



## Paleovegetation changes accompanying the evolution of a riverine system at the BK paleoanthropological site (Upper Bed II, Olduvai Gorge, Tanzania)



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### ABSTRACT

Paleovegetation studies are essential to ecologically frame hominin evolution. The analysis of the phytolith content of 22 paleosol samples collected along the vertical sequence of the channel containing the BK (Bell's Korongo) archaeological levels, provided evidence of the paleovegetation that accompanied the evolution of the riverine system that formed this site 1.353 million years ago, when climate was particularly arid. The analysis reveals the abundance of forest indicator phytoliths (46% to 92% of the assemblages), rare grass silica short cells and sedges phytoliths (up to 15% of assemblages), and palms (up to 10% of the phytolith assemblages). The vegetation of the BK fluvial system was therefore characterized by abundant woody plants. It did not vary significantly diachronically in the period of time under scrutiny. The alluvial paleovegetation corresponds well to the fluvial dynamic that formed BK, including the presence of sterile samples recovered in areas where the water traction changed the soils frequently. This spot of dense paleovegetation together with the fluvial watercourse (in a paleolandscape likely dominated by sparse/open vegetation) could have been attractive, seasonally, for animals and hominins.

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### 1. Introduction

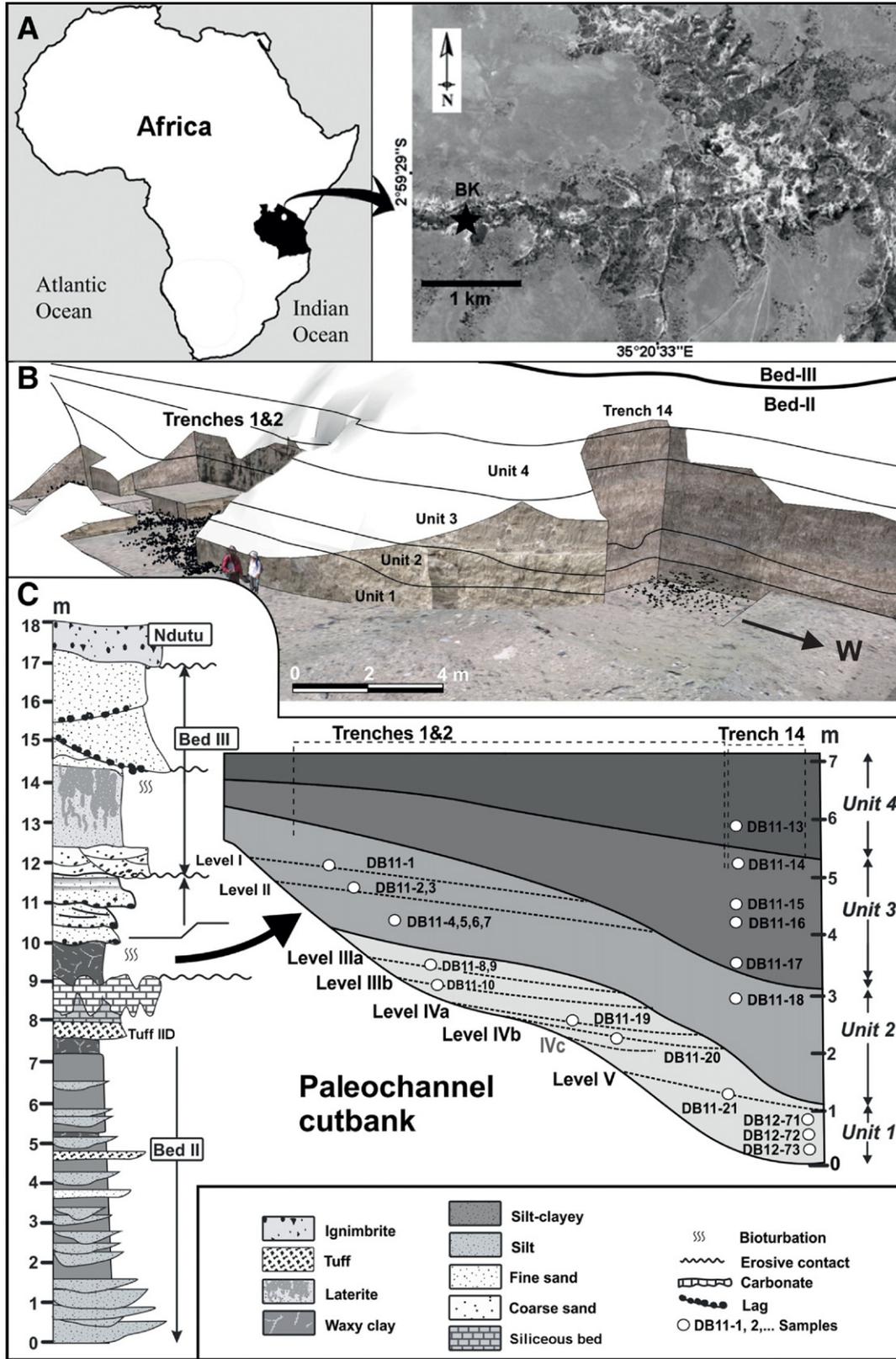
Olduvai Gorge in North Tanzania is a world famous area, which has provided a large number of hominin remains (Leakey, 1971), and which continues to be actively investigated as it still provides exceptionally well-preserved Lower to Upper Pleistocene paleontological and archaeological sites, with hominin remains, anthropogenically modified bones, and stone artifacts from the most primitive Oldowan to the late Acheulean culture (e.g. Domínguez-Rodrigo et al., 2007; Diez-Martín et al., 2015). In the southern branch of Olduvai side gorge, one site named the Bell's Korongo site (hereafter BK) was discovered in 1935, and first excavated in the 1950s (Leakey, 1971). Placed in the stratigraphy at the top of sedimentary Bed II, it overlies Tuff IID, which is dated to  $1.353 \pm 0.035$  Ma (Domínguez-Rodrigo et al., 2013). From the archaeological and taphonomical point of view, BK is a well-studied site where numerous artifacts and animal remains were recovered

(Diez-Martín et al., 2009; Domínguez-Rodrigo et al., 2009, 2014; Organista et al., 2015, 2017). Several excavations were carried out in the 1950's and 1960's, revealing a very rich assemblage of bones and stone tools (over 6800 stone items), classified as belonging to the Developed Oldowan B complex (Leakey, 1971). The BK bone assemblage excavated by Leakey showed a substantial portion of bones with marks made by hominins (Egeland et al., 2007; Monahan, 1996). New excavations by TOPPP (The Olduvai Paleoanthropology and Paleoecology Project) have allowed recovering another 1500 lithic pieces (Diez-Martín et al., 2009) and among them, cutting tools, which support the consumption of small to large carcasses by hominins at the site. Recent analyses support the interpretation of BK as an anthropogenic site where hominins were modifying and consuming small and middle-sized carcasses, as well as a substantial amount of megafaunal carcasses (Domínguez-Rodrigo et al., 2009, 2014; Organista et al., 2015, 2017), in agreement with previous interpretations (Egeland and Domínguez-Rodrigo, 2008; Monahan, 1996). BK has the highest hominin input from all the Bed II sites (Domínguez-Rodrigo et al., 2009, 2014; Egeland and Domínguez-Rodrigo, 2008; Organista et al., 2015, 2017).

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The BK site corresponds to a riverine system where conglomeratic sandstone filled channels eroded into siliceous earthy claystone (Domínguez-Rodrigo et al., 2014; Hay, 1976; Leakey, 1971). In the trench initially excavated by TOPPP where 13 geological levels were

identified, most sediments are fine-grained, which suggests that a distal alluvial sedimentary environment created this sequence (Domínguez-Rodrigo et al., 2009) (Fig. 1). To date, paleovegetation reconstructions are not available for BK site, or elsewhere in the Gorge for this time



**Fig. 1.** A) Approximate position of BK site in the Olduvai Gorge. B) 3D scheme showing position of BK trenches. C) Stratigraphic section across the Bed II–Bed III and Ndotu units in BK (left), and detailed stratigraphic position of the phytolith samples (right). Modified from Domínguez-Rodrigo et al. (2014).

period around 1.3–1.4 Ma (Barboni, 2014). Only carbon isotopic data indicate that  $C_4$  plants, most likely grasses were abundant in the paleovegetation (Cerling and Hay, 1986). At Peninj, situated about 80 km northeast from Olduvai, pollen data indicate that the vegetation was dominated by grasses and local freshwater swamps were present, but large scale paleolandscape is described as a savanna grassland in which trees and shrubs were scarce around 1.4 Ma (Domínguez-Rodrigo et al., 2001).

In order to constrain paleoenvironmental factors that may have triggered the evolution of certain hominin behaviors, paleoenvironmental reconstructions including paleovegetation are necessary. In this regard, we have analyzed the phytolith remains recovered from several paleosurfaces recorded along the stratigraphic sequence of the BK site. The reconstruction of the evolution of the paleovegetation of this riverine system over time will provide a paleoecological framework that will help setting into context the anthropogenic site of BK and contribute to understand the interactions of hominins with fauna and with their environment. We chose to use phytoliths at BK because they offer a better percentage of recovery than pollen grains at Olduvai sites (Bonnefille, 1984), and are more informative than carbon isotopes to document plant functional types present at any given site (Cerling and Hay, 1986; Sikes and Ashley, 2007). Plant macro-remains were not found preserved at BK but are common at other sites in the gorge (e.g. Bamford, 2012).

## 2. Material and methods

### 2.1. Geological description of the site

BK site includes seven archaeological levels in a large meandering channel that flowed from south to north from Mt. Lemagrut and into the paleolake at the center of the basin at the end of Bed II (Domínguez-Rodrigo et al., 2013). The deposits correspond to fluvial channel infills formed during a dry period (G.M. Ashley, pers. com., 03/2017). The BK river incised 4–5 m cutting down older deposits including a carbonated paleosurface (Fig. 1). The different archaeological levels are contemporaneous to the channel infill process, which is complex in a meandering river. The fluvial infill is composed of four large sedimentary units, corresponding to lateral accretion surfaces and low angle cross-bedding. Therefore, every sedimentary body is tilted to the deepest part of the river, creating an inclined isochron. In each unit, high and low energy deposits occur, in the lower and upper part respectively. Unit 1 is erosive and contains the archaeological levels V (oldest), IVb, IVa, IIIb and IIIa (youngest) (Fig. 1C). Unit 1 includes several sub-units composed of fine or coarse sediments. Sediments from Trenches 1 and 2 were sampled in the point-bar surface where scours and swales alternate. Scours reworked the point-bar surface during bankfull events, changing slightly the original position of bones placed in the paleosurface (Organista et al., 2017). Reworking processes remove fine sediments and plants along scours, whereas these stay in swales (see e.g. similar pattern in Mara river, Fig. 2A). Westward (in Trench 14), Unit 1 is composed of high-energy materials (very coarse sands and gravels) with fine sediment materials above them. Unit 2 is the next lateral accretion unit, composed of low energy sediments, silts and clays in the eastern part (Trenches 1 and 2). Archaeological levels I and II are located in this area in two horizontal paleosurfaces. Westwards, Unit 2 eroded the upper part of Unit 1, including archaeological levels IIIa, IIIb, IVa, IVb, and IVc (Fig. 1). The erosion process was followed by the deposition of gravels and coarse sands during the high flow stage. Once the flow dismissed, fine sediments were also deposited in this area (Trench 14) and paleosols developed (Fig. 3). Unit 3 partially eroded Unit 2, including archaeological levels 1 and 2. In Trench 14, Units 2 and 3 are mainly represented by silts and clays similar to overbank deposits in a floodplain. Lastly, Unit 4 represents the silting phase and the beginning of deposition outside the channel, in a wide



Fig. 2. Modern river setting. A: Mara River, Tanzania. The picture shows the alternation of areas covered by bushes and herbaceous plants and of areas uncovered by vegetation as proposed for Trenches 1 and 2 of BK (Photo by David Uribebarrea). B: Olduvai River, Tanzania. Maasai herders dig in the dried riverbed to access the fresh water that is available (just 30–50 cm below the surface in this example) during the dry season (Photo by D. Barboni, June 2014).

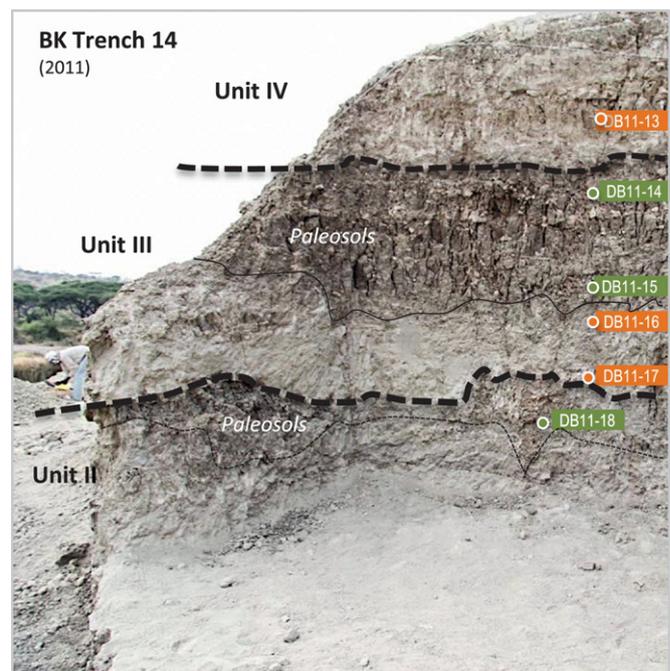


Fig. 3. Photograph of BK Trench 14 as it was excavated in 2011, and position of the sedimentological units and phytolith samples. (Photo by D. Barboni, positioning of the geological units by D. Uribebarrea).

floodplain. The tops of unit II and III are clayey. They exhibit vertic features and included carbonate nodules typical of Vertisols (Fig. 3).

## 2.2. Phytolith sampling and analysis

We collected and analyzed the phytolith content of 24 paleosol samples from BK site (Table 1). Samples were collected by D. Barboni (during the 2011 and 2012 field seasons) in three different trenches (1, 2 and 14) along the vertical stratigraphic sequence. Samples from Trench 1 comprise archaeological levels 1 to 3 and Trench 2 includes the level 4. These trenches are placed where the highest concentration of cut-marked bones have been recovered. Trenches 1 and 2 were placed in the paleo-river channel. Trench 14 was placed to the west of Trenches 1 and 2 and is placed in the paleo-river flood plain (Fig. 1).

Samples were prepared for phytolith analyses by treatment of dry sediments (6–8 g) with pure HCl (33%) for 1–2 h to remove carbonates, and then with H<sub>2</sub>O<sub>2</sub> (30%) at 80 °C to remove organic matter. Clays were deflocculated with sodium hexametaphosphate (NaPO<sub>3</sub>)<sub>6</sub> buffered at pH 7, and removed by decantation. Separation of phytoliths from heavy minerals was made using a ZnBr<sub>2</sub>–HCl heavy liquid set at a density of 2.3 g·cm<sup>-3</sup>. The residue was mounted in benzyl benzoate. Phytolith identification and counting was carried out at magnification ×400. Counts reached 200 phytoliths per sample whenever possible.

Phytoliths were described following the international code for phytolith nomenclature (Madella et al., 2005). They were classified according to their morphology and size, and subsequently grouped according to their most probable (but not exclusive) botanical origin based on comparisons with published reference collections available to date (e.g., Piperno, 1988; Ollendorf et al., 1992; Strömberg, 2003; Mercader et al., 2009; Garnier et al., 2012; Albert et al., 2016; Arráiz, 2016; Collura and Neumann, 2016) (Appendix A). Phytolith morphotypes typical of woody plants (e.g. the globular decorated) and those identified by Collura and Neumann (2016) as diagnostic of wood and/or bark tissues (e.g. parallelepiped/cubic/ovate (blocky) bodies with granulate surface) were assigned to the non-botanical “Forest Indicator” (FI) category (Fig. 4). The FI category is used here as a proxy for trees and

shrubs following previous phytolith work at Olduvai (Ashley et al., 2010a, 2010b; Barboni et al., 2010; Arráiz et al., n.d., 2017) and elsewhere (see review in Strömberg (2004)). The Grass category includes grass silica short cells (GSSCs) only: rondel, saddle, trapeziform short cells (also called trapezoid), and lobate phytoliths (bilobate, cross, and polylobate morphotypes) (Fig. 4). The grass/sedge category includes the silicified bulliform cells produced by Poaceae and Cyperaceae, and the hexagonal/round platelets (or hat-shaped) morphotype diagnostic of Cyperaceae. The taxonomical attribution of phytolith morphotypes to plant taxa proposed here (see details in Appendix A) is tentative, and will likely improve in the future as more modern phytolith reference collections become increasingly available. In the samples we analyzed, some morphotypes were found very well preserved (e.g. Fig. 4B), while others exhibited features of dissolution and, rarely, of zeolitization (e.g. Fig. 4D). Zeolites such as phillipsite and analcime were also observed as individual minerals in our residues following phytolith extractions (Fig. 4G–H).

## 3. Results

Six out of the 22 paleosol samples collected in the BK site were found totally sterile (DB11-3, -4, -6, -7, and -9 from Trench 1, and DB11-19 from Trench 2), and <80 phytoliths could be counted in samples DB11-13 and DB12-71 (Fig. 5, Appendix A). Diatoms were sparsely observed in two samples from Trench 14, but in too low abundance to provide any ecological signal (18 valves in DB11-18, 1 valve in DB12-71). Micrometric zeolites were observed in all samples, and in greatest abundance in Trench 14 where they may represent up to 65% of the particles extracted (Fig. 5). Zeolites were also found most abundant in the two sub-sterile samples DB11-13 and DB12-71 (Fig. 5). The abundance of unidentified and damaged phytoliths, however, does not appear to be correlated with the abundance of zeolites (Fig. 5). Yet, the residues mounted for microscopic observation and counting of phytoliths include many 5- to 10-µm-diameter particles, other than recognizable phytoliths or zeolites. These particles, which are dark under crossed nichols, could be highly altered phytoliths. They were not counted, and therefore, our quantification of unidentified/damaged phytoliths is probably largely under-estimated.

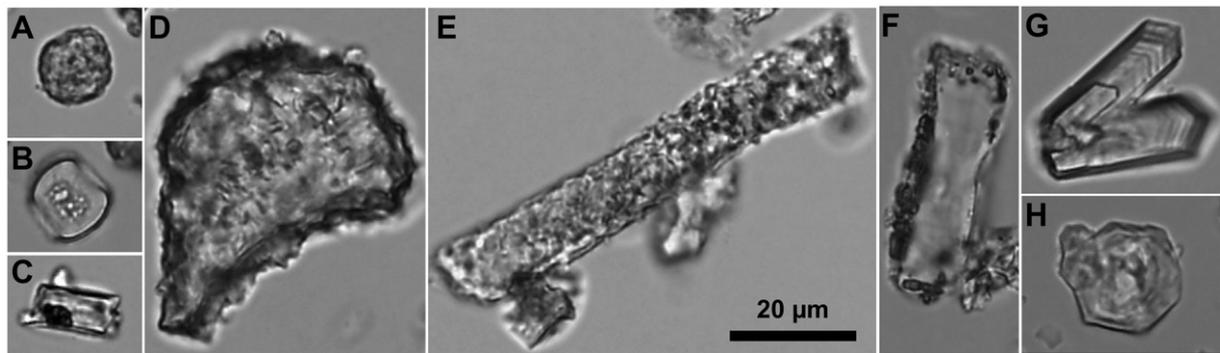
Phytoliths in the productive samples were relatively rare compared to the number of zeolites and particles present, but some were surprisingly well preserved (Fig. 4). A total of 39 different morphotypes were observed, described, and counted separately (Appendix A). Most morphotypes could be attributed to a possible botanical producer group/signal (Fig. 5). Phytoliths of the forest indicator (hereafter FI) category, essentially blocky bodies/sclereids and globular granulate phytoliths clearly dominate the assemblages ( $\mu = 67\% \pm 14\%$ , average and standard deviation) (Fig. 5). Palm phytoliths occur in seven samples only, three of them being from archaeological levels II, IVb and V. They represent 1 to 10% of the total phytolith assemblages. Grass silica short cells (GSSCs) are also scarce, with percentages < 15%, but they occur in all the productive samples. Among GSSCs, trapeziform short cells and rondels are the most represented (< 1–7%). Silicified bulliform cells and platelets (hat-shaped) are rare and represent <5% of the total phytolith assemblages. Fern phytoliths (20 to 80 µm-long parallelepipedal bodies, faceted with sharp edges) occur in few samples, mainly from Trench 14. In summary, little differences are observed between units, trenches or between samples even when non-diagnostic and damaged phytoliths are excluded (Fig. 6).

## 4. Discussion

The presence of sterile and sub-sterile samples may be explained by the river setting, which does not favor the settlement of particles, and/or by the repeated lake flooding which made the soils alkaline. Paleolake Olduvai was saline/alkaline and its seasonal flooding increased the soil pH, which could trigger phytolith dissolution. Flooding frequency and

**Table 1**  
List of samples studied for their phytolith content at BK archaeological site.

Sample ID	Arch. level	Lab #	Sediment type	n phytoliths
BK Trench 1 (2.9660°S, 35.3243°E)				
DB11-1	I	55/1	Cemented carbonate	215
DB11-2	II	55/2	Cemented carbonate	250
DB11-3	II	55/3	Cemented carbonate	Sterile
DB11-4	–	55/4	Tuffaceous clay	Sterile
DB11-5	–	55/5	Tuffaceous clay	178
DB11-6	–	55/6	Tuffaceous clay	Sterile
DB11-7	–	55/7	Tuffaceous clay	Sterile
DB11-8	IIIa	55/8	Clay	218
DB11-9	IIIa	57/1	Silty clay	Sterile
DB11-10	IIIb	57/2	Silty clay	257
BK Trench 2 (2.9660°S, 35.3243°E)				
DB11-19	IVa	51/3	Silty clay	Sterile
DB11-20	IVb	51/4	Silty clay	132
DB11-21	V	51/5	Silty clay	147
Trench 14 (2.966083°S, 35.324250°E)				
DB11-13	–	57/3	Tuffaceous silt	79
DB11-14	–	57/4	Tuffaceous clay (green waxy vertisol clay with peds)	229
DB11-15	–	57/5	Clay, with carbonates (green waxy vertisol clay with peds)	125
DB11-16	–	57/6	Tuffaceous silt, under carbonate calcrete	320
DB11-17	–	57/7	Tuffaceous clay	312
DB11-18	–	57/8	Silty clay (green waxy vertisol clay with peds)	185
DB12-71	V	58/1	Waxy clay	51
DB12-72	–	58/2	Waxy clay	138
DB12-73	–	58/3	Silty clay	236



**Fig. 4.** Micrographs of phytoliths (A–F) and zeolites (G–H) found in samples from BK archaeological site, Olduvai Gorge. Phytoliths: A: Globular granulate; B: Saddle regular; C: Trapeziform short cell (trapezoid); D: Fan shaped bulliform cell; E: Elongate; F: parallelepiped/cubic/ovate (blocky) bodies with granulate surface. Zeolites: G: phillipsite; H: analcime.

pH influence the solubility of biogenic silica such as phytoliths start losing their surface decorations (Frayse et al., 2006; Cabanes et al., 2011; Cabanes and Shahack-Gross, 2015) or serve as nuclei for zeolite crystallization (Arráiz et al., n.d., 2017). In the BK paleosol samples, however, the zeolites we observed in large amounts are phillipsite and analcime (Fig. 4G–H). These zeolites are volcanic minerals (Hay, 1963), and their presence in BK samples is likely due to the erosion and sediment transport from the slopes of Lemagrut volcano located southeast of BK (Domínguez-Rodrigo et al., 2014). Phillipsite and analcime are the most common zeolites in fluvial deposits, while lake deposits are characterized by other zeolites such as clinoptilolite and chabazite (e.g. Hay and Sheppard, 2001; Mees et al., 2007). Also, unlike in the older Zinj paleosurface of Lower Bed I (1.84 Ma), we have rarely observed zeolitized phytoliths that could suggest phytolith dissolution due to alkaline soil conditions (Arráiz et al., n.d., 2017). There is also no apparent correlation between the abundance of zeolites and the abundance of unidentified and/or damaged phytoliths in the samples we analyzed here that would indicate phytolith dissolution or zeolitization. An allochthonous input of phytoliths from the highlands, however, cannot be excluded.

Phytolith assemblages of BK site are characterized by the abundance of the Forest Indicator category and very weak representation of grass silica short cells (GSSCs), which suggests that the paleovegetation of BK was dominated by trees and/or shrubs during deposition times. None of the BK samples analyzed had a sufficient number of globular granulate and/or of GSSC phytoliths to calculate the D/P index (Bremond et al., 2005) and, hence, quantitative comparison with modern samples was not carried out. Among the FI category, we note that most FI phytoliths are blocky bodies, and not the globular granulate and decorated phytoliths. Globular granulate phytoliths are exclusively produced by woody plants (in all plant parts including wood, bark, leaves), but some trees and shrubs species do not produce them at all (Collura and Neumann, 2016). For example, they are rarely found in the surface soils under Afromontane forests in East Africa (Barboni et al., 2007) and in temperate trees in general (Collura and Neumann, 2016). Blocky bodies are produced in many silica-rich African woody plants (e.g. Mercader et al., 2009), and some are diagnostic to species, e.g. the Blocky with irregular projections typical for *Kigelia africana* (Collura and Neumann, 2016). Unfortunately, when we carried out the phytolith analysis of the BK samples, such detailed information on the taxonomical resolution of blocky phytoliths as recently published by Collura and Neumann (2016) was not yet available to us to provide here a more detailed woody plant inference.

Among the grass silica short cells found at BK, the trapeziform short cells are the most represented. This is surprising in a tropical environment, because these morphotypes are generally found in present-day grass species with  $C_3$  photosynthetic pathways, such as those occurring at high elevation in the tropics and/or growing under permanent soil moisture in Africa today (Barboni and Bremond, 2009; Rossouw and

Scott, 2011; Cordova, 2013). Trapeziform short cell phytoliths are not observed in any of the surface soil samples analyzed so far from the Olduvai – Crater Highland – Serengeti – Eyasi – Manyara region (Albert et al., 2016; Arráiz, 2016). At Olduvai, trapeziform short cell phytoliths were observed in older paleontological sites from sedimentary Bed I, such as FLK N (Barboni et al., 2010) and Zinj sites (Ashley et al., 2010a; Arráiz et al., n.d., 2017). Several proxies have provided evidence for a densely wooded environment, and it is now established that patches of densely wooded (with trees and/or bushes) were occurring locally in the paleolandscapes in areas under the influence of groundwater (Ashley et al., 2010a, 2010b; Barboni et al., 2010; Arráiz et al., n.d., 2017), and this, despite the presence of  $C_4$ -savanna like vegetation at the landscape scale (Bonnefille, 1984; Cerling and Hay, 1986; Magill et al., 2013; Barboni, 2014). At BK, we found trapeziform short cell phytoliths, as well as fern and sedge phytoliths, and abundant FI. The abundance of trees and/or shrubs and of  $C_3$  helophytic grasses, ferns and sedges at BK 1.35 million years ago in a fluvial context is plausible despite a very arid climate. This reconstructed vegetation fits well with the paleoecological information from the avifauna remains found at BK, which suggest a low energy river with presence of trees and bushes near the river bank (M. Pernas-Hernández, pers. comm., 05/2016), and with the faunal assemblages from BK sites which indicate open grass-dominated vegetation at the landscape scale (Domínguez-Rodrigo et al., 2014; Organista et al., 2017). More generally, our paleovegetation reconstruction for BK site fits well with the low woodland paleoenvironments inferred from the mammal fauna throughout Bed II (Kovarovic et al., 2013).

The results reflect a vegetation that fits well with the geological reconstruction of BK. The sedimentary environment in which BK was formed was a low energy alluvial system with alternating distributary channels (chute-channels) and low energy interchannel areas (Domínguez-Rodrigo et al., 2014). The whole system evolved into a final phase in which the fluvial channel was filled with sediments (silting phase). Sediments from Trenches 1 and 2 were sampled in the point-bar, where chute-channels eroded and mobilized fine sediments due to water traction. The chute-channels alternated with small interfluvies where fine sediment was retained, allowing the development of soil and vegetation (as seen in a modern river, Fig. 2A). This alternation may explain the occurrence of sterile samples (DB11-3, 4, 6, 7, 9, and DB11-19) near productive samples. On the contrary, Trench 14 was located in the river channel but in a more evolved state in which floodplain sediments (silts and decantation clays) accumulated. This low energy system retained humidity and allowed the development of deep and mature soils.

Paleo-lake Olduvai was a playa lake. It therefore changed in size seasonally but also according to longer term precessional cycling, which determined its maximum size (Ashley, 2007). BK was formed during a dry period when Olduvai paleolake had almost disappeared (Hay, 1976; Kovarovic et al., 2013; Garrett, 2017). Today, such arid conditions

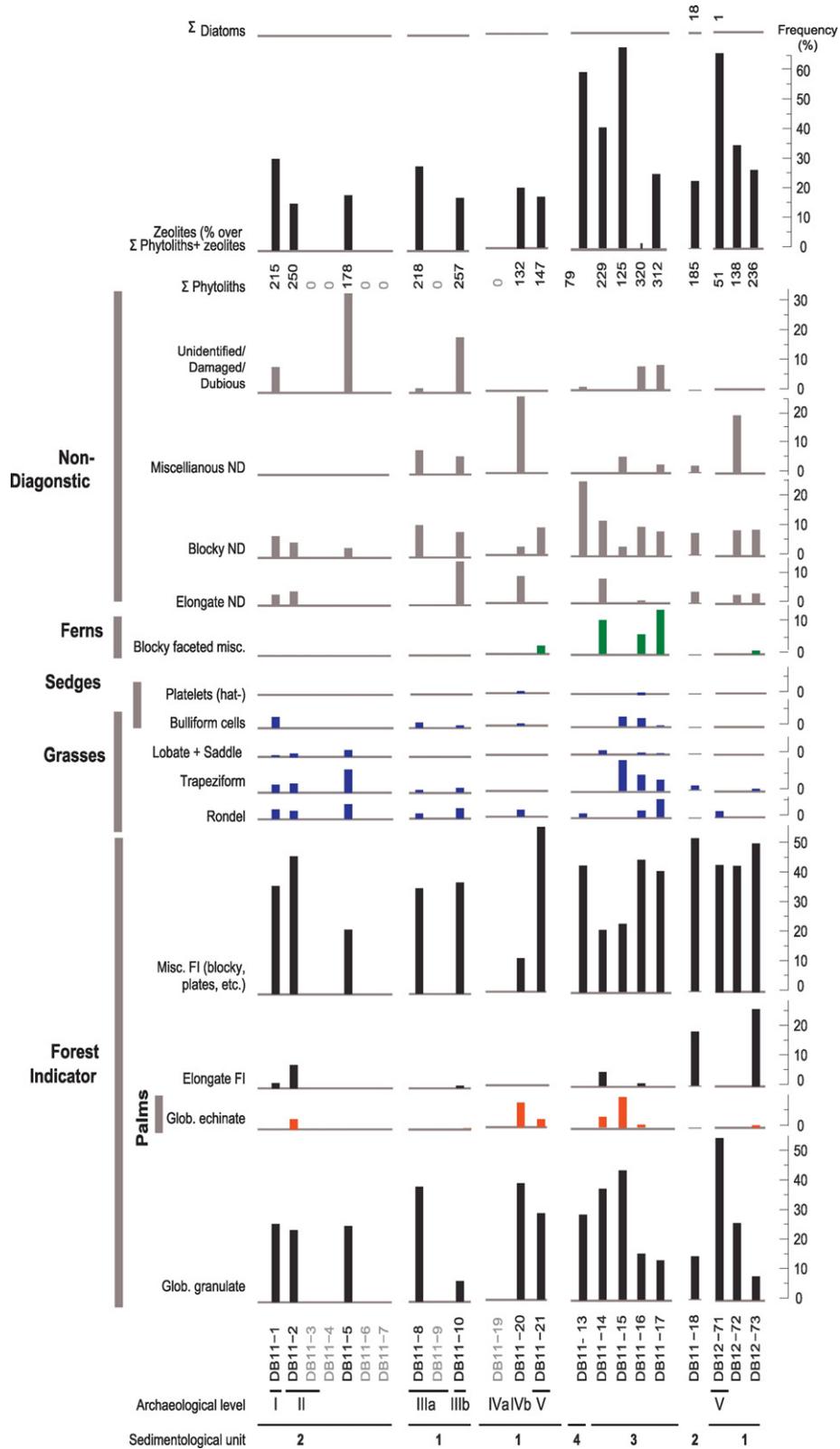


Fig. 5. Relative abundance (in percentage) of phytolith main morphological categories in samples from the BK archaeological site, Olduvai Gorge, Tanzania.

prevail in the area and the vegetation is dominated by short and medium grasslands with *Sporobolus* and *Digitaria* species in the Serengeti Plains, *Acacia* – *Commiphora* bushlands in the lower slopes of the Crater Highlands (Herlocker and Dirschl, 1972). Near the playa Lake Manyara, the alkaline grassland contrasts with the woody vegetation accompanying the perennial streams, which drain into the lake. The

riparian forests include medium size trees of e.g. *Warburgia ugandensis*, *Syzygium guineense*, *Ekebergia capensis*, *Croton macrostachyus*, *Tamarindus indica* or *Trichilia roka* (Greenway and Vesey-Fitzgerald, 1969; Loth and Prins, 1986). The abundance of woody plants at BK site is therefore plausible given the riparian context and despite the arid climate.

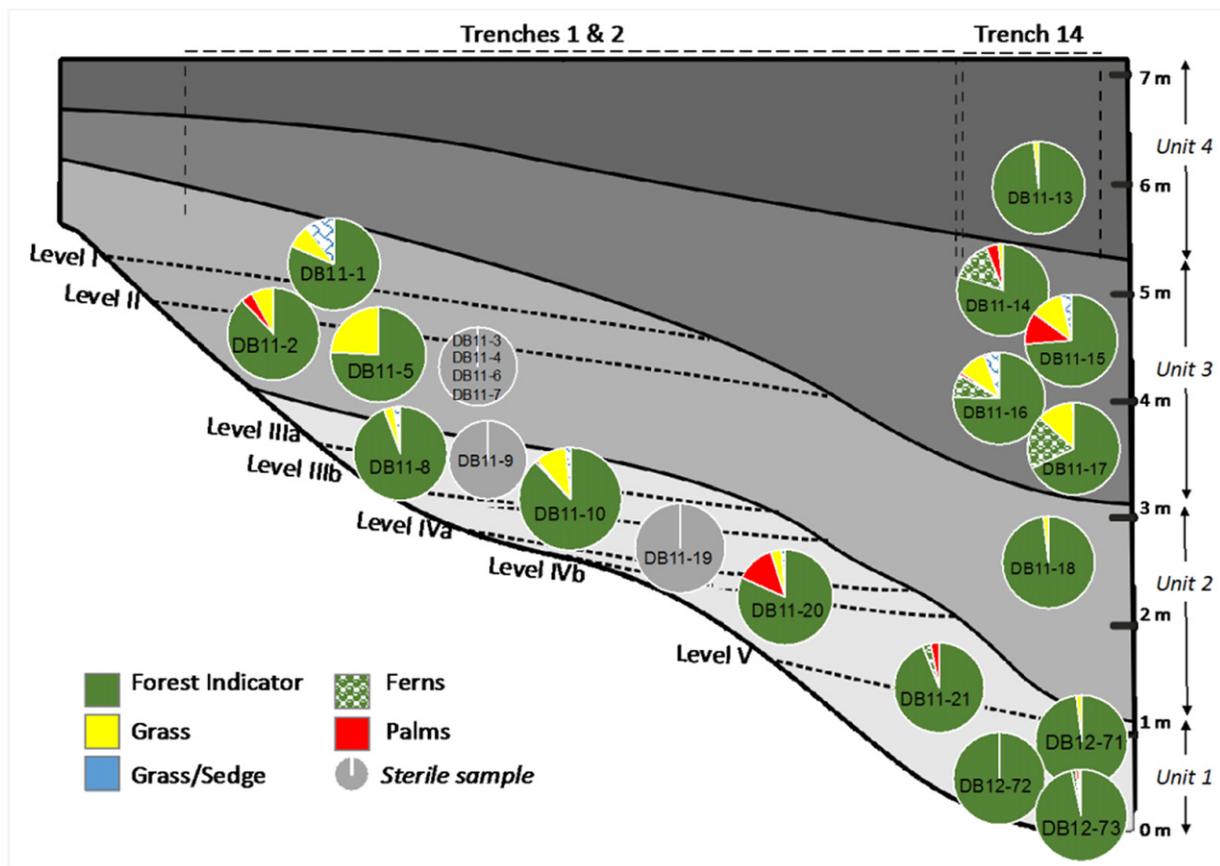


Fig. 6. Relative abundance of phytoliths grouped by botanical attribution shown here as pie diagrams placed according to the stratigraphic position of the samples in archaeological Trenches 1, 2, and 14 at BK site, Olduvai Gorge, Tanzania.

BK phytolith assemblages also indicate the presence of palms. Palms in riparian settings occur today along several seasonal rivers in the Serengeti Plains, and near Lake Manyara and Lake Eyasi. Albert et al. (2015) analyzed several samples from these areas and found that palms are under-represented in surface soil phytolith assemblages, in which globular echinate phytoliths rarely account for >10%. Arráiz (2016) found that globular echinate phytoliths represent up to 30% in the northeastern side of lake Eyasi where *Hyphaene* are dominant in the vegetation. Bremond et al. (2005) found the highest percentage of globular echinate phytoliths in a surface sample from a *Raphia* swamp in Cameroon. Although more studies are needed, this comparison suggests that, like for bulliform cells in grasses, the mass of phytoliths produced by palm trees may be correlated with the rate of evaporation (i.e. the amount of water passing through the plant). At a given evaporative demand, the more water is available at the root level, the more silica is accumulated in the leaves (Issaharou-Matchi et al., 2016). We hypothesize that this pattern may be particularly true for monocotyledons like palms (Arecaceae), grasses (Poaceae) and sedges (Cyperaceae). In the BK samples, globular echinate phytoliths represent <10%, like in modern dry land soil samples. Yet, a transfer function between the percentage of globular echinate phytoliths and the abundance of palms in the paleovegetation cannot be given, first, because too few modern studies are available for calibration, and second, because the function may be biased by the water availability at the root level, as explained here above.

In a generally dry period, the presence of woody riverine vegetation, which provides resources (e.g. fruits of tamarind tree are edible) and refuge, and a river, which provides freshwater, suggest that BK acted as an attractor to hominins and other animals. Yet, rivers were probably seasonal, and surface water may only have been readily available during the wet season, while digging would have been required during the dry

season to access water below the surface in the river bed (see modern example in Fig. 2B). In BK, as well as in other sites in Olduvai Gorge (e.g., sites of Zinj Complex, Uribealrrea et al., 2014; Domínguez-Rodrigo and Cobo-Sánchez, 2017), a large number of bones exhibit percussion marks and cut marks. These bone remains are associated with large assemblages of stone tools. All these data suggest primary access to fleshed carcasses by hominins. BK has been described as an anthropogenic site created by butchering activities over time (Diez-Martín et al., 2009; Domínguez-Rodrigo et al., 2009; Egeland and Domínguez-Rodrigo, 2008; Organista et al., 2017). Level IVb in BK has been interpreted as a site in which hominins carried out butchering activities. The outstanding amount of raw lithic material seems to exceed the amount necessary to produce the tools for butchering. Thus, in level IVb, other hominin activities besides butchery (e.g. digging?) may have been carried out (Domínguez-Rodrigo et al., 2014). As observed for anthropogenic sites of Lower Bed I, such as those of the Zinj complex (FLK Zinj, PKT, and DS sites, dated 1.84 Ma), it appears that dense vegetation together with freshwater (river or groundwater spring) were powerful environmental triggers for animals and hominins (e.g. Arráiz et al., n.d., 2017; Ashley et al., 2010a; Barboni, 2014).

## 5. Conclusions

Despite the fact we studied 22 samples, the data we provide here give some information regarding the evolution of vegetation through time but in a very localized area and very specific riverine environment. This analysis is not meant to provide a landscape scale reconstruction of the paleovegetation of the site around 1.34 Ma. Our phytolith results from BK site reflect a vegetation clearly dominated by woody plants (trees, and most likely shrubs). This riparian vegetation corresponds

to the environment that formed BK, which deposits represent a low energy alluvial system with alternating distributary channels and low energy inter-channel areas. The vegetation of BK did not change significantly over the time under scrutiny here around 1.34 Ma. Given the arid climatic context at that time, it is very unlikely that the wooded area inferred here was extensive. Rather, BK site was formed within a gallery forest or riparian woodland, while the surroundings were likely dominated by sparse/open grass-dominated vegetation.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2017.05.010>.

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