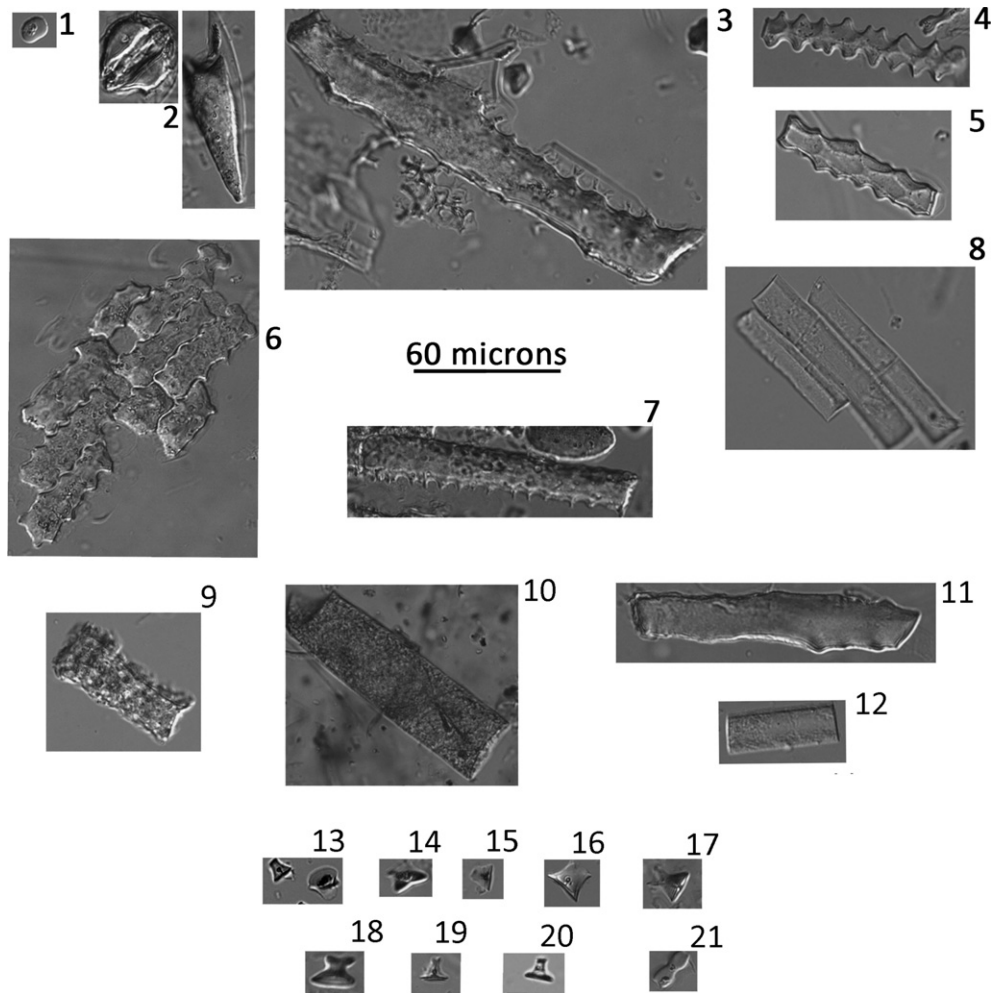


Fig. 5. (1) Saddle ovate, *Aristida junciformis* (Stapf) De Winter. (Culm/Leaf/Inflorescence). (2) Stomata and scutiform, *Pennisetum polystachion* (L.) Schult. subsp. *polystachion*. (Culm/Leaf/Inflorescence). (3) Tabular dendriform, *Eragrostis* spp. (Culm/Leaf/Inflorescence). (4) Tabular crenate, *Oplismenus* spp. (Culm/Leaf/Inflorescence). (5) Tabular crenate (facetate texture), *Oplismenus* spp. (Culm/Leaf/Inflorescence). (6) Tabular crenate, *Cynodon* spp. (Culm/Leaf/Inflorescence). (7) Tabular dendriform, *Eragrostis* spp. (Culm/Leaf/Inflorescence). (8) Tabular elongate, *Sporobolus consimilis* Fresen. (Culm/Leaf/Inflorescence). (9) Tabular scrobiculate, *Oplismenus* spp. spp. (Culm/Leaf/Inflorescence). (10) Tabular scrobiculate *Oxytenanthera abyssinica* (A. Rich) Munro. (culm). (11) Tabular sinuate, *Eragrostis* spp. (Culm/Leaf/Inflorescence). (12) Tabular thin, unidentified Poaceae. (Culm/Leaf/Inflorescence). (13) Tower, *Eragrostis racemosa* (Thunb.) Steud. (Culm/Leaf/Inflorescence). (14) Tower, *Brachyachne* spp. (Culm/Leaf/Inflorescence). (15) Tower, *Oreobambos buchwaldii* K. Schum. (Culm/Leaf/Inflorescence). (16) Tower, *Sporobolus africanus* (Poir.) Robyns & Tournay. (Culm/Leaf/Inflorescence). (17) Tower horned, *Oxytenanthera abyssinica* (A. Rich) Munro. (culm). (18) Tower horned, *Oxytenanthera abyssinica* (A. Rich) Munro. (culm). (19) Tower wide, *Panicum* spp. (Culm/Leaf/Inflorescence). (20) Tower wide, *Sporobolus consimilis* Fresen. (Culm/Leaf/Inflorescence). (21) Bilobate (saddle trend) *Eragrostis* spp. (Culm/Leaf/Inflorescence).

Table 4

Summary statistics of major phytolith classes as they relate to the Poaceae subfamilies studied in this article. According to our microscopy observations, cluster analysis, and PCA we collapsed several morphotypes under the following 10 major classes.

Subfamily	Class										Totals
	Bilobate ^a	Carinate ^b	Conical ^c	Ovate ^d	Cross ^e	Saddle Long ^f	Saddle Plateau ^g	Saddle ^h	Tower ⁱ	Trapeziform Crenate ^j	
*Arundinoideae	40.36%	0.00%	0.00%	0.08%	0.00%	0.00%	25.28%	19.83%	14.45%	0.00%	100.00%
Bambusoideae	16.61%	9.88%	0.00%	3.03%	0.00%	36.25%	0.00%	2.81%	31.43%	0.00%	100.00%
Chloridoideae	9.75%	0.00%	5.41%	0.00%	1.20%	4.76%	0.00%	45.54%	30.85%	2.49%	100.00%
Panicoideae	73.67%	0.00%	0.00%	0.15%	12.13%	0.00%	0.00%	0.00%	14.05%	0.00%	100.00%

^a Bilobate concave outer margin long shaft; bilobate concave outer margin short shaft; bilobate convex outer margin long shaft; bilobate convex outer margin short shaft; bilobate flattened outer margin long shaft; bilobate flattened outer margin short shaft; bilobate nodular, bilobate notched/flared outer margin long shaft; bilobate notched/flared outer margin short shaft.

^b Carinate.

^c Conical.

^d Ovate.

^e Cross.

^f Saddle long; saddle long, wavy edge.

^g Saddle plateau.

^h Saddle; saddle ovate; saddle squat.

ⁱ Tower; tower bevelled; tower horned; tower wide.

^j Trapeziform crenate.

Chloridoideae assigned to the Bambusoideae and two to the Panicoideae. Correct classification amongst the saddle-free Panicoideae increased marginally from 89% to 92% but this small increase in success amongst the Panicoideae came at a large cost to the Chloridoideae, diminished the overall correct classification rate, and weakened the cross-validated results between the complete sample and jackknife results.

We also employed DA to test whether the relative proportions of C₃ and C₄ grasses in a given assemblage could be predicted. Three Panicoid specimens in our botanical collection could not be assigned to either pathway and therefore had to be excluded from this run, reducing overall sample size to 51 specimens (10 samples = C₃; 41 samples = C₄). The best classification is achieved using five phytolith morphotypes only: Bilobate, Carinate, Conical, Saddle, and Tower (Appendix C, supplementary material online). The full sample and jackknifed classifications produced identical results with an overall correct classification of 92% (Appendix D, supplementary material online). One C₃ specimen (*Oreobambos buchwaldii* K. Schum – Bambusoideae) was misclassified as a C₄ grass and two C₄ specimens (*Coelorchis* spp. and *Urochloa* spp. – Panicoideae) were misclassified as C₃ grasses. The tendency for misclassification to occur is highest amongst the Panicoideae (the subfamily for which pathway could not be established *a priori* in three cases), albeit at a low rate. This may be due to high frequencies of saddles amongst C₄ Arundinoideae and Chloridoideae specimens and their almost complete absence amongst C₃ specimens; that is, subfamily-related phytolith morphotype frequencies appear to influence the results of carbon pathway group classification to an unknown degree.

We ran our Cluster and Principal Component analyses on the full dataset, removing the morphotypes that did not load per iteration until our data reached a simple structure in which each remaining morphotype loaded to only one component (Appendix E, supplementary material online). The cluster ordination of the full dataset

was initially conducted on the basis of both linkage distance among phytolith morphotypes and their associations. The resulting dendrogram (Fig. 6) shows saddles to be a very dissimilar group. Notice the large distance between the nexuses that separate saddles and bilobates. For the full dataset, we found that 25 phytolith morphotypes created 10 principal components (78.83% of the total variance). Of these 10 components, 7 of them refer to short cell phytoliths and represent 47.92% of the total variance. The short cells thus grouped reflect similar data patterns and therefore stand for seven sets of meaningful associations. In order of relevance, these include (1) bilobate convex outer margin long shaft/saddle plateau/tower bevelled, (2) carinate/ovate, (3) tabular elongate/tower wide, (4) saddle/saddle squat, (5) bilobate notched or flared outer margin long shaft/bilobate notched or flared outer margin short shaft, (6) polylobate/tabular facetate, and (7) blocky crenate/saddle ovate/tabular thin. The PCA plot in rotated space for components 1 and 2 (Fig. 7) clearly shows that most long cells, bulliforms, scutiforms and vessel conduits cluster distinctly from short cells.

We also assessed our dataset for statistical indicators of taxonomic affiliation as well as environmental predictors as determined by grass subfamily and tribe. When the full dataset is employed the ensuing CA (Fig. 8) shows several kinds of taxonomic resolution. The highest taxonomic refinement (Fig. 8, lower and middle sections) is provided by some members of the Bambuseae, Cynodonteae, and Andropogoneae, for they cluster together with little or no interference from other tribes. Similar distinctiveness can be appreciated among the Aristideae and Arundineae. A large group of Panicoids (Fig. 8, upper section) allows for identification to the subfamily level, but it is incapable of discriminating tribes: it mixes up the Andropogoneae, Arundinelleae, and Paniceae. The cluster with the lowest taxonomic potential (it groups Bambusoids, Chloridoids and Panicoids together) combines the Andropogoneae, Aristideae, Cynodonteae, and Paniceae (Fig. 8, middle to lower section).

Table 5

Results from Discriminant Analysis.

	Arundinoideae	Bambusoideae	Chloridoideae	Panicoideae	Percent correct
Arundinoideae	2	0	0	3	40
Bambusoideae	0	3	3	0	50
Chloridoideae	0	1	13	2	81
Panicoideae	0	0	3	24	89
Total	2	4	19	29	78

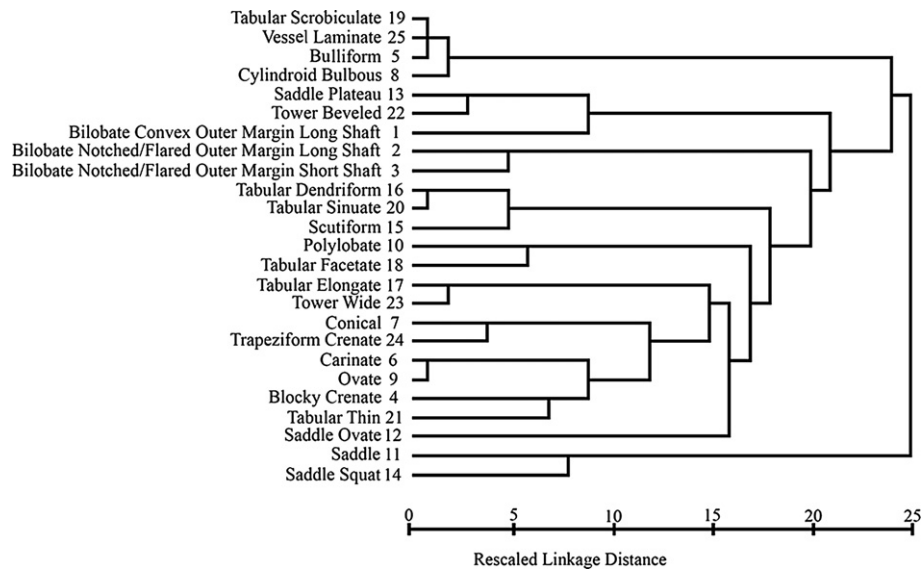


Fig. 6. Hierarchical Cluster Analysis by SPSS 15: Dendrogram displaying rescaled distance among principal phytolith morphotypes in the full dataset. See [Appendix A](#) for sample numbers.

Second, we used a simplified dataset containing ten generic classes of short cells (see above) to test the taxonomic capabilities of our data in a simplified format. The Cluster Analysis plots one class far apart from the rest ([Appendix F](#), supplementary material online). This class comprises the towers. Increasing similarity is seen among the following tandems: (1) conical/trapeziform crenate, (2) saddle plateau, and (3) carinate/ovate respectively. Importantly, four of these ten simplified classes were dropped by the PCA (first 2 axes account for 59.98% of the variance; 77.38% for all 3 components) because of their inability to load cleanly to one component only ([Appendix G](#), supplementary material online). These multiple loaders are Bambusoid, Chloridoid, and Panicoid grasses (including the bilobate, cross, long saddle, and saddle classes). The CA of the collapsed dataset ([Appendix H](#), supplementary material online) confirms that taxonomic refinement at

the tribe level can be observed for one group only (the same group described in the CA as the most powerful discriminator). Yet, the consolidation of major phytolith classes did not help in clarifying taxonomic membership for the rest of the assemblage. The collapsing of several morphotypes into generic classes obscures the taxonomic nuances observed in the CA of the entire dataset except for highly idiosyncratic specimens.

5. Discussion and concluding remarks

This paper has provided a phytolith reference collection of grasses growing in the most widespread ecosystem within the Zambebian regional centre of plant endemism, and it naturally complements local reference collections of phytoliths from trees and bushes ([Mercader et al., 2009](#)). Phytolith production varies

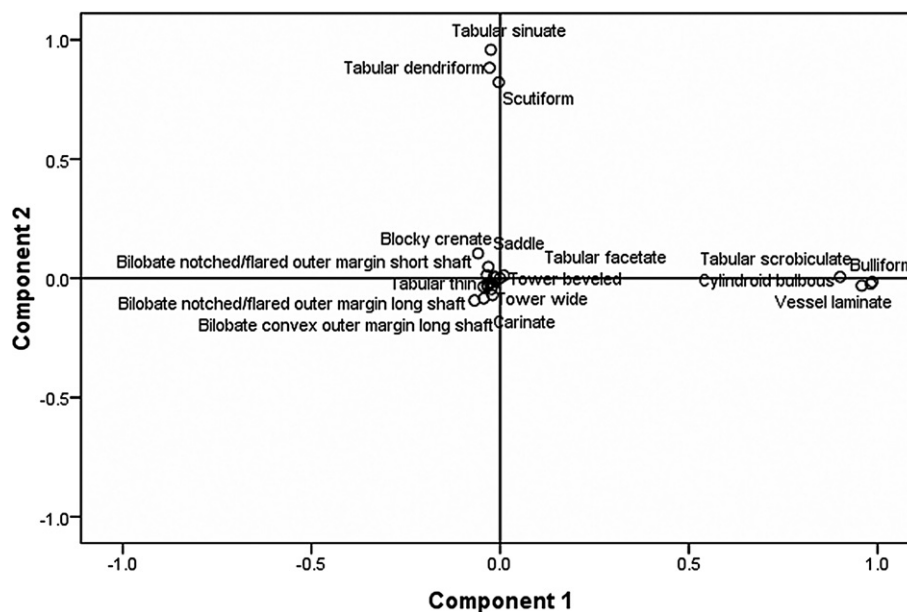


Fig. 7. Principal Component Analysis: Component Plot (1 and 2) in rotated space. Rotation Method: Varimax with Kaiser Normalization. Rotation converged in 7 iterations.

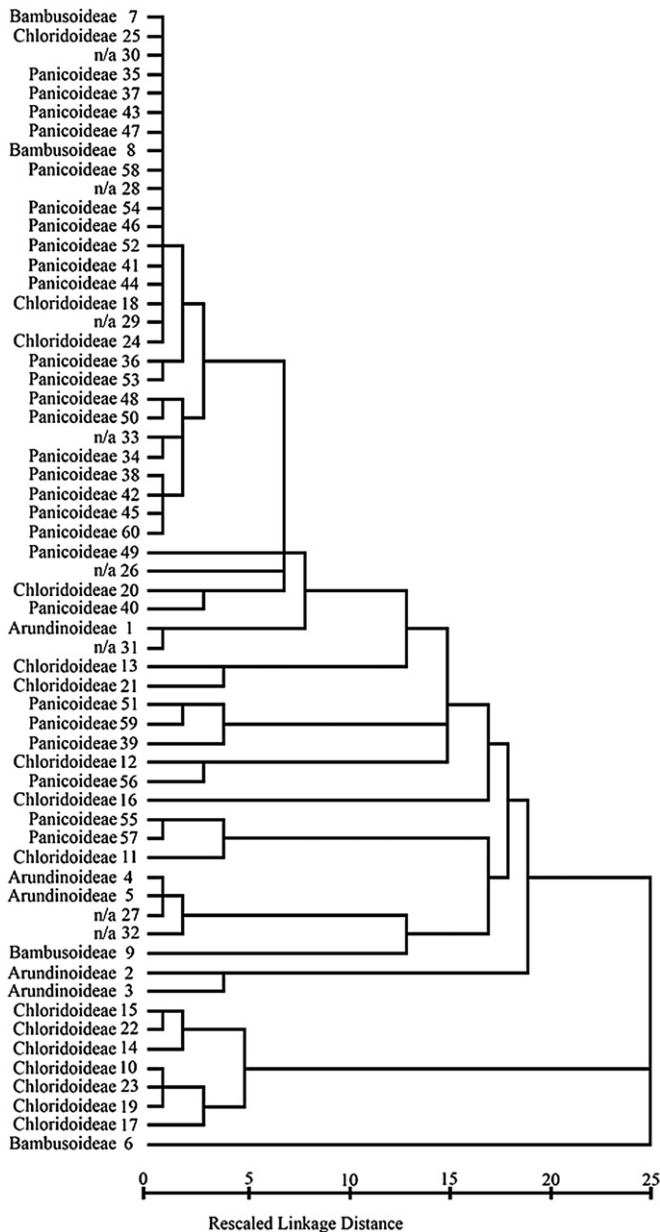


Fig. 8. Hierarchical Cluster Analysis by SPSS 15: Dendrogram displaying rescaled distance among subfamilies in the full dataset. See Appendix A for sample number details.

greatly among different genotypes of the same plant species and plant part (Epstein, 1994). With some exceptions, lower phylogenetic orders produce more phytoliths, although it is known that many basal monocots are non-producers (Prychid et al., 2004) and, contrarily, that some of the most derived clades produce high numbers of phytoliths (Hodson et al., 2005). In addition, external factors, such as the concentration of silica in soils, impact the plant's uptake of silicon (Henriet et al., 2006, 2008). Silicon was found to be a high prominence mineral plant constituent in miombo grasses and sedges. This is in contrast with reported lower silica concentrations among local dicotyledonous plants in which average phytolith production relative to the plant's dry weight is 1.42% ($n = 156$; range: 21.792–0.005%) (Mercader et al., 2009) compared to 4.72% for grassy species ($n = 58$ range: 23.300–0.658%) (this study). Notice that top producers among the trees make as much silica as top producers among the grasses.

Nonetheless, the poorest silica-producing grass still makes many more phytoliths than the poorest arboreal phytolith maker. Normally, however, local grasses would release three and half times more phytoliths into the soil than do trees and bushes (cf. Albert et al., 2000, pp. 942).

Average ash production is very similar for arboreal and non-arboreal taxa (7.8% versus 7.2% respectively): airborne/colluvial dispersion of phytolith-loaded ash across the landscape has sources of comparable magnitudes. Unlike local woody species, the grassy cover from Niassa produces mostly small to medium size phytoliths, most of which are $<20\ \mu\text{m}$ in maximum length. From a textural point of view, contrarily to what has been observed for arboreal miombo phytoliths (Mercader et al., 2009), the surface quality of grassy phytoliths, especially those seen in short cells, is mostly psilate.

Overall, the idealized Zambezian grassy phytolith spectrum is dominated by a small subset of Poaceae short cells, which include five morphotypes conventionally associated with Panicoid grasses (Bilobate concave outer margin long shaft, Bilobate concave outer margin short shaft, Bilobate convex outer margin long shaft, Bilobate convex outer margin short shaft, Cross; $n = 6452$), one morphotype commonly seen in Chloridoid taxa (saddle, $n = 1572$), and two types that appear across subfamily boundaries (tower, tower horned; $n = 2254$) We also document polylobates, which are frequent in the Panicoideae. Neither bulliform cells nor scutiforms nor long cells provide taxonomic resolution. The globular psilate deserves attention because smooth spheroids are produced by both arboreal and non-arboreal species. There is no doubt that globular psilates are a far more common occurrence among the trees and bushes than they are in grassy plants. Among arboreal dicots, globular psilates grade 4th in the overall production rank and amount to $\sim 10\%$ of the total assemblage (Mercader et al., 2009) in contrast with a much lower rank (17th) and count (2%) among the grasses (this study).

Because grass subfamilies are specially adapted to succeed under specific precipitation and temperature regimes (Tieszen et al., 1979; but see Taub, 2000), phytolith identification to the subfamily level allows for detailed reconstructions of paleograsland composition, as well as ancient temperature and moisture availability at the time of production (e.g. Brown, 1984; Fredlund and Tieszen, 1994; Bremond et al., 2005). We do not see phytolith morphotypes that all C_3 grasses share and C_4 plants do not. Neither are there morphotypes unique to C_4 grasses as a group. So while there are morphotypes that identify individual C_3 or C_4 genus or species, there are no morphotypes that identify pathway. That said, there are no carinate phytoliths in C_4 grasses (carinate phytoliths identify *Leptaspis cochleata* Nees ex Steud – Pharoideae), there are no conical phytoliths in C_3 grasses (conical phytoliths are found in C_4 *Bewsia biflora* (Hack.) Goossens and *Chloris virgata* Swartz – Cynodonteae), and they both are rare in other C_4 grasses. Within the C_3 group, bilobates and towers do consistently associate at similar ratios ($\sim 50/50$); while in the C_4 cohort bilobates ($\sim 50\%$), saddles ($\sim 25\%$) and towers ($\sim 25\%$) appear together.

Statistical analysis has long been used to identify variables that may classify unknown specimens into known categories because of its ability to detect group-indicators (or predictor phytoliths) and quantify the score on which such grouping variables indicate membership to a given group (Huberty, 1994). Upon testing the ability of classic short cell identification schemes (Twiss et al., 1969) to indicate membership to a given grass subfamily, we see that these succeed in estimating membership, but do so with reservations. Without being exhaustive (see details in statistical section above), we noticed that some grasses behave like counterparts in unrelated subfamilies, for example our trapeziform crenate (also known as “trapezoid sinuous”, Brown, 1984, pp. 349) derives from

the common Zambesian chloridoid *Bewsia biflora* (Hack.) Goossens, not from the Pooideae. Likewise, shapes that somewhat resemble the long saddles from C₃ bambusoids can be found in the C₄ chloridoid *Brachyachne* spp. Bilobates are created by non-Panicoid species of the genus *Eragrostis* (C₄ Chloridoid). These bilobates, with their saddle-like 3-D morphology (Fig. 5 (25)), diverge from classic Panicoid profiles; yet, the same genus produces bilobates that could be confused for true Panicoid types. Arundinoid bilobates display large sizes and thin, slender shafts, unseen among the Panicoids. The towers from C₃ *Oreobambos buchwaldii* K. Schum, a Bambusoid, make this grass behave like C₄ Chloridoids and Panicoids. Lastly, there are C₄ Panicoids such as *Coelorachis* (Andropogoneae) and *Urochloa* (Paniceae) that, unlike all other Panicoids, produce scarce bilobates.

In conclusion, we have provided the first quantitative taxonomy of grass phytoliths for the largest phytochorion of sub-Saharan Africa. This taxonomy, in conjunction with earlier phytolith work on local dicotyledonous plants (Mercader et al., 2009), is the most extensive phytolith key for any African ecoregion, totaling 42 families, ~100 genera, and ~125 species of vascular plants from Northern Mozambique. The next logical step to take in regional phytolith research should be a detailed account of phytoliths deposited in local topsoils underneath living plants (e.g. Barboni et al., 2007; Bremond et al., 2008). These soil horizons represent the interface between existing vegetation communities and the inevitably distorted fossil assemblages that the paleobotanist normally uses for environmental reconstruction. The soil's phytolith contents, by comparison with the control sample derived from plants themselves, may help resolve methodological issues without which future paleoecological and paleoclimatic interpretations in the study area will be fraught with difficulty. What portion of biogenic silica is lost to burial? Do buried phytolith assemblages reflect the vegetation growing locally at the time of sampling and the relative biomass proportions of arboreal to non-arboreal taxa, or do they represent a biased and condensed palimpsest developed over the course of several plant generations and thus is only partially reflective of extant vegetation (Fredlund and Tieszen, 1994: 329; Thorn, 2008, pp. 30)? Most importantly, does silica from living plants and topsoils represent two faces of the same analog or, more likely, do they stand for divergent analytical scales that should be characterized individually and calibrated against each other prior to attempting paleoecological reconstruction?

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jas.2010.03.001.

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