



Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania

Doris Barboni ^{a,*}, Gail M. Ashley ^b, Manuel Dominguez-Rodrigo ^{c,d}, Henry T. Bunn ^e,
Audax Z.P. Mabulla ^f, Enrique Baquedano ^{c,g}

^a CEREGE (UMR6635 CNRS/Université Aix-Marseille), BP80, F-13545 Aix-en-Provence cedex 4, France

^b Dept of Earth & Planetary Sciences, Rutgers University, Piscataway, NJ 08854-8066, USA

^c IDEA (Instituto de Evolución en África), Museo de los Orígenes, Plaza de San Andrés 2, 28005 Madrid, Spain

^d Dept. of Prehistory, Complutense University of Madrid Ciudad Universitaria s/n, 28040 Madrid, Spain

^e Dept of Anthropology, University of Wisconsin-Madison, 1180 Observatory Drive, Madison, WI 53706, USA

^f Archaeology Unit, P.O. Box 35050, University of Dar es Salaam, Dar es Salaam, Tanzania

^g Museo Arqueológico Regional de Madrid, Plaza de las Bernardas, Alcalá de Henares, Madrid, Spain

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ABSTRACT

The phytolith content of 10 samples collected immediately under Tuff IF (~1.785 Ma) at FLK N and other surrounding localities (~2 km²) provides a direct botanical evidence for woody vegetation in the eastern margin of Olduvai Gorge during uppermost Bed I time. Observation and counting of 143 phytolith types (5 to >150 μ) reveal dense but heterogeneous woody cover (~40–90%) of unidentified trees and/or shrubs and palms associated to the freshwater springs surrounding FLK N, and more open formation (presumably ~25–70% woody cover) in the southeast at localities VEK, HWK W and HWK E. The paleovegetation is best described as groundwater palm forest/woodland or bushland, which current analogue may be found near Lake Manyara in similar hydrogeological context (freshwater springs near saline/alkaline lake). Re-evaluating the published pollen data based on this analogy shows that 70% of the pollen signal at FLK N may be attributed to thicket-woodland, *Acacia* groundwater woodland, gallery and groundwater forests; while <30% is attributed to swamp herbage and grasslands. Micro-botanical, isotopic, and taphonomical studies of faunal remains converge on the same conclusion that the area surrounding FLK N, which attracted both carnivores and hominins in the early Pleistocene, was densely wooded during uppermost Bed I time.

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Introduction

Archaeological artifacts including stone tools and abundant bones attest to the repeated presence of ancient hominins in the Olduvai Gorge since at least ~1.84 Ma (Leakey, 1971; Blumenshine et al., 2003). Intensive archaeological and geological research have recently been resumed at locality FLK N in Bed I. Detailed taphonomical investigation showed that bone accumulations at this locality were most likely the results of carnivores (felids and hyenas) rather than hominins, despite the repeated occurrence of stone tools in archaeological levels 1 to 6 (Dominguez-Rodrigo et al., 2007; Bunn et al., 2010). What factors prompted hominins and carnivores to repeatedly visit FLK N are still unknown.

Early hominin behavior (hunting, scavenging, etc.) and repeated occupation of a site could be explained by some aspects of the natural environment, which might be viewed hospitable if it provides food, drinkable water, and shelter. FLK N was located in the floodplain of

paleolake Olduvai (Hay, 1976), in which water was saline (e.g., Hay and Kyser, 2001; Deocampo et al., 2009), that is most likely not potable. Earlier studies suggested predominant grasslands during upper Bed I time (Bonnefille and Riollet, 1980; Bonnefille et al., 1982; Bonnefille, 1984; Bamford et al., 2008), somehow in contradiction with analyses of the paleosols and the fauna, which suggested mixed C3–C4 vegetation (Cerling and Hay, 1986; Sikes and Ashley, 2007) and most likely a complete range of open- to closed-vegetation environments (Plummer and Bishop, 1994; Fernandez-Jalvo et al., 1998; Andrews and Humphrey, 1999). Vegetation is one of the important aspects that paleoenvironmental reconstructions, therefore, still need to address.

Micro-botanical remains such as phytoliths offer the possibility to investigate the structure of past vegetation at the local scale. These biogenic silica particles are highly distinctive among the Poaceae (grasses) (Twiss et al., 1969), several domesticated plants (Piperno, 2009), and numerous monocots and dicots (Piperno, 2006, p. 7). After the plants decay, phytoliths are deposited and integrated into the soils. They may be dispersed by wind and runoff, but most likely to a lesser extent than pollen, which may travel distances of over 100 km (Okubo and Levin, 1989). In contrast to pollen grains, which are

* Corresponding author. CEREGE (UMR6635 CNRS/Université Aix-Marseille), BP80, F-13545 Aix-en-Provence cedex 4, France. Fax: +33 442 971 540.

E-mail address: barboni@cerge.fr (D. Barboni).

degraded or destroyed under oxidizing conditions that occur in soils and lake sediments undergoing frequent subaerial exposure, phytoliths are found well-preserved in paleosols even as old as the Miocene and Pliocene (WoldeGabriel et al., 2009). In Africa, where phytolith assemblages from soil humic horizons were calibrated in terms of vegetation physiognomy and climate parameters (Alexandre et al., 1997; Bremond et al., 2005a,b; Barboni et al., 2007; Bremond et al., 2008), it is now established that important features of the vegetation are well reproduced by surface soil phytolith assemblages, particularly local variations in the woody cover between forest and savannas (Bremond et al., 2005a).

As a complement to studies of the paleoenvironments (Ashley et al., 2010), bone taphonomy (Bunn et al., 2010; Dominguez-Rodrigo et al., 2010), and lithic technology (Diez-Martin et al., 2010), we provide here new phytolith data from FLK N and surrounding localities to characterize the paleovegetation that surrounded an early Pleistocene site that was repeatedly visited by hominins and carnivores. We focused on uppermost Bed I (~1.785 Ma, Hay and Kyser, 2001) and constrained our sampling accordingly to get vegetation inferences at the local scale. Our phytolith results are compared to stratigraphically equivalent pollen data (Bonnefille, 1984) that we re-evaluated using vegetation data from nearby Lake Manyara (Greenway and Vesey-Fitzgerald, 1969), whose hydrogeological context is similar to Olduvai upper Bed I (i.e., freshwater springs near alkaline lake; Ashley et al., 2010). Our results and conclusions challenge earlier paleobotanical studies (Bonnefille, 1984; Bamford et al., 2008) by providing evidences for groundwater palm forest/woodland or bushland, a paleoenvironmental setting that would explain the remarkable concentration of fossils and stone tools at this specific location in the Gorge of Olduvai.

General setting

Olduvai Gorge is a steep-sided west–east valley (1350–1500 masl) in the Serengeti Plain near the western margin of the Eastern Rift Valley in northern Tanzania (Fig. 1). The present climate is semi-arid. Vegetation of the Serengeti Plain is grassland with *Commiphora* scrub and scattered *Acacia* (Herlocker and Dirschl, 1972). Southeast of the Olduvai Gorge, highlands >2000 masl include volcanic centers such as Ngorongoro,

Lemagrut, and Olmoti. The Gorge cuts across a 50-km-wide rift-platform basin located between Precambrian basement to the west and the Pleistocene Ngorongoro Volcanic Highland to the east. The basin fill is now disrupted by rift-parallel faults and separated into blocks. The sediments are 100 m thick and composed largely of reworked volcaniclastic sediment and air-fall tuffs deposited in a shallow semi-arid fluvial–lacustrine basin (Hay, 1976). The sedimentary record contains a rich faunal and cultural record of early hominins and thus is also important to human evolutionary studies (Leakey, 1971; Bunn and Kroll, 1986; Blumenschine and Masao, 1991; Peters and Blumenschine, 1995; Ashley, 2000; Dominguez-Rodrigo et al., 2007).

The basin stratigraphy overlies volcanics dated at ~2.0 Ma and is divided into a series of six beds. The stratigraphic interval targeted for study is early Pleistocene in age and located immediately below the Olduvai subchron (CN2), a short paleomagnetic reversal within the Matuyama chron. The top of the subchron is dated at 1.785 Ma (Berggren et al., 1996). Bed I is the lowest unit of the Olduvai Beds. It is marked by Tuff IA at the base and capped by Tuff IF (~1.785 Ma) (Hay and Kyser, 2001) (Fig. 2). The oldest hominin remains lie a short distance beneath Tuff IB; the others lie at varying levels between Tuffs IB and IF (Leakey, 1971; Hay, 1976). The sedimentary deposits of middle to upper Bed I are a package of lake, lake margin and wetland sediments that have been interpreted to represent a sequence of lake fluctuations (wet/dry periods) driven by 19–23 ka precession (Milankovitch) cycles over about a 50-ka interval (Ashley and Hay, 2002; Ashley, 2007). The sediments are interbedded volcaniclastic-sourced lithologies: “waxy” claystones (smectitic), tuffaceous siltstones and “earthy” claystones, a siliceous lithology composed of phytoliths, diatoms, siliceous plant remains and windblown detritus (Ashley and Hay, 2002). Discontinuous beds of ash, sandstone, limestone and thin diatomites make up the rest of the record. The waxy claystones represent higher lake levels (wetter periods) and the interbedded earthy claystones represent a wetland that flourished during times of lower lake levels (drier periods).

New geological information from six excavations in upper Bed I within a 15,000 m² area surrounding FLK N archaeological site revealed thick carbonate tufa beds and mounds within the dominant lacustrine clay (Ashley et al., 2010). Tufa occurs in all sections except the archaeological site (FLK N), and the thickest accumulation is at FLK O2

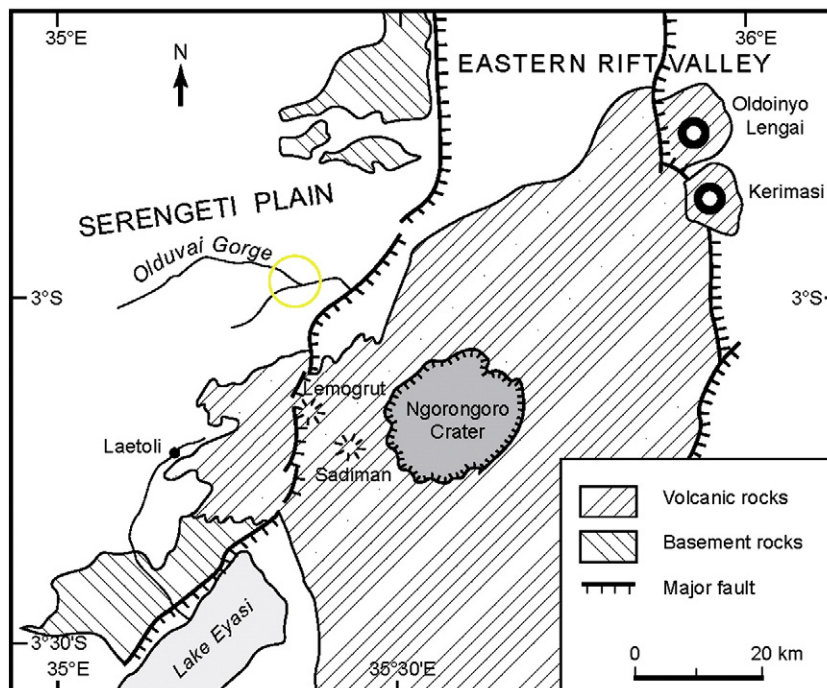


Figure 1. Regional map, Olduvai Gorge, Tanzania.

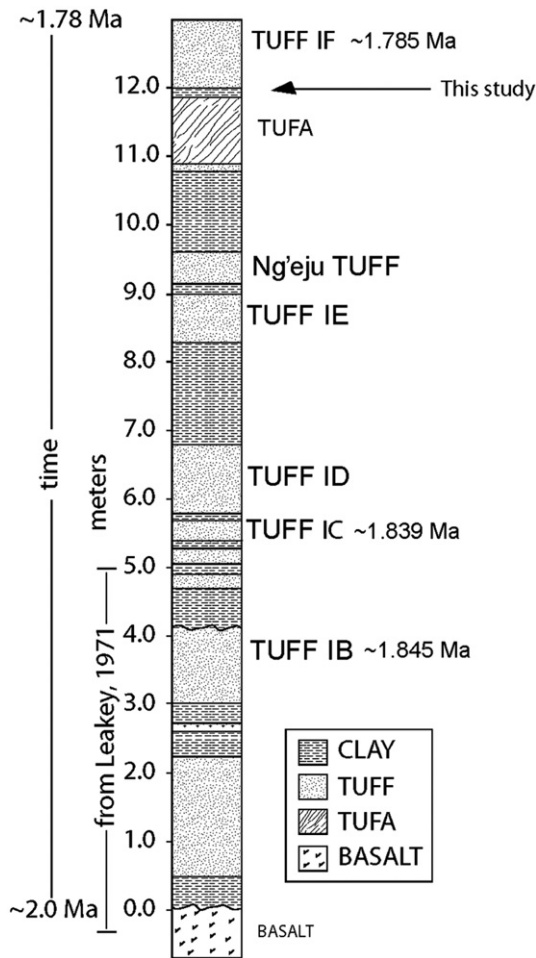


Figure 2. Stratigraphy of Bed I, Olduvai Gorge, Tanzania.

(Fig. 3). The stable isotope signatures of the tufa deposits document that the water was sourced from precipitation, and the physical association of the water with faults indicates precipitation from groundwater. Water appears to have come up along two fault lines (FLK and Zinj faults). The freshest water was associated with the Zinj fault, whereas water flowing from the FLK fault experienced extensive evaporation. Seepage from groundwater-fed springs and seeps had most likely kept the ground of surrounding lowlands wet, and standing water must have been locally present. The timeframe for a 5-cm deposit is calculated to be 500 yr in average (0.5 mm/yr), based on the sedimentation rate calculated from the thickness of non-volcanic sediments accumulated between dated Tuff IB and IF (Hay and Kyser, 2001; Ashley, 2007).

Material and methods

Field sampling

To reconstruct paleovegetation at the local scale, we sampled age-equivalent levels at several localities in the Olduvai Gorge (Fig. 3). Our sampling was restricted to 5 cm immediately below Tuff IF (Fig. 2). Samples were collected in stratigraphic sections at FLK, FLK W, FLK NW, FLK N (Ashley et al., 2010), and at VEK, HWK W and HWK E localities where Tuff IF is also exposed (Hay, 1976). Overall, 14 samples were collected in an area of about 2 km² (Table 1). Prior to Tuff IF deposition this area was located on a broad lake margin flat, occasionally flooded by paleolake Olduvai, which shoreline lied 1–2 km westward (Ashley et al., 2010). At a given sampling spot, the outcrop was scraped clean to expose the green to brown waxy clay under Tuff IF. About 20 g of clay was sampled at each spot.

Laboratory procedure for phytolith extraction and counting

Samples were prepared for phytolith analyses by treatment of 8–10 g of sediments with pure HCl (33%) in Pyrex beakers for 4 h to remove carbonates, and then with pure H₂O₂ (30%) at 70°C to remove organic matter. H₂O₂ was changed daily until the reaction ceased. Clays were dispersed with a solution of sodium polyphosphate (NaPO₃, 0.1%, buffered at pH 7) and removed by decantation and centrifugation. Separation of organic silica from the mineral fraction and concentration of phytoliths was achieved using ZnBr₂ heavy liquid set at a density of 2.3. Residue (including phytoliths) was rinsed and dried before storage. The sediment was not sieved to avoid any potential over-representation of small phytoliths (Strömberg, 2004). The extracted material, including phytoliths and any other particles of specific gravity <2.3, was mounted using glycerin to allow rotation and observation of the particles in the three dimensions. Observations and counting were done under optical microscope at 500× magnification. Micrographs were taken on extra slides prepared with Canada balsam (Fig. 4).

All isotropic particles (even though their overall morphology was unusual or looked altered by dissolution processes) were described, drawn, and counted separately (Appendix A). Counting was carried out until reaching 200 phytoliths or until the material was exhausted. Among the 14 samples analyzed, four were considered sub-sterile (Table 2).

Phytolith types and taxonomic interpretation

Phytoliths were classified according to their morphology and size, and described following the international phytolith nomenclature (Madella et al., 2005) and Strömberg (2003). Phytolith taxonomic identification, which is not straightforward was tentatively carried out here by comparison with published photographs and descriptions (Runge, 1999; Ball et al., 2002; Strömberg, 2003, 2004; Piperno, 2006; Mercader et al., 2009), cross-checking of references, and our personal experience with modern soil phytolith data (Barboni et al., 2007).

In Olduvai upper Bed I samples we recognized 143 different phytolith types, including many characteristic types of woody plants (Appendix A). The globular bodies (6–50 μ) are produced by monocotyledons and dicotyledons, woody and herbaceous plant taxa (e.g., Strömberg, 2003; Prychid et al., 2004). Globular granulate phytoliths occur mainly (but not exclusively) in tropical woody dicotyledons (e.g., Piperno, 1988). They are reliable indicators of the tropical woody cover because their abundance in soil samples increases with increasing density of tropical broadleaved trees and shrubs at low and mid-elevation (Bremond et al., 2005a; Barboni et al., 2007; Bremond et al., 2008). The globular echinate and micro-echinate phytoliths with well-defined, evenly distributed spines, are exclusively produced by palms (Arecaceae) (Tomlinson, 1961), without further taxonomic resolution despite variations in their sphericity, size, and spines length/shape (Albert et al., 2009). Globular echinate and micro-echinate bodies with spines distributed unevenly or in a fuzzy pattern, and with more or less marked ridges (phytoliths Glo-18, -19, and -24, Appendix A) resemble silica bodies produced by Marantaceae and Costaceae species (Strömberg, 2003, 2004), and were therefore given such taxonomic interpretation. Globular phytoliths, smooth/psilate, with tubercles or vague facets were also counted separately. Those tuberculate were not assigned to Restionaceae (Prychid et al., 2004) because of their spherical 3D morphology (Restionaceae phytoliths are pyramidal, Cordova C.E., personal communication, 2009). The striated, onion-like bodies (6–50 μ) that we observed are angular or spheroidal, sometimes vaguely keystone, with sharp edges and concentric striations. They resemble vesicular infillings of ligneous plants (Strömberg, 2003, 2004). S-bodies or sclereids (20–60 μ) include smooth, porcelain-like silica bodies of irregular shape, with longitudinal facets, or angular, shard-like bodies (Strömberg, 2003). They resemble silicified terminal tracheids (Postek, 1981) or

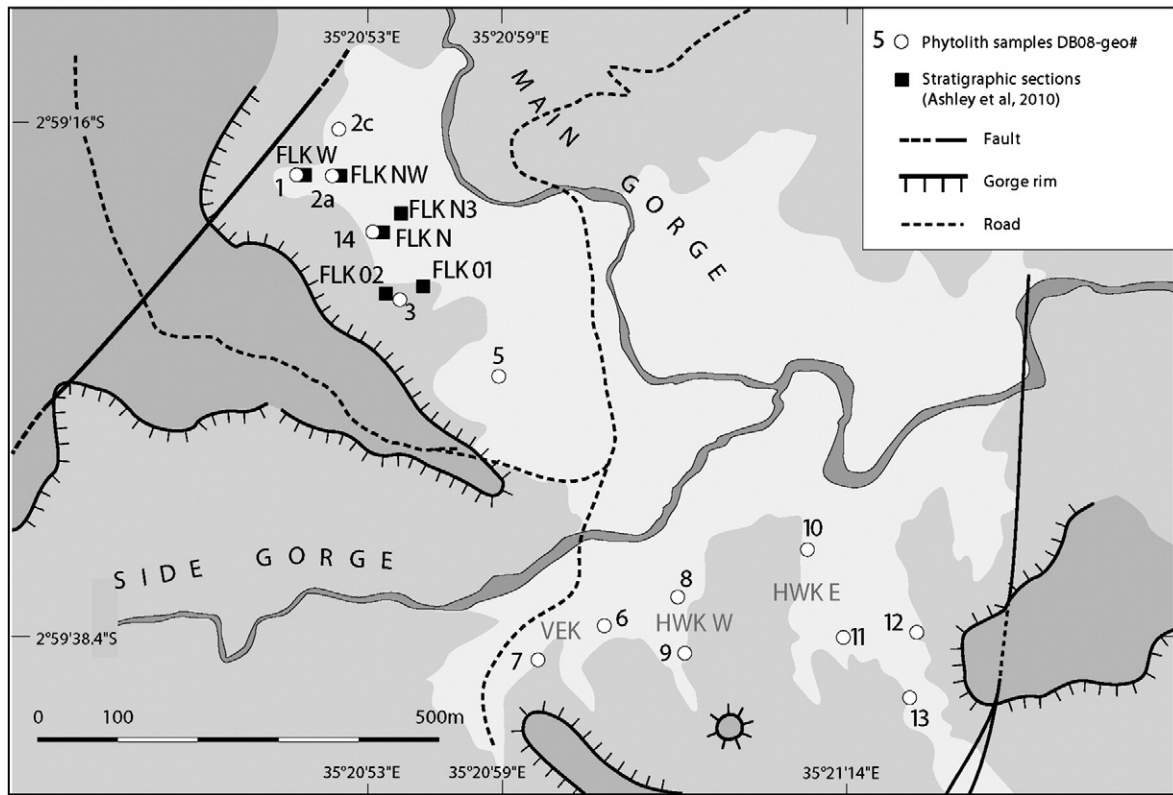


Figure 3. Map of the junction area in Olduvai Gorge, showing the spatial distribution of the phytolith samples from uppermost Bed I and the stratigraphic sections. All samples were collected less than 5 cm under Tuff IF. Thick tufa (spring) deposits occur in all sections except at FLK N archaeological site.

scleireids (Piperno, 1988) observed in lignified plants such as *Uapaca* in East Africa (Mercader et al., 2009), and are therefore considered forest indicators. We are aware, however, that it is possible that some of these particles may be non-biogenic silica, such as volcanic glass shards.

The 43 different grass silica short cells (GSSCs) that we observed belong to the categories Bilobate, Cross, Pyramidal, Oblong, Polylobate, Rondel, Saddle, and Trapeziform short cell. Their size range is 10–35 (exceptionally 80) μm. Strong correlations exist between GSSCs, grass sub-families, and some aspects of the environment in East Africa such as altitude, water- and light-availability (Barboni and Bremond, 2009). Saddles are typical for light-loving grasses favoring open and arid habitats, while Bilobates are typical for moisture-loving grasses favoring shade and/or mesic to hydric habitats. Polylobate trapeziform (or Trapeziform sinuates) short cells are typical for high-

elevation grasses of the Pooideae sub-family, which extant species only occur above 2000 masl in Africa (Livingstone and Clayton, 1980). Rondel, Pyramidal and Trapeziform short cells are redundant to some C4-xerophytic grasses of the Chloridoideae subfamily and some C3-high-elevation grasses of the Pooideae and Danthonioideae subfamilies (Barboni and Bremond, 2009). In modern soils, percents of Rondel and Trapeziform short cells increase with increasing abundance of Pooideae in the vegetation and, therefore, are a useful proxy for tracing the occurrence of C3-Pooideae and elevation/temperature (Bremond et al., 2008). At low and mid-elevation, however, phytoliths cannot distinguish between C3 and C4 grasses, due to an overlapping phytolith signal between shade-loving and moisture-loving grasses (Barboni and Bremond, 2009).

Some phytoliths among the categories Plate, Elongate, and Blocky parallelepipeds were tentatively assigned to woody plants, sedges, or grasses (Appendix A). Large tabular bodies (25–200 μm) were observed in several samples. Some are thin (<15 μm), with or without longitudinal parallel lines of material that is “made of transparent, opaque silica with small black (organic?) grains inside and have a verrucate, somewhat diffuse (not well-defined) surface” (Strömberg, 2003). Others are thick (>15–20 μm) polyhedral plates with more or less sinuous outlines, sometimes ornamented. Those with tubuliferous internal structure resemble the polyhedral epidermal cells produced by *Cyperus* sp. (Ball et al., 2002), and were therefore tentatively assigned to sedges. We considered Pla-10 (thick plate with sinuous contour) a forest-indicator phytolith, because it resembles silicified epidermal cells shaped like jigsaw-puzzle pieces (although not in aggregates) described for some woody dicotyledons (Bozarth, 1992). Blocky silicified bodies (10–180 μm) include acicular hair cells and cuneiform bulliform cells produced by grasses, plus others that strongly resemble the “tabular thick lacunate” bodies documented from miombo tree species (Mercader et al., 2009). Several polyhedral and parallelepiped bodies resemble the silicified polyhedral bulliform cells observed in grasses (Twiss et al., 1969) and sedges (Barboni and Novello, unpublished) and were,

Table 1
Precise localization of the phytolith samples collected under Tuff IF, uppermost Bed I, Olduvai Gorge, Tanzania.

Sample #	Lab #	Lat S	Lon E	Locality ^a
DB08-Geo1	18/6	2°59'18.4"	35°20'834'	FLK NN
DB08-Geo2c	19/3	2°59'16.3"	35°20'51.8"	
DB08-Geo2a	18/7	2°59'18.2"	35°20'51.6"	
DB08-Geo14	20/4	2°59'20.8"	35°20'53.4"	FLK N
DB08-Geo3	18/8	2°59'24.0"	35°20'54.4"	FLK
DB08-Geo5	19/2	2°59'27.1"	35°20'58.9"	-
DB08-Geo6	19/4	2°59'37.9"	35°21'3.6"	VEK
DB08-Geo7	19/5	2°59'39.4"	35°21'0.7"	
DB08-Geo8	19/6	2°59'36.7"	35°21'6.8"	HWK W
DB08-Geo9	19/7	2°59'39.1"	35°21'7.1"	
DB08-Geo10	19/8	2°59'34.6"	35°21'12.5"	HWK E
DB08-Geo11	20/1	2°59'38.4"	35°21'14.1"	
DB08-Geo12	20/2	2°59'38.1"	35°21'17.2"	
DB08-Geo13	20/3	2°59'40.9"	35°21'16.9"	

All samples were collected <5 cm under Tuff IF.

^a From Hay (1976).

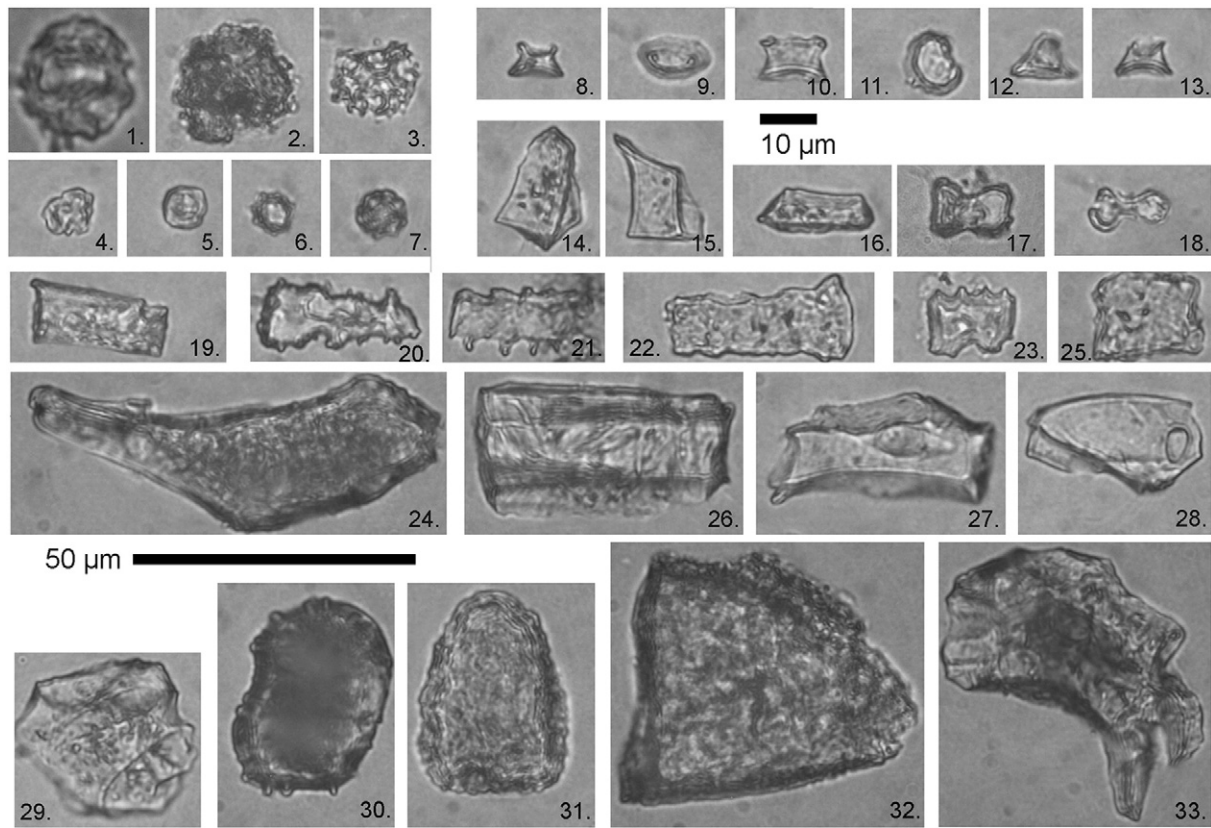


Figure 4. Selected phytolith types observed in samples from uppermost Bed I, Olduvai Gorge, Tanzania. 1–7: Globular types, 1: tuberculate (Glo-20, Appendix A), 2: granulate (Glo-4,5), 3: micro-echinate fuzzy (Glo-19), 4: granulate d8–15 µ (Glo-3), 5: smooth/psilate (Glo-28), 6,7: echinate with distinct spines (Glo-13); 8–13: Rondel-type Grass silica short cells (GSSCs), 8,13: conical, top spiked (GSSC-26), 9: conical, top truncated (GSSC-27), 10,12: conical, top keeled (GSSC-25), 11: tabular slightly crescent-shaped (GSSC-36), 14–15: Pyramidal short cell types (GSSC-22), 16: Oblong trapeziform short cell type (GSSC-16), 17: Bilobate thick shank round lobes (GSSC-8), 18: Bilobate round lobes (GSSC-4); 19–24: Elongate types, 19: smooth glass-rod type body, straight (EI-2), 20,21: tabular or slightly cylindrical, tuberculate (EI-12), 22: tabular with sinuous edges (EI-14), 23: cylindrical body sinuous, smooth surface (EI-11), 24: cylindrical body granulate, curved (EI-4); 25–27: Blocky types, 25: cubic body with granulate surface (Blo-31), 26: hexagonal with bulliform-type texture (Blo-19), 27: parallelepiped body smooth, pinched-point (Blo-27); 28–29: dubious morphotypes that may be non-biogenic glass shards or phytoliths, 28: may be identified as thin biogenic silica plate, edge or surface lacunate (Pla-3), 29: may be identified as sclereid (S-1); Other Blocky types: 30,31: ovate, granulate/tuberculate surface (Blo-31), 32: Tabular thick lacunate body large (Blo-23), 33: cuneiform irregular with bulliform-type texture (Blo-25).

Table 2
Phytolith counts summarized, uppermost Bed I, Olduvai Gorge, Tanzania.

Phytolith main categories ^a	Taxonomy	Localities sampled under Tuff IF ^b /DB08-sample #													
		FLK NN			FLK N			FLK –		VEK		HWK W		HWK E	
		1	2c	2a	14	3	5	7	6	8	9	10	11	12	13
Globular granulate	FI	164	65	70	40	128	22		91	150	77	60	16	7	
Globular echinate	Palm	7		1	40	1			5	6	16	20	51	1	
Globular echinate/micro-echinate/ridges	Mar/Cos?				28	1							10		
Globular tuberculate/faceted/smooth	FI	10		3	3	1	2		2				9	9	
Globular (other)	–										5				
Striated/onion-like	FI				1				8						
Plates (other)	–				8										
Plates (grass types)	Grass/Sedge?			51						0	8	22			
Plates (FI)	FI									6		1			
Sclereids	FI	2		12	7					4		39	8	1	
Mesophyll-type bodies	Grass											1			
Elongate (others)	–			9						3	2	14	1		
Elongate (FI types)	FI		11	8	20	4				8	3	14	6		
Elongate (grass types)	Grass?									4	2	17	5		
Blocky (others)	–	15	101	26	23	51	1		28	65	71	61	20	7	
Blocky bodies (FI types)	FI			19	36	4						1	1		
Acicular hair cells	Grass/Sedge	1			1					12	4				
Fan-shaped and parallelepiped bulliform cells	Grass/Sedge	7	23	3	14	14			9	24	5	34	7	1	
Grass silica short cells	Grass	2.5		7.5	7				7	49	27	220	54	2	
Dubious	–					3	2				1	2			
SUM phytoliths		209	200	210	228	207	27	0	150	335	224	506	188	28	
Diatoms				2											

^a Detailed counts of phytolith types are in Appendix A.

^b Localities after Hay (1976).

therefore, tentatively assigned to a Grass/Sedge category. Elongate bodies (12–360 µm) have circular, triangular or irregular transverse sections, and smooth, rough, granulate, tuberculate, or lacunate surface. Among the Elongate types, three were attributed to grasses, and five were considered forest indicators because they resemble types produced by miombo tree species (Mercader et al., 2009). Others were considered non-diagnostic (Table 2, Appendix A).

Analytical treatment applied to re-evaluate the published pollen data

Olduvai fossil pollen record is characterized by abundant herbaceous taxa (mostly grasses and sedges), which account for 50% to 90% of the total pollen count and make the signal of arboreal taxa indistinct. However, the pollen diversity (119 taxa identified in the 11 productive samples) is surprisingly high for an arid paleo-climatic context (Bonnefille, 1984). To re-evaluate the pollen signal for Olduvai upper Bed I, we considered the ecological affinity of the plant species associated with each fossil pollen taxon for vegetation types that may occur nowadays in a hydrogeological context similar to Olduvai upper Bed I, namely freshwater springs near saline or alkaline lake (Ashley et al., 2010). In the surroundings of Olduvai, we chose Lake Manyara, because its vegetation was extensively described (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986). To calculate a measure of the relative importance of each potential vegetation type at FLK N and FLK (where fossil pollen data are available) we used the matrix of pollen percentages by sites in combination with a taxa–vegetation matrix created with Lake Manyara botanical relevés and vegetation descriptions, and the African Pollen Database inventory (Vincens et al., 2007) (Appendix B). Scores for vegetation types are calculated as follow:

$$S_a = \sum_{i=1}^n \delta_{ia} \sqrt{P_i}$$

where S is the score of vegetation type a , n is the number of pollen taxa with extant species in vegetation type a , and P is the relative abundance of the pollen taxon. $\delta_{ia} = 1$ if taxon i occurs in vegetation type a and $\delta_{ia} = 0$ if not. The calculation of vegetation scores goes some way towards compensating for the fact that pollen taxa may occur in more than one vegetation type. It also takes into account the pollen taxa diversity and the excessive weight of over-represented taxa (Prentice et al., 1996).

Results

Phytolith relative abundance and paleovegetation

All productive samples had phytoliths globular granulate attributed to woody dicotyledons, which indicates the presence of trees and/or shrubs in the paleovegetation (Table 2) (Fig. 5). Forest-indicator phytoliths, including globular ornamented bodies (granulate, echinate, tuberculate, etc.) plus the striated/onion-like bodies and sclereids were found most abundant at FLK N (sample 14) and FLK NN (sample 1). Grass silica short cells (GSSC, diagnostic of Poaceae) were found rare to absent (<4%) at FLK and FLK N, but numerous and diverse at VEK, HWK W and HWK E (up to 47%), which attest to the presence of grasses in the southeast of the junction, not at the FLK N archaeological site (Fig. 6). Palm phytoliths (globular echinate) were abundant in samples at FLK N (17%) and HWK E (27%) in association with phytoliths that are globular echinate with small (micro) spines arranged in a fuzzy pattern, which we (tentatively) assigned to the tall understory monocots Marantaceae/Costaceae. Palms (and maybe Marantaceae/Costaceae) may, therefore, have been locally abundant in the paleolandscape.

The presence of silicified bulliform cells and the almost complete absence of grass silica short cells in samples from FLK N and surrounding

northwestern localities strongly suggest the presence of rare grasses submitted to high water availability (Madella et al., 2009) and/or sedges (Barboni and Novello, unpublished data) in the paleoenvironment. The relative abundance of bulliform cells is <10% and similar in all samples (Fig. 5), which suggests little drought stress for the grasses and/or sedges in the junction area.

For all but one sample, the counts of GSSCs are low (0 to <50 phytoliths). For sample 10 at HWK E a statistically valid count of 220 GSSCs could be reached (Table 2, Appendix A). The assemblage (Fig. 7) is characterized by Polylobate trapeziform (2.4%) (typical for C3-Pooideae high-elevation grasses), and Rondel (64%), Oblong (9%), and Trapeziform short cells (7%).

Other silica bodies such as the Elongate phytoliths, the medium-size (40–60 µm) and large (>60 µm) parallelepipeds (blocky-type phytoliths) and Plates, were found abundant in most samples (Fig. 3). However, their taxonomic origin is, so far to our knowledge, unclear.

Discussion

The phytolith data suggest abundant woody plants including trees and/or shrubs, and palms with little to no grasses but probably some sedges, in the paleovegetation around FLK N during uppermost Bed I time (~1.785 Ma). Around FLK N, the paleovegetation is best described as a groundwater forest/woodland or bushland. Less than 1.5 km to the southeast, the presence and relative abundance of grasses attests for a more open vegetation (such as wooded grassland *sensu* Sikes and Ashley, 2007), where trees and/or shrubs and palms were scattered.

Assuming our sampling of the first few centimeters under Tuff IF and the low sedimentation rate of 0.5 mm/yr (Hay and Kyser, 2001; Ashley et al., 2010) have provided contemporaneous samples, the heterogeneity of the vegetation cover over such small area cannot be explained by climate. Instead, the heterogeneous vegetation cover between localities around FLK N and HWK E is most likely the result of local favorable factors in the environment, such as fresh groundwater. Availability of fresh groundwater would have helped sustain dense arboreal vegetation even under attested semi-arid climate (Bonnefille, 1984; Cerling and Hay, 1986; Plummer and Bishop, 1994; Sikes and Ashley, 2007; Bamford et al., 2008). The presence of freshwater springs is attested by the presence of thick tufa beds in the 15,000 m² area around FLK N, but not at the exact location of FLK N archaeological site, which is interpreted to be higher (+1 m relief) (Ashley et al., 2010). Higher relief implies better drained soils and may, therefore, explain why palm phytoliths are found most abundant at FLK N (sample 14, Fig. 4). Compared to modern phytolith data (Barboni et al., 2007), the abundance of Globular phytoliths (~85% around FLK N, ~55% around VEK and HWK in average) suggests a dense woody cover around FLK N similar to current dense forests, and more open woody cover further to the southeast, similar to current Sudano–Zambesian miombo forests.

Locally dense vegetation with palms and sedges but few grasses in the vicinity of freshwater springs is a paleoenvironmental context associated to a saline paleolake that is analogous to present setting around Lake Manyara. Indeed, an evergreen groundwater forest currently occurs in the northern area of the nearby saline and alkaline Lake Manyara despite the low annual rainfall (ca. 650 mm/yr) and prolonged dry season (ca. 7 months) (Greenway and Vesey-Fitzgerald, 1969). This forest is a three-story formation, which includes the palm *Phoenix reclinata* at the intermediate level, and some grasses, reeds and other flowering plants at the lower level. This forest is supported by groundwater from the high water table fed by seepage from the volcanic rock of the rift wall. The groundwater forest occurs on the upper part of the alluvial fans, close to the spring head (Loth and Prins, 1986). Total cover of woody species exceeds 80% (predominantly *Trichilia roka*, *Rauvolfia caffra*, *Croton macrostachyus*, *Ficus sycomor*, *Tabernaemontana usambarensis*, and the perennial herb *Hypoestes verticillaris*); in semi-open places, grass colonies of *Panicum deustum*, *P. trichocladum* and *Setaria plicatilis* occur.

Uppermost Bed I Olduvai, Tanzania

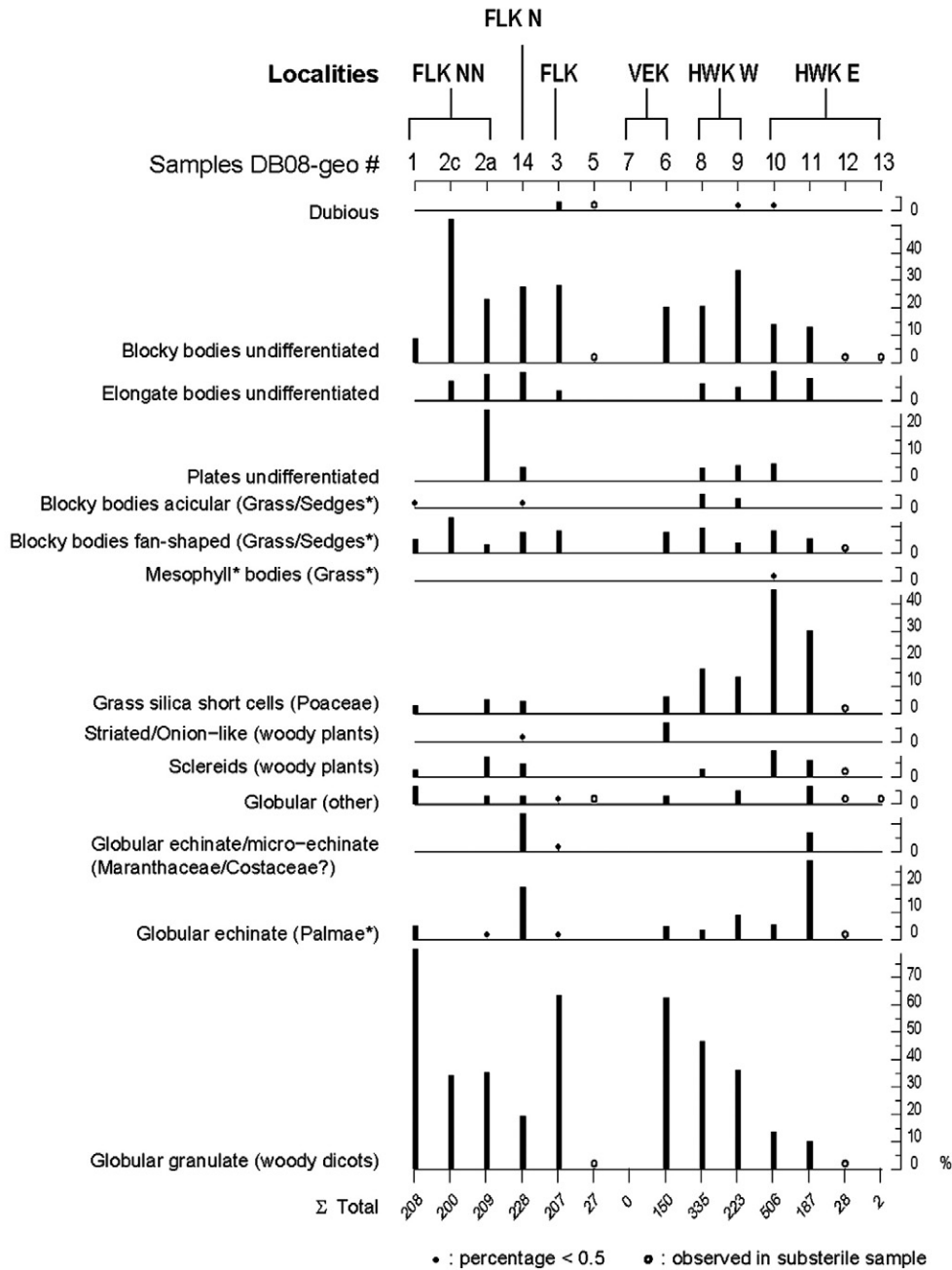


Figure 5. Relative abundance of phytoliths (main categories) observed in the samples collected <5 cm under Tuff IF, uppermost Bed I, Olduvai Gorge, Tanzania. * means phytolith type.

On drier ground beneath the trees, the reed *Cyperus alternifolius* may be very common. In locally better drained areas, the forest is replaced by bushland (20–60% woody cover, predominantly shrubs of *Salvadora persica*, *Maerua tripylla*, trees of *C. macrostachyus*, and *Cynodon* grasses). The palm *P. reclinata* in association with trees of *Acacia xanthophloea* and the grass *Chloris gayana*, occurs away from the springs on the lower parts of the alluvial fans, and may locally cover >50% of the ground. The wooded grasslands (with scattered trees of *Croton m.* and abundant *Cynodon dactylon* grasses) occur where water from the springs stagnates (Loth and Prins, 1986). Where the water table is too high, the forest is replaced by swampy glades in which tall reeds of *Typha* and *Cyperus immensus* predominate. Hence, the key environmental factors differentiating vegetation types within the semi-arid ecosystem of Lake Manyara,

such as around most of the rift valley lakes of East Africa, are primarily the distance to the lake (which controls soil salinity) and the distance to the springs or perennial rivers (which controls freshwater availability) (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986).

Our interpretation of the phytolith assemblages is that, locally, around FLK N where freshwater springs occurred, paleovegetation was as densely wooded as the present *Salvadora* bushlands or the groundwater forest of Lake Manyara (>60% woody cover), which is more than was suggested by previous macro-botanical (Bamford et al., 2008) and pollen studies (Bonnieffle, 1984). Silicified mats of fossil grass clumps were found preserved under Tuff IF at FLK N, VEK, HWK W, and HWK E localities and farther east in the Gorge (Bamford et al., 2008). Evidence for grasses is confirmed by our phytolith results at VEK, HWK

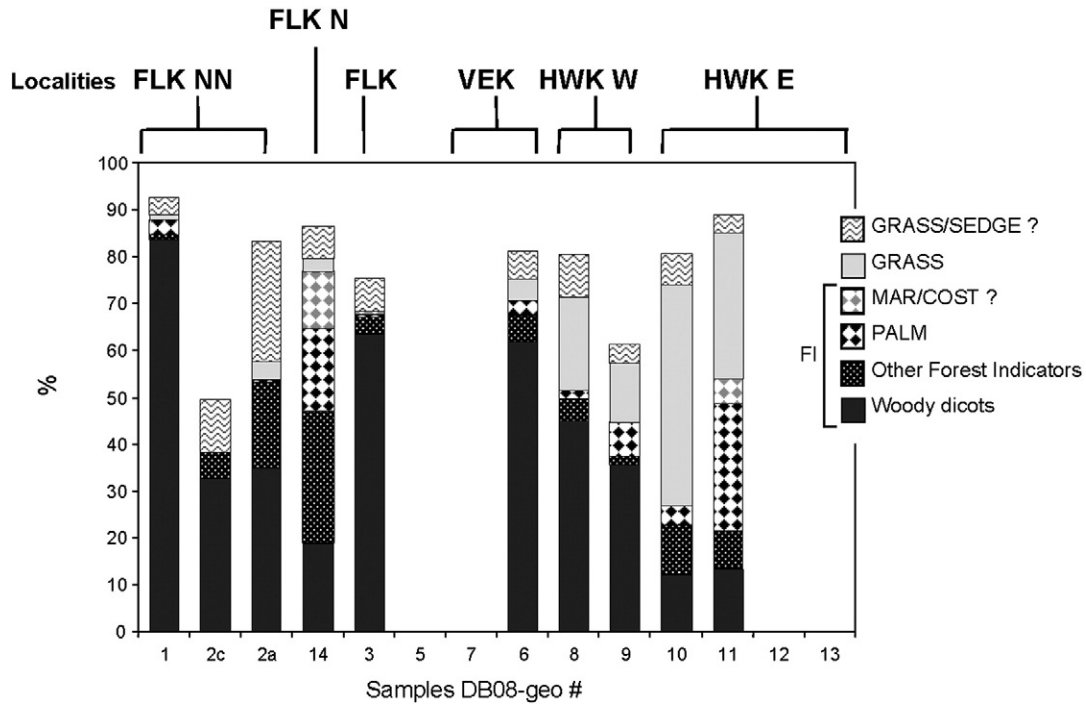


Figure 6. Relative abundance of phytolith indicators of grasses, sedges, Marantaceae/Costaceae?, palms, and woody plants observed in our samples collected <5 cm under Tuff IF, uppermost Bed I, Olduvai Gorge, Tanzania. See text and Appendix A for the taxonomical attribution of phytolith types. Totals do not reach 100% because the percentage of phytoliths with unknown taxonomical origin and dubious 3D morphology is not null. FI: Forest indicators.

W, and HWK E, but not near FLK N, where few to no grass phytoliths were found in the five samples we studied. It is not clear where exactly at FLK N the macroplant layer is exposed, and how distant it is from our phytolith samples. However, given that semi-arid tropical vegetation is highly heterogeneous and grasses are ubiquitous, grass patches and patches of woody plants co-occur over small (<25 m²) areas. Although a silicified wood (approximately dated to 1.8–1.75 Ma) identified as *Guibourtia coleosperma* (Caesalpinaceae) was found at HWK E (Bamford, 2005) and up to 70% of “wood/bark” phytoliths were counted in three samples from HWK E (Bamford et al., 2008), the presence of well-preserved *in situ* fossilized grass mats was interpreted as open continuous grassland on well-drained soils throughout the Gorge during uppermost Bed I time (Bamford et al., 2008). The grass cover may not have been continuous, however, because our repeated

sampling of uppermost Bed I confirms the presence/abundance of forest-indicator phytoliths, and because silicified grass layers were not observed where we sampled for this phytolith study (except at HWK E, Fig. 3).

The silicified macroplant remains are localized records of vegetation, preserved if particular conditions are met (Carson, 1991). Hence, it cannot be ruled out that they may give only a partial (biased) vision of a plant community that was restricted to a specific local context as noted for Lower Bed II (Albert et al., 2006). As observed today around Lake Manyara, vegetation cover is highly heterogeneous over short distances because it is highly sensitive to local hydrogeologic conditions. Perennial overland flows of freshwater from the springs are responsible for sharp changes in the vegetation structure (from forest with >80% woody cover to grassland with <2% woody cover) over small distances (<1 km), and grasses occur in pockets at various locations (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986).

Contrary to macro-botanical remains, pollen data are most likely to represent the regional (paleo) vegetation. Despite being plausibly older than our phytolith samples (<5 cm below Tuff IF), two pollen samples from 30 to 10 cm below Tuff IF in the FLK area (samples FLKN1i and FLKa) are available for comparison (Bonnefille, 1984). Both indicate abundant grasses and sedges in the vegetation, and the presence of drought-adapted trees and shrubs of the Sudano-Zambezian phytochorion and Afromontane taxa in the nearby highlands. We note, however, that several of these pollen taxa represent plants such as *Achyranthes*, *Salvadora*, *Acacia*, and *Phoenix* that are common in the present bushlands and *Acacia* woodland that occur next to the groundwater forest of Lake Manyara. Others such as Capparidaceae represent common shrubs of the riverine vegetation on the low alluvial terraces and back swamps and which are regularly flooded during the wet season, but suffer water shortage during dry season (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986) (Appendix B).

The re-evaluation of the pollen data using Lake Manyara as modern analogue, and an approach that allows multiple ecological affinities for pollen taxa and lowers the weight of high pollen

Grass silica short cells at HWK E (sample DB08-geo10)

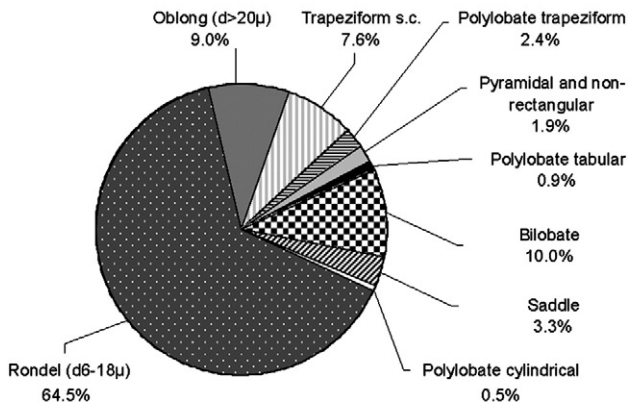


Figure 7. Pie diagram of the relative abundance of grass silica short cell types (GSSCs) in sample DB08-geo10 at locality HWK E, uppermost Bed I, Olduvai.

producers, reveals that 70% of the pollen signal could be in fact attributed to woody plant formations, including the thicket-woodland of the escarpment, the gallery forests along seasonal streams, the *Acacia* groundwater woodland, and the groundwater forest (Fig. 8). Less than 30% of the fossil pollen signal is attributed to the swamp herbage and grassland despite the over-representation of pollen from heliophilous herbs and grasses. Change in the percentages of Cappariaceae pollen between sample FLKN1i and FLKa was interpreted as a change in climate toward drier conditions (Bonnefille, 1984). However, the analogy with Lake Manyara vegetation suggests that different local hydrogeological conditions such as changes in soil alkalinity/salinity and/or distance to the freshwater springs rather than climate may have induced such change in the pollen composition. Overall, however, both pollen samples show similar vegetation patterns. This re-evaluation indicates that although grasses were most abundant in the paleolandscape, other plant formations such as groundwater woodland, forest, and thicket-woodland were also most likely present around FLK N during upper Bed I time (Fig. 8).

The phytolith data are also in agreement with carbon isotopes from Bed I (and lowermost Bed II), which indicate abundant C3 biomass and, therefore, implies that the vegetation included trees and shrubs (40–60% woody cover) or that there were more higher altitude grasses (Cerling and Hay, 1986; Sikes and Ashley, 2007). The abundance of woody plants is indicated by the abundance of forest-indicator phytoliths and the low number of grass silica short cells in most samples from around FLK (Fig. 6). Sample 10, which produced abundant grass silica short cells, also indicates that high-elevation C3 grasses were most likely present in past grass cover during uppermost Bed I time, because phytoliths Rondel, Oblong, Trapeziform short cells and Polylobate trapeziform (typical for East African C3-Pooideae grasses, Barboni and Bremond, 2009) represent ~86% of the GSSCs (Fig. 7). In East Africa, such high values are observed in Afromontane soils at high elevation (>2800 masl), where the grass cover is exclusively composed of C3-Pooideae and Danthonioideae grasses (Bremond et al., 2008). Chloridoideae grasses such as *Cynodon* and *Sporobolus* (C4) produce high amount of Rondel and Trapeziform short cells (Bamford et al., 2006), which may contribute to high Ic values despite the absence of Pooideae in the grass cover. This is confirmed by high Ic values of 31% to 63% that were obtained from the edaphic grasslands near the Olbalbal depression (East of Olduvai Gorge) (Barboni et al., 2007). Hence, until repeated sampling confirms

the pattern, the abundance of C3-Pooideae grasses in the paleo grass cover (that would argue for lower than present paleo-temperatures at Olduvai during uppermost Bed I and/or higher atmospheric CO₂ level) is not ascertained.

The phytolith data are also in agreement with the faunal remains from upper Bed I. The abundance of acelaphini and antilopini at the top of Bed I has been interpreted as indicators of open environment (Gentry and Gentry, 1978; Kappelman, 1984; Shipman and Harris, 1988). A comparative ecomorphological analysis of middle and upper Bed I bovids confirmed a drying trend across the sequence but contradicted the taxon-based interpretation by showing that most of the bovids were adapted to a complete range of open (predominantly) to closed-vegetation environments (Plummer and Bishop, 1994; Andrews and Humphrey, 1999). More specifically, bovids adapted to mixed and closed-vegetation habitats were almost a third more abundant than predicted by a taxon-based analysis. *Antidorcas recki*, one of the two most abundant taxa at FLK N, was ecomorphologically classified as having an intermediate habitat adaptation. Plummer and Bishop (1994) argued against the use of grassland-dominated ecosystems as a proxy for the Olduvai Bed I sequence and mentioned that ecosystems with a greater proportion of mixed and closed habitats would be more adequate. Taphonomic and paleoecological interpretation of micromammals also suggest the presence of a very rich woodland/forest in the lower section of Bed I changing to more open woodland in the upper section of the sequence. FLK N2 and FLK N6 show an even proportion of gerbillinae and muridae, suggesting an important presence of woodland around FLK N (Fernandez-Jalvo et al., 1998). It should be stressed that the presence of open-vegetation bovids at some of the Olduvai Bed I sites does not necessarily indicate open landscape at the setting where these sites clustered, as shown by the gerbil component of the assemblage relative to murine that was taphonomic in origin: predators (owls) obtained their prey somewhere else and brought them into the site. The ecological analysis based on the FLK N microfauna indicates a woodland that was denser than any savanna woodland from modern savannas (Fernandez-Jalvo et al., 1998).

Taphonomic and paleoecological interpretation of the macrofaunal remains from FLK N also showed that the main taphonomic agent/carnivore responsible for the accumulation of *Parmularius* and *Antidorcas*, the two predominant taxa in the assemblage was a highly-specialized predator (felid) (Dominguez-Rodrigo et al., 2007,

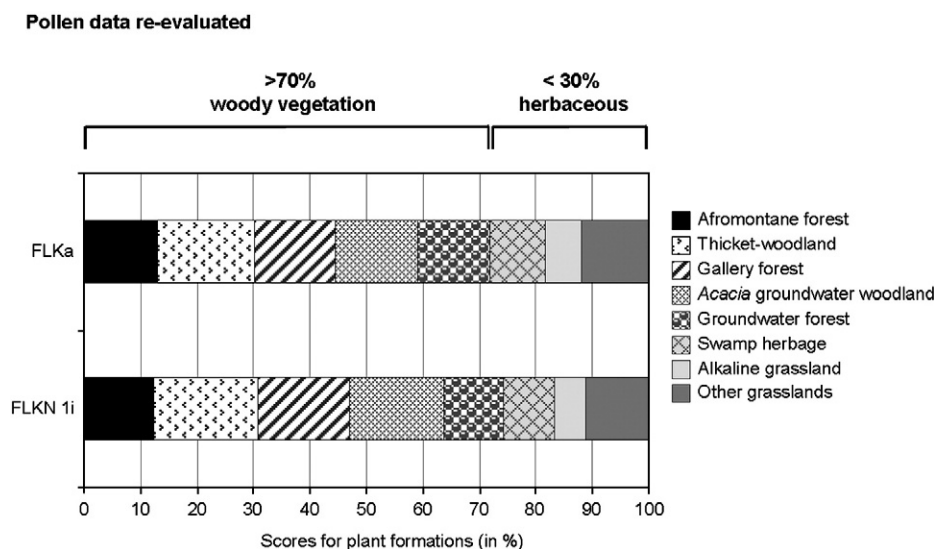


Figure 8. Re-evaluated fossil pollen data by Bonnefille (1984).

pp 269–278). Dominguez-Rodrigo et al. (2007) argued that site formation could be understood as a very low-competitive setting (enabling the preservation of a large portion of complete long bones and many axial bones which would have disappeared in open habitats) probably used as a refuge by those predators. They may have preyed on the game occupying the grassland part of the landscape and transported their prey into the more wooded part of the ecosystem. The contrasting settings (grassland, forest/woodland, and bushlands) and presence of freshwater springs in the vicinity of FLK N would explain the repeated occupation of this area by carnivores and hominins over the millennia and, thus, the impressive thickness of the FLK N deposit. The isotopic analysis of the enamel of three specimens of *Homo habilis* from lower and uppermost Bed I revealed that their diet was dominantly C3 (van der Merwe et al., 2008). The enamels indicate 23% of C4 biomass for OH7, 27% for OH62, and 49% for OH65. Of these, OH7 and OH62 are from Olduvai East (east of paleolake Olduvai, like the area under study here) and OH65 is from Olduvai West. Grassy woodland/woody grassland with ~50% woody cover is also indicated in the western margin of the Olduvai Basin, some 15 km to the west of FLK N (Sikes and Ashley, 2007). The spatial extent of woodland/bushland suggests that the resource-rich woody vegetation that was available to hominins in the surrounding of paleolake Olduvai was probably the densest in the vicinity of FLK N.

To interpret these phytolith data, we relied on published material (e.g., Strömberg, 2003), but phytolith reference collections specific to African plants are rare (Ball et al., 2002; Mercader et al., 2009; Rossouw, 2009). We are aware that some assignments to plant taxa may be re-evaluated in the light of new studies on modern plant material. This is the reason why we provide our raw counts, the phytolith type descriptions, and some micrographs to allow further and/or improved paleoenvironmental interpretations of upper Bed I paleovegetation. The modern phytolith study by Mercader et al. (2009) showed that woody plants from the Sudano–Zambezian flora produce lacunate phytoliths, a feature of the phytolith surface that resembles dissolution pits. This work on fresh plant specimen was inspiring and brought confidence that the unfamiliar silica bodies that made up the phytolith assemblages of upper Bed I could carry a strong vegetation signal, which is now confirmed by our results and in agreement with the re-evaluated pollen data and faunal studies.

Conclusions

Our phytolith-based paleoenvironmental reconstruction of a paleo-groundwater forest close to the spring heads where FLK N was formed and bushlands to wooded grasslands at localities away from the springs resembles today's vegetation around Lake Manyara. Using Manyara botanical relevés, a re-evaluation of the fossil pollen data confirms that woody vegetation types (including the thicket-woodland from the escarpments, the *Acacia* groundwater woodland, and the gallery and groundwater dense forests) were also present in the surroundings of FLK N during uppermost Bed I time. Microbotanical, isotopic, and taphonomical studies of faunal remains now converge on the same conclusion that the area surrounding FLK N, which attracted both carnivores and hominins in the early Pleistocene, was locally densely wooded during uppermost Bed I time.

Supplementary materials related to this article can be found online at doi:10.1016/j.yqres.2010.09.005.

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