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Alpine grassland palaeoecology of the Virunga Volcanoes, East Africa: A new phytolith record from Mt. Muhavura

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ABSTRACT

This study presents a first attempt at using phytoliths from a high-altitude crater lake as a palaeoecological tool at a tropical montane site. Mt. Muhavura (4127 m asl) at the border of Uganda and Rwanda is part of the Virunga volcanoes located in the Albertine Rift, one of the most biodiverse areas in Africa. To investigate the potential of phytoliths to record grassland history in an Afroalpine environment, a unique and little studied ecosystem, we analysed the phytolith content of 37 sediment samples from a 159 cm sediment core from the crater lake at the summit of Mt. Muhavura representing the last ca. 2400 years BP. Ten plant species from the Alpine belt were also analysed for their main phytolith morphotypes. Phytoliths from the sediments were grouped into 12 main categories and the most frequently occurring individual morphotypes were bilobate (33%), oblong (16%), elongate (17%) and globular psilate (13%). The phytolith assemblage consists predominantly of phytoliths characteristic of grasses (70%). A literal interpretation of the results would be that Panicoideae grasses (mainly C_4) that are characteristic of warm and wet climate and C_3 Pooideae subfamily grasses characteristic of cold climate/high altitude have co-existed throughout the late Holocene in this belt. As only C_3 cold climate grass subfamilies are known to occur at this altitude today, the abundance of short cell phytoliths (bilobates) typical of Panicoideae grasses in the lake sediments at this altitude presents a new perspective to the phytolith discussion. The C_3 Pooideae grasses analysed did not produce bilobates. In this study, the phytolith index, Ic that is used as a proxy of past grass subfamily dominance is not representative of the taxonomic significance for which it is known. This study suggests that caution needs to be taken when using bilobate morphotypes and the Ic as indicators of grass subfamily dominance at high altitude on East African mountains as the bilobates may not be taxonomically representative of the grasses for which they are typically known. This highlights the inherent problem of phytolith redundancy even at an altitude where C_3/C_4 grass distribution is better delineated.

1. Introduction

Several pollen-based studies in East Africa have presented evidence of natural vegetation change during the early Holocene and of both natural and human-induced changes during the late Holocene. They particularly indicate vegetation changes due to a general transition from warm and wet climatic conditions in the early to mid-Holocene to drier conditions in the late Holocene (e.g. Taylor, 1990, 1992; Bonnefille and Mohammed, 1994; Umer et al., 2007; Rucina et al., 2009; Finch and Marchant, 2011; McGlynn et al., 2013). In Uganda, several studies have reported aridity-induced environmental changes over the last ca. 2000 years, although most are often also linked to forest clearance (e.g. Taylor, 1990; Taylor et al., 1999; Lejju et al., 2005; Ssemanda et al., 2005; Russell et al., 2007; Lejju, 2009). At medium altitudes, pollen and charcoal records have provided evidence of environmental change in montane sites of south western Uganda that attest to a long period of human impact and vegetation change during the late Holocene (e.g. Taylor, 1990, 1992; Marchant and Taylor, 1998). Anthropogenic activities and their impacts on the vegetation during the last two millennia have also been reported at high altitude in East Africa on

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mountains such as Mt. Kenya (e.g. Rucina et al., 2009) and on the little-studied Virunga volcanoes (McGlynn et al., 2013).

In recent decades, palaeoecological research has been conducted on East African mountain ecosystems to understand their response to past climatic changes (e.g. Livingstone, 1967; McGlynn et al., 2010 (Rwenzori Mountains, Uganda); Thompson et al., 2002; Schüler et al., 2012 (Mt. Kilimanjaro, Tanzania); Street-Perrott et al., 1997; Olago et al., 1999; Karlen et al., 1999; Wooller et al., 2000; Barker et al., 2001; Ficken et al., 2002 (Mt. Kenya); Mumbi et al., 2008; Finch and Marchant, 2011; Finch et al., 2014 (Eastern Arc Mountains, Tanzania)). Despite the many records documenting ecosystem response to past environmental changes in East Africa, uncertainty remains regarding how vegetation has varied during the last two millennia, especially at high altitude, as most pollen and charcoal studies do not clearly elucidate this period (Lamb et al., 2003). Furthermore, studies in East Africa often concentrate on longer time scales that deal with wide-scale regional transitions in vegetation and climate and rarely with local plant community transitions. This is largely because pollen, the most commonly used palaeoecological tool, usually provides a broader regional record. As a result, vegetation response to short term climatic variability in the recent past of East Africa is poorly understood and yet such knowledge would be of great relevance for land-use management and conservation policy (Lamb et al., 2003).

Phytoliths are a more apt tool to reconstruct past local plant communities because they generally do not undergo aerial transportation and are normally deposited in sites close to the parent plant (Pearsall, 2000; Wallis, 2001). Phytoliths are microscopic silica bodies that are produced within and between plant cells when plants absorb soluble silica during water uptake (Carter, 1998; Lu and Liu, 2003). When plants die, the organic material decomposes, releasing the inorganic phytoliths directly into the soil, creating an *in situ* record of the vegetation cover of the plants that produced them (Lu and Liu, 2003). Phytoliths are produced in many plant families but are distinctive and abundant in the grass family, a major component of Afromontane vegetation. Unlike pollen analysis and carbon isotope analysis of organic matter, that are unable to distinguish between different types of grasses, phytolith analysis can to some extent identify the grass family to the subfamily level. Phytoliths can distinguish C_3 grasslands (high altitude/cold climate grasses of the subfamily Pooideae that use C_3 photosynthesis) from C_4 grasslands and distinguish between C_4 grasslands dominated by C_4 warm humid climate grasses (grasses of the subfamily Panicoideae) and those dominated by C_4 warm dry climate grasses (the subfamily Chloridoideae) (Twiss, 1992; Barboni et al., 1999; Piperno, 2006; Bremond et al., 2008). However, because of issues of multiplicity (the production of several different phytolith forms within a single plant species) and redundancy (similar phytolith forms being produced by several plant species), it is difficult to assign a definite taxonomic classification to a specific morphotype (Rovner, 1971). For example, in East Africa, some grass species of the subfamily Chloridoideae were found to produce rondels and did not produce the saddle type that is typical of this subfamily (Bamford et al., 2006; Barboni and Bremond, 2009). In addition, bilobates that are typical for the subfamily Panicoideae are also produced in some grass species of the subfamilies Pooideae, Bambusoideae, Arundinoideae (Twiss, 1992; Piperno and Pearsall, 1998; Rossouw, 2009; Mercader et al., 2010) and Danthonioideae (Watson and Dallwitz, 1992; Reimer and Cota-Sanchez, 2007; Rossouw, 2009; Cordova and Scott, 2010). Arundinoideae and Bambusoideae grasses are the most redundant of the five main grass subfamilies, producing nearly all of the morphotypes that are typical for the Pooideae, Panicoideae and Choridoideae grass subfamilies (Kondo et al., 1994; Piperno and Pearsall, 1998; Bremond et al., 2008).

In East Africa, few studies have used phytolith analysis for palaeoenvironmental reconstructions – existing examples are from Kenya (Maitima, 1997), Tanzania (Albert et al., 2006; Bamford et al., 2006; Barboni et al., 2010; Rossouw and Scott, 2011; Albert and Bamford, 2012) and Uganda (Lejju et al., 2005; Lejju, 2009). However, no study has yet attempted to use phytoliths as a palaeoecological tool on tropical African mountains at the altitude presented here. Various studies on East African mountains indicate that different environmental factors such as temperature, water availability and elevation influence the distribution of grass subfamilies on these mountains, with temperature being the most important determinant of the occurrence of C_3 and C_4 grasses (Tieszen et al., 1979; Livingstone and Clayton, 1980; Young and Young, 1983). For this reason, almost no C_3 grass species occur below 2000 m asl and no C_4 grasses occur above 3000 m asl (all heights are given in metres above sea level). At high altitudes, the response of grass flora to environmental changes is more accurately detected because of the sensitive nature of the grasses to temperature compared with low altitude areas in East Africa (Livingstone and Clayton, 1980). Therefore, plant microfossils that are not carried over long distances might be able to provide local palaeotemperature estimates, as the more insensitive low altitude grasses would not make the fossil record ambiguous (Livingstone and Clayton, 1980).

Mountain vegetation is particularly sensitive to climate change and is a rich source of biodiversity that needs to be monitored to avoid extinction of plant and animal species that survive in such environments (Court-Picon et al., 2007). The shifting snowlines on East African mountains are indicative of the sensitive nature of these mountains to register past environmental shifts (Rucina et al., 2009). Palaeoecological research has shown that such sensitivity to environmental changes on mountains such as Mt. Kenya and Mt. Rwenzori allows us to understand the impact of natural drivers on climate and vegetation as well as human induced impacts over long time scales (Karlen et al., 1999; McGlynn et al., 2010). More recently, rapid glacial retreat over the 20th century has been observed on the Rwenzori Mountains within the Albertine Rift in western Uganda (Hemp, 2005; Taylor et al., 2007) and Mt. Elgon in eastern Uganda has in recent times undergone massive landslides (Claessens et al., 2007) indicating a change in regional environmental conditions. Because human activity is largely absent at such high altitudes, mountains provide an opportunity to study non-anthropogenic drivers of environmental change. The Virunga volcanoes are located within the Albertine Rift – one of the most important conservation areas in Africa, containing more vertebrate species than any other region on the continent with the highest vertebrate endemism in mainland Africa, and which is home to endemic and globally threatened species such as the mountain gorilla (Plumptre et al., 2007). The Virunga volcanoes are of great importance in regional hydrology and ecosystem services, which currently support livelihoods in the surrounding areas (Kalina, 1993; Lejju, 1999). Until recently, no attention has been paid to the long-term environmental history of the Virunga volcanoes, compared with other mountains in East Africa and yet they are part of current major global conservation efforts. A pollen study in the Virunga volcanoes has provided evidence of the natural impact of increasing aridity on the vegetation at higher altitudes over the last 4500 cal BP and human impact on vegetation at lower elevations on these mountains is more pronounced ca. 900 cal BP (McGlynn et al., 2013).

Here we present a new phytolith record, the first at this elevation in Africa, that provides insights into past grassland composition in the grass-dominated Alpine belt of Mt. Muhavura. This study tests the potential of phytoliths to reconstruct grassland history in the Alpine belt and infer associated environmental conditions. The study set out to; a) examine if phytoliths occur in sufficient

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amounts in the alpine lake sediments, b) explore their distribution in the sediment profile and attribute them to specific plant taxa found at the site and c) establish the type of phytoliths found in selected alpine plants. In this study, 37 sediment samples from an alpine lake and ten alpine plant species were analysed for their phytolith content to study the phytoliths characteristic of alpine grassland and document their potential to reconstruct the vegetation history of this mountain.

2. Description of study area

2.1. Geographical setting

The Virunga volcanoes are a chain of eight volcanoes in East and Central Africa along the borders of Uganda, Rwanda and the Democratic Republic of the Congo (DRC) (Fig. 1), located in the western arm of the East African Rift Valley (the Albertine Rift). In Uganda, they are located within Mgahinga Gorilla National Park (MGNP) in Kisoro district in south-western Uganda (Fig. 1). MGNP consists of the northern slopes of three volcanoes, all of which are extinct: Mt. Muhavura (4127 m) and Mt. Gahinga (3475 m) shared between Uganda and Rwanda, and Mt. Sabinyo (3635 m) at the borders of Uganda, Rwanda and the DRC (Fig. 1). The park is located at the edge of the Albertine Rift at latitude 1° 23′ S and longitude 29° 39′ E, with terrain ranging from gentle slopes at lower elevations (2227 m) to steep slopes at high altitudes (4127 m) (Lejju, 2004). Mgahinga Gorilla National Park in Uganda is contiguous with the Volcanoes National Park in Rwanda and Virunga National Park in the Congo forming a much larger ecosystem, the Virunga Conservation Area, that covers about 430 km^2 (Bygott and Hanby,

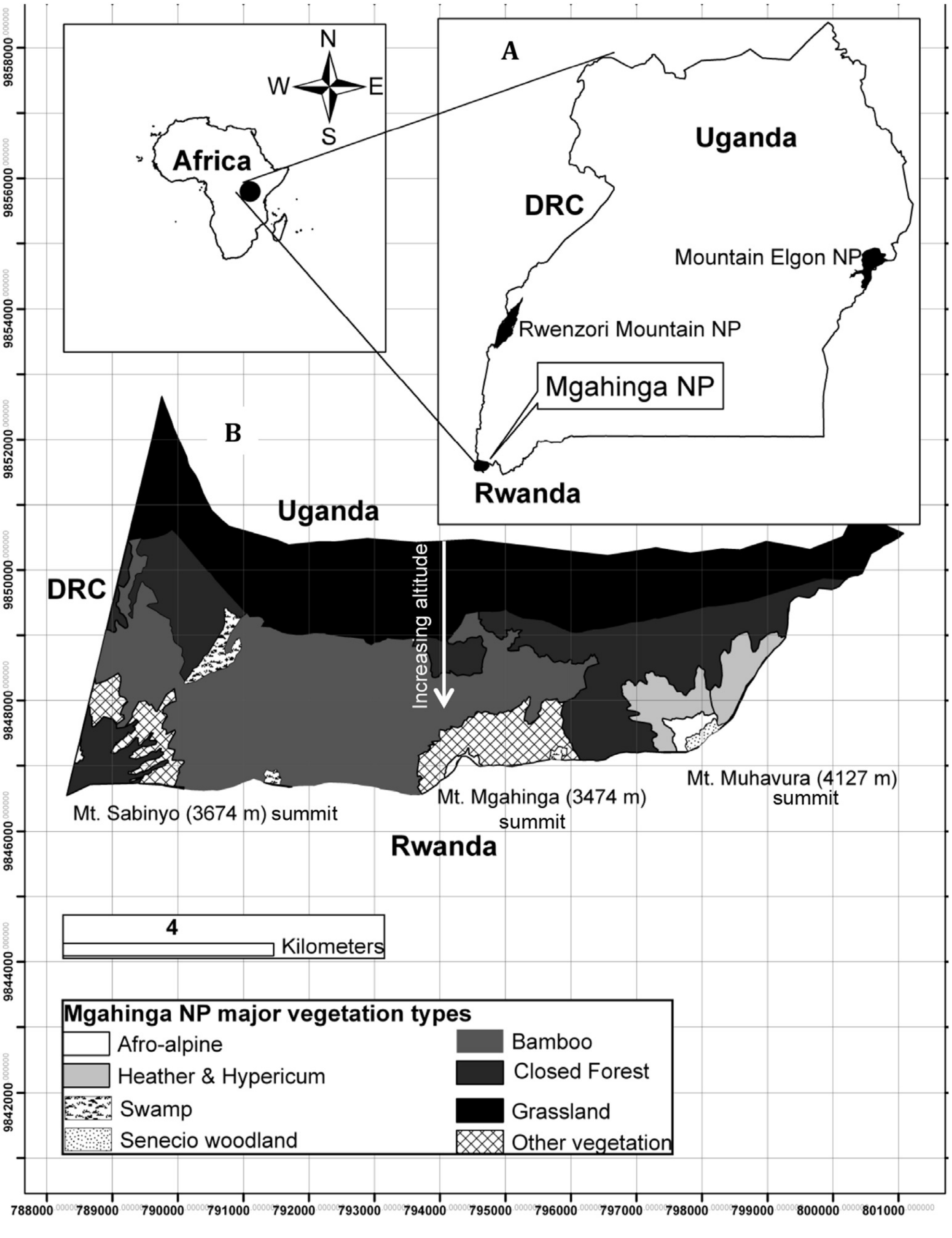

Fig. 1. Map of Uganda showing the location of Mgahinga Gorilla National Park (MGNP), other mountain parks and the vegetation map of MGNP showing from mountain base to summit the vegetation types found on the three volcanoes; Sabinyo, Gahinga and Muhavura.

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1998). Mt. Muhavura, the focus of this study, lies partly in MGNP in Uganda and Volcanoes National Park in Rwanda. Mt. Muhavura is shaped as an almost perfect cone (Fig. 2) with a small, shallow and almost circular crater lake at its summit (1° 23.0′S, 29° 40.7′ E, 4127 m asl) (Fig. 3b). The lake is approximately 25 m in diameter with a maximum water depth of 1.6 m.

2.2. Modern climate

The park lacks continuous climatic records and those that are available are very recent. Existing data indicates that the Virunga volcanoes generally receive higher rainfall than the surrounding plains (Cunningham et al., 1993). Day temperatures in the Virunga volcanoes are reported to range from about 4 °C at the highest elevation (4127 m) to 18 °C at the lowest elevations (2381 m) (Lejju, 1999). Situated almost on the equator, there is little difference in day length and annual mean temperature throughout the year, but the monthly rainfall and day–night temperatures vary considerably. The rainfall pattern in the area is characterised by two wet seasons (March–April and October–December, coinciding with the equinoxes) and two dry seasons each year (January–February and May–August, coinciding with the solstices) with an average rainfall of 1650 mm per year in MGNP (Adams and Infield, 1998). The climate of the Afroalpine belt (usually above 3600 m) on East African Mountains is that of nightly frosts and intense sunshine during the day throughout the year (Hedberg, 1970).

2.3. Modern vegetation

The mountains in this region have a marked altitudinal zonation (Fig. 2) common to mountains in tropical Africa creating similar vegetation belts that may have variations among them due to differences in local factors (Hedberg, 1951; Livingstone and Clayton, 1980). From the base of Mt. Muhavura is the Montane Forest Belt, followed by the Subalpine/Ericaceous Belt and finally the Afroalpine Belt at the top (Fig. 2). Some of the belts are split into different zones according to their dominant plants (Kalina, 1993; see Fig. 1).

The Montane Forest Belt (ca. 2380 m–3000 m, Fig. 2) consists of the montane woodland zone (represented by Closed Forest in the legend in Fig. 1), the *Hagenia-Hypericum* zone and the bamboo zone with the montane woodland zone as the lowest vegetation zone of Mt. Muhavura within once cultivated grassland (Fig. 1; Kalina, 1993; Lejju, 2004). The montane woodland zone is characterised by the grasses *Pennisetum clandestinum*, *Hyparrhenia* sp. and *Eragrostis lasiantha* among others and at higher altitudes shade-loving grasses such as *Panicum adenophorum*, *Digitaria uniglumis*, *Pennisetum trachyphyllum and Setaria orthosticha* (Snowden, 1933). Planted woodlots of exotic species are concentrated at the boundary of the park within the local community. Forest regeneration is observed in the lower montane forest belt (Lejju, 1999, 2004). This zone is followed by the *Hagenia-Hypericum* zone where the temperate genera of grasses include: *Festuca*, *Bromus*, *Calamagrostis* and *Avenastrum*. Other grasses include: *Hyparrhenia mobukensis* covering a large area on Mt. Muhavura, *Andropogon amethystinus* (prelevant at high altitudes up to 3350 m), *Pennisetum* spp., *Panicum* spp. and less frequently *Eleusine jaegeri* (Snowden, 1933). The bamboo (*Sinarundinaria alpina*) zone exists at higher elevations of the Montane Forest Belt in the Virunga Volcanoes (Lejju, 2004; Fig. 2) and according to Snowden (1933), it is almost absent from Mt. Muhavura but it is reported to reach 2900 m on western Muhavura (Bussmann, 2006).

The Subalpine/Ericaceous Belt (3000 m–3600 m, Fig. 2) consists of the ericaceous zone that marks the cessation of trees and bamboos and an increase of ericaceous shrubs (heath) up to 3700 m (Bussmann, 2006). It is represented by the 'Heather and Hypericum' vegetation types in Fig. 1, and is characterised by the Ericaceae shrubs of *Erica arborea* and *Philippia johnstonii*. Dominant grass species are *Andropogon amethystinus*, *Festuca abyssinica* and *Poa* spp. On the dry eastern escarpment of Mt. Muhavura, the *Hagenia* forest is replaced by Afroalpine grassland with no ericaceous shrub as on the more humid western slope (Bussmann, 2006).

The Subalpine Belt is then followed by the Alpine Belt (3600 m–4127 m, Figs. 1 and 2, partly shown in Fig. 3b at the summit) which shows less plant diversity and is characterised by mosses, *Alchemilla* and grasses as the main ground cover, while giant *Senecio* and *Lobelia* are the two dominant shrubs rising above the ground (Snowden, 1933; Kalina, 1993; Lejju, 2004). In the vegetation map (Fig. 1), this belt is represented by 'Afroalpine' and '*Senecio* woodland' vegetation types. Important non-grass species in this zone are *Senecio alticola*, *Lobelia wollastonii*, *Helichrysum* spp., *Swertia* spp. and *Luzula volkensii* (Snowden, 1933). Grasses found here are *Festuca abyssinica*, *Poa annua*, *Poa leptoclada*, *Deschampsia flexuosa*, *Deschampsia ruwenzorensis* and *Anthoxanthum nivale* (Snowden, 1933; Lejju, 1999) all belonging to the C_3 subfamily Pooideae (Watson and Dallwitz, 1992). At the top of this belt is the crater lake from which the sediment cores for this study were taken and it is presently surrounded by grasses and a few stands of other Afro-alpine vegetation such as *Lobelia* spp. (Fig. 3b).

3. Materials and methods

3.1. Sediment coring, physical analysis and chronology

Sediment cores were extracted from the crater lake at the summit of Mt. Muhavura in July/August 2008 using a Renberg

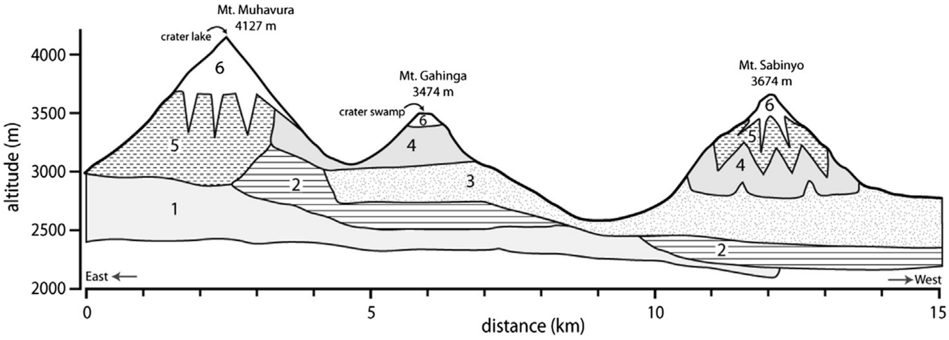

Fig. 2. Vegetation zonation of the northern slopes of the three easternmost Virunga Mountains (Mts. Muhavura, Mgahinga and Sabinyo): 1 = Regenerating montane woodland (former farmland); 2 = Montane woodland (lower montane forest); 3 = Bamboo; 4 = Hagenia/Hypericum zone (Upper montane forest) 5 = Ericaceous/subalpine vegetation; 6 = Afroalpine.

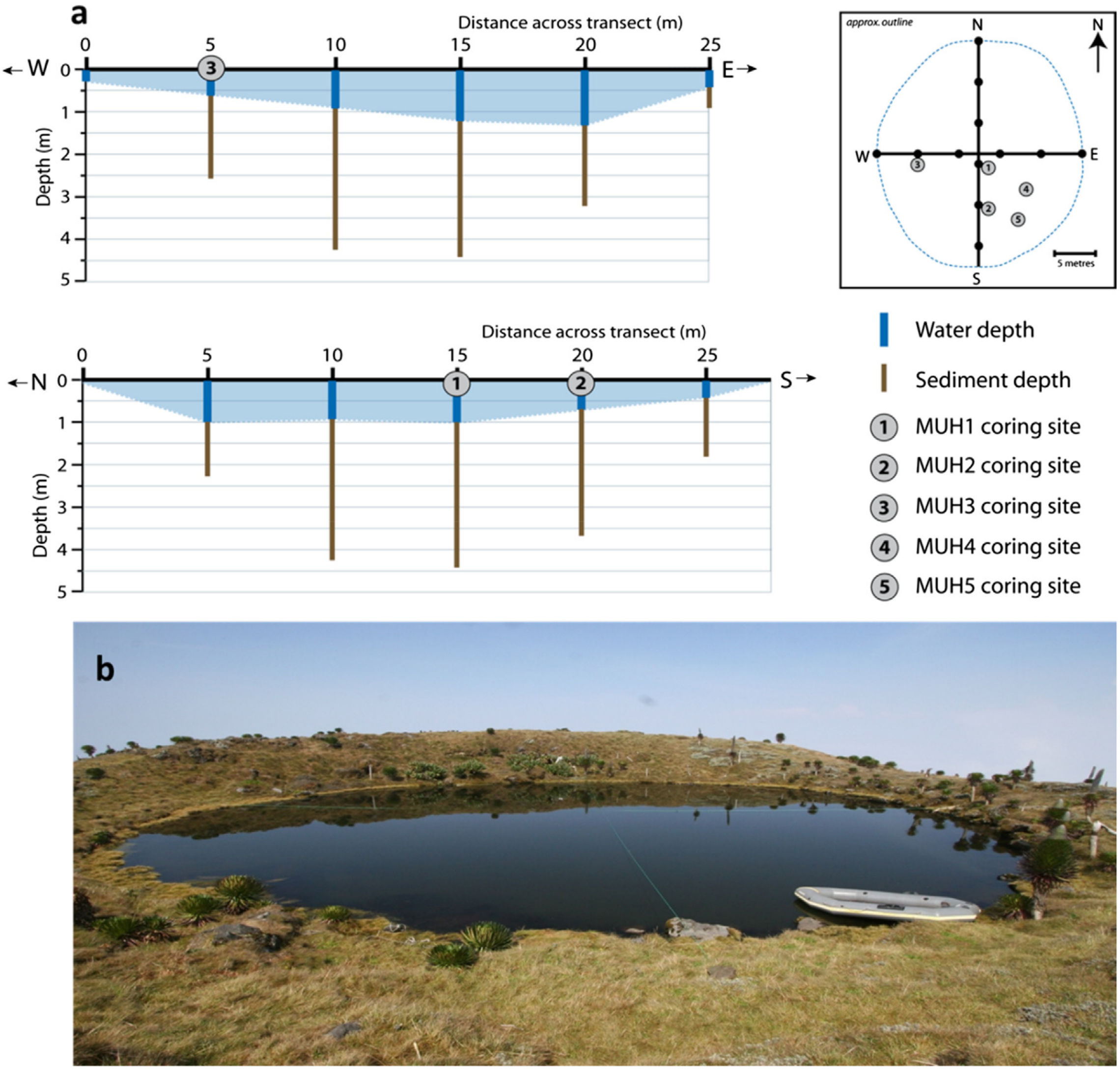

Fig. 3. (a) Bathymetry showing the distances on transects along the diameter of the lake where the cores MUH3 and MUH5 (this study), MUH2 and MUH4 (McGlynn et al., 2013) were taken from. (b) The crater lake at the summit of Mt Muhavura (1° 23.0′S, 29° 40.7′ E, 4127 m asl).

gravity corer for the upper most section of the lake sediments and a modified Livingstone piston corer for the deeper, more consolidated sediments, consisting of two contiguous cores forming the core MUH3 (50–159 cm). The topmost sediments (0–24 cm, MUH5) were extruded in 1 cm increments into labelled zip-lock bags in the field immediately after extraction from the lake while the deeper sediments were wrapped in clingfilm and aluminum foil following extrusion as whole cores, and transported to Mbarara University of Science and Technology for storage and analysis. Their physical properties were described following the Troels-Smith system (Troels-Smith, 1955; Fig. 6). A total of 37 sediment samples at intervals varying between 1 cm and 5 cm were analysed for their organic matter and phytolith content in this study.

The amount of organic and inorganic matter in the sediment profile for the consolidated sediments was determined by percentage loss on ignition (% LOI) technique described in Heiri et al. (2001). The chronology of the core is roughly estimated from the age of a well-dated core, MUH2, from the same lake (McGlynn et al., 2013) by matching the cores' stratigraphy and % LOI. The cores were taken approximately 8 m apart in the 25 m diameter crater lake (Fig. 3). The homogenous organic-rich sediments in both core sequences had a conspicuous brown layer towards their base and both points are marked by a sharp decline in % LOI (Fig. 6). In MUH2, this point is estimated to date ca. 2400 cal yr BP (McGlynn et al., 2013). Another decline in % LOI is observed towards the top of both cores although it is less marked in the core for this study.

3.2. *Phytolith analysis: modern alpine plants*

Leaf blades from ten plant species comprising of five families from the Alpine Belt of Mt. Muhavura were analysed for their phytolith types only. Table 1 shows the plant species analysed and their photosynthetic pathway (Boom, 2004). The four grass (Poaceae) species were identified as *Poa annua*, *Deschampsia flexuosa*, *Festuca abyssinica*, *Agrostis* sp., all belonging to the C_3 subfamily Pooideae. The non-grasses consisted of six species belonging to four families: *Luzula abyssinica* (Juncaceae), *Luzula johnstonii* (Juncaceae), *Ranunculus oreophytus* (Ranunculaceae), *Helichrysum formossisimum* (Asteraceae), *Romulea congolensis* (Iridaceae) and *Dendrosenecio* sp. (Asteraceae). The plants analysed are herbaceous apart from the *Dendrosenecio* sp., which is arborescent. They provided a reference collection that to some extent aided identification and association of phytoliths in the sediment profile.

Table 1
Plant species sampled in the Alpine belt with their photosynthetic pathway (Boom, 2004).

Family and subfamily	Species	C_3/C_4
Poaceae		
Pooideae	*Poa annua*	C_3
Pooideae	*Deschampsia flexuosa*	C_3
Pooideae	*Festuca abyssinica*	C_3
Pooideae	*Agrostis* sp.	C_3
Juncaceae	*Luzula abyssinica*	C_3
Juncaceae	*Luzula johnstonii*	C_3
Ranunculaceae	*Ranunculus oreophytus*	C_3
Asteraceae	*Dendrosenecio* sp.	C_3
Asteraceae	*Helichrysum formossisimum*	C_3
Iridaceae	*Romulea congolensis*	C_3

Phytolith extraction from the modern plants followed the wet oxidation method described in Pearsall (2000). Each specimen was washed in liquid soap and rinsed several times with distilled water. Organic material was digested by adding about 20 ml concentrated nitric acid to the samples and placing them in a hot water bath for about 2–3 h until all the organic material was dissolved (solid potassium chlorate was added as a catalyst). Samples were then centrifuged at 2000 rpm for 10 min, decanted and rinsed thrice with distilled water and the residue was mounted onto microscope slides, oven dried and made permanent using DPX. Phytoliths formed in plant tissues were viewed using a light microscope at ×400 and ×1000 magnification and photographs taken using a Panasonic DMC-F3 digital camera. The main phytolith morphotypes found in the plants analysed are shown in Fig. 4.

3.3. Phytolith analysis and counting: lake sediments

Phytolith morphotypes were extracted following standard procedures described in Pearsall (2000) and Piperno (2006). The procedure involved treating approximately 3 g of sediment with 10% hydrochloric acid in a hot water bath to remove carbonates, washing in distilled water by centrifuging and decanting. Organic matter was removed from the samples by adding 30% hydrogen peroxide and placing in a hot water bath. Samples were sieved through a 250 μm sieve and clay-size particles were removed by gravity sedimentation. The final residue containing phytoliths and diatoms was placed on microscope slides and placed in an oven to dry and then made permanent using DPX. Phytoliths were counted using a Zeiss CP-achromat light microscope at ×400 magnification. Abundances were estimated by scanning the whole slide to make an approximation of only the main taxonomically important phytolith types. Known phytoliths that are present in the sediments but were not counted are the acicular hair cells/trichomes, stomata and parallelepiped bulliform (Madella et al., 2005). This is because they are not of major taxonomic importance and/or because they are common in grasses which were already over represented by various morphotypes diagnostic of the whole grass (Twiss et al., 1969; Piperno, 1988; Stromberg, 2003). Selected morphotypes are shown in Fig. 5 and the relative abundance (%) of the main phytolith morphotypes counted is graphically represented in Fig. 6.

3.4. Phytolith classification

Phytolith morphotypes typical of Poaceae were classified according to the classifications of Twiss et al. (1969), Twiss (1992), Alexandre et al. (1997), Carnelli et al. (2004), Piperno (2006), Barboni and Bremond (2009) amongst others, while other phytoliths were classified according to Runge (1999), Albert et al. (1999) and Piperno (2006). They were named according to the ICPN Working Group of Madella et al. (2005). Detailed descriptions of each morphotype were presented in Murungi (2013). Table 2 shows the main phytolith categories and their taxonomic attributions as deduced for this study. Table 3 shows the estimated count data of the main phytolith morphotypes observed.

Table 2
Main phytolith morphotypes identified in the Mt. Muhavura sequence and the taxonomic attributions deduced for this study.

Morphotypes	Taxonomic attribution for this study	Main references
Cross, bilobate, cylindric polylobate (lobates)	Arundinoideae/Danthonioideae, Ehrhartoideae grass subfamilies	Twiss 1992; Piperno and Pearsall, 1998; Mercader et al., 2010; Novello et al., 2012
Saddle	Arundinoideae/Danthonioideae subfamilies	Twiss, 1992; Bremond et al., 2008; Mercader et al., 2010; Novello et al., 2012
Rondel, Oblong and Trapeziform short cell	Pooideae subfamily	Twiss, 1992; Barboni and Bremond, 2009; Cordova, 2013; this study
Trapeziform sinuate	Pooideae subfamily	Twiss et al., 1969; Bremond et al., 2008; this study
Rectangular	Pooideae subfamily	Twiss et al., 1969; Kondo et al., 1994; this study
Cuneiform bulliform	Poaceae, Juncaceae?	Twiss, 1992, this study
Elongate (psilate & Echniate)	Monocots, Dicots	Runge, 1999; Thorn, 2001, 2004; Piperno, 2006; this study
Globular psilate	Monocots, Dicots	Piperno, 2006, this study

Phytolith types were grouped into twelve main categories as: (1) cross, (2) bilobate, and (3) cylindrical polylobate (grouped together with bilobate during counting and all three are referred to as 'lobates' hereafter). The (4) saddle type (short and long). The (5) rondel-shaped were in various forms and correspond to the pooid type of Twiss et al. (1969) and to the towers, conical, and pyramidal types described in Kondo et al. (1994); Fredlund and Tieszen (1994). Conical rondels were counted separately from the more trapezoidal rondels. The (6) oblong-shaped are elliptical in outline and appear longer than they are broad (Madella et al., 2005). They correspond to the pooid types of Twiss et al. (1969) and they are referred to as 'rondels' in Piperno (2006) and as 'rondels elliptical base' in Barboni and Bremond (2009). Oblong morphotypes are therefore rondels but have been separated from those with a trapezoidal outline, and unless specified, the term rondel here encompasses oblong. The (7) trapeziform sinuate has a general trapezoidal outline with a crenate/sinuous base (Kaplan et al., 1992; Carnelli et al., 2004). The trapeziform with a bilobate or polylobate base are included in this group because they are linked to a similar plant origin (Piperno, 2006). The (8) rectangular/square have in some cases a crenulated margin along one side (it is also a trapeziform sinuate but was separated from those with both sides sinuate and are more trapezoidal) and resemble pooid types of Twiss et al. (1969). The (9) trapeziform short cell types are similar to the trapezoids described

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by Kaplan et al. (1992) and Carnelli et al. (2004). The trapezifrom short cell in this study is a rondel with a wider trapezoidal outline. The other types were the (10) cuneiform bulliform phytolith (Twiss et al., 1969; Kondo et al., 1994), the (11) Elongate type (psilate and echinate long cells) (Thorn, 2001, 2004) and finally the (12) globular psilate (smooth sometimes with slightly rough surface) (Piperno, 1988, 2006; Mercader et al., 2009).

3.5. Phytolith/vegetation indices

Three phytolith indices (ratios) have been proposed by various authors to make inferences of the dominant grass subfamily, tree cover density and climate. These are the climatic index (Ic), the aridity index (Iph) and the Dicotyledonous/Poaceae index (D/P) (Diester-Haass et al., 1973; Twiss, 1992; Alexandre et al., 1997; Bremond et al., 2005; Puerto et al., 2006; Bremond et al., 2008). For the grasses these ratios are calculated using only phytolith types that have been described as typical or dominant in a given grass subfamily. Two indices were calculated in this study: Ic and Iph.

1) Ic is the percentage of short cell phytoliths mainly produced by subfamily Pooideae grasses relative to the sum of short cell phytoliths mainly produced by Pooideae, Panicoideae and Chloridoideae subfamily grasses (Twiss, 1992; Bremond et al., 2008).

$$\mathrm{Ic}\ (\%) = \frac{\text{Rondel} + \text{Trapeziform short cell} + \text{Trapeziform sinuate}}{\text{Rondel} + \text{Trapeziform short cell} + \text{Trapeziform sinuate} + \text{Cross} + \text{Bilobate} + \text{Saddle}} \times 100$$

Where rondel, trapeziform short cell and trapeziform sinuate represent subfamily Pooideae phytoliths; cross and bilobate are for Panicoideae grasses while the saddle phytoliths are for Chloridoideae grasses (Twiss et al., 1969; Twiss, 1992; Fredlund and Tieszen, 1994; Barboni et al., 1999).

Grasslands dominated by C_3 Pooideae grasses (cold climate grasses) should produce high Ic values while grasslands dominated by C_3/C_4 Panicoideae grasses (warm moist climate) and C_4 Chloridoideae grasses (hot dry climate grasses) should have low Ic values (Bremond et al., 2008). However, as previously mentioned, the abundance of species of the grass subfamilies Arundionoideae and Bambusoideae in the vegetation can add statistical noise to the Ic signal (Bremond et al., 2008). For Ic, a value of 50% indicates the crossover point between grass subfamilies (Bremond et al., 2008). This study on selected mountains in East Africa found that Ic is a good proxy for estimating proportions of C_3 −Pooideae, Arundinoideae and Bambusoideae which increase with elevation versus Panicoideae grasses that decrease with increasing elevation (Bremond et al., 2008).

2) The Iph is the percentage of C_4 Chloridoideae short cell phytolith types relative to the sum of C_4 Chloridoideae and the mainly C_4 Panicoideae short cell phytolith types (Diester-Haass et al., 1973; Bremond et al., 2008) i.e.

$$\mathrm{Iph}(\%) = \frac{\text{Saddle}}{\text{Saddle} + \text{Cross} + \text{Bilobate}} \times 100$$

For Iph, a minimum value of 30% distinguishes C_4-tall grasses (Panicoidae) from C_4-short grasses (Chloridoideae), (Alexandre et al., 1997). C_4 grasslands dominated by Panicoideae grasses yield a low aridity index (Iph) while those dominated by C_4 Chloridoideae grasses yield a high Iph (Diester-Haass et al., 1973; Bremond et al., 2008). It has been shown that Iph is a good proxy of Chloridoideae grasses versus Panicoideae grasses (Alexandre et al., 1997; Fredlund and Tieszen, 1997). However, Iph proved not to be a relevant proxy at high elevation on tropical mountains as these grasses generally do not occur above certain altitudes and the phytolith morphotypes used to calculate it are produced in small amounts by C_3 (Pooideae and Arundinoideae) grasses that flourish at high elevation (Bremond et al., 2008).

The D/P index is the ratio of phytoliths diagnostic of tropical woody dicotyledons (the globular granulate type) versus short cell phytolith diagnostic of grasses i.e. D/P (%) = Dicots/(Grass short cells) × 100. It is used to infer woody cover density (Alexandre et al., 1997; Bremond et al., 2008). Because of the absence of the globular granulate phytoliths that are typical of woody dicots (Alexandre et al., 1997), the phytolith index D/P could not be calculated in this study.

4. Results

4.1. Phytolith occurrence in modern alpine plant species

All the C_3 grasses of the subfamily Pooideae analysed produced morphotypes that are known to be typical of these grasses (Twiss et al., 1969; Twiss, 1992; Piperno, 2006; Barboni and Bremond, 2009). The grass silica short cells (GSSCs) observed in the four grass species analysed are: the trapeziform short cells, trapeziform sinuate/polylobate, rectangular shaped, oblong shaped and rondels (Fig. 4). They also produce other phytolith types i.e. globular psilate phytoliths, cuneiform shaped phytoliths, elongates and trichomes. Conical rondels (with pointed or flat tops) (Fig. 4a.1–a.5, b.6, b.7) were common in *Deschampsia flexuosa*, *Agrostis* sp. and *Festuca abyssinica*; trapeziform short cells (Fig. 4 e.g. a.7, a.9, b.4) and trapeziform sinuate (Fig. 4 e.g. a.8, b.1, b.3) in *Deschampsia flexuosa* and *Agrostis* sp.; and oblong phytoliths in *Festuca abyssinica* (Fig. 4c.1, c.2). A flared saddle like shape was observed in *Agrostis* sp. (Fig. 4b.10). For the non-grasses, phytoliths were not as common as in the grasses and are not well represented. It is only the *Luzula* spp. (family Juncaceae) that produced phytoliths some of which appear quite similar in outline to some GSSCs if at all they were not mere contaminations as they were often sighted only once. *Luzula johnstonii* consisted of globular psilate, cuneiform bulliform, elongate, a sort of rondel and a long conical shape that may be a hair cell (Fig. 4f) while *Luzula abyssinica* had elongates, a sort of long conical shape, a saddle, a bilobate and a trichome (Fig. 4e). *Ranunculus oreophytus* (Ranunculaceae) produced globular psilates (with slightly rough surfaces); *Romulea congolensis* (Iridaceae) produced oval shapes with tapering ends, slightly squared shapes and globular psilates; *Helichrysum formossisimum* (Asteraceae) showed forms that appeared elongate and a dendritic wide elongate was observed, while the *Dendrosenecio* sp. (Asteraceae) did not seem to produce phytoliths.

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Table 3
Main phytolith morphotype abundance (in %), from the Mount Muhavura crater lake sediment sequence indicating total counts.

Sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
sample depth (cm from top)	0.5	1.5	2.5	3.5	5.5	9.5	12.5	14.5	17.5	19.5	20.5	21.5	22.5	23.5	52.5	56.5	62.5	66.5	72.5
Bilobate	25.3	45.4	46.3	28.6	54.4	57.1	28.8	42.8	47.7	50.4	42.4	53.2	44.9	53.4	13.5	18.2	29.1	16.0	23.8
Cross	1.1	2.4	2.7	1.0	0.6	1.9	0.0	0.0	0.0	0.0	1.3	4.0	1.4	2.1	0.0	0.6	0.8	1.3	1.3
Short Saddle	6.9	13.2	16.8	7.9	8.3	5.8	5.2	5.0	10.8	8.4	3.3	9.7	3.6	9.0	1.0	0.0	2.3	1.3	3.8
Long Saddle	0.0	1.1	0.0	1.3	0.0	2.1	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.6	0.0	1.3
Oblong	23.0	1.3	1.2	16.5	4.6	0.5	31.5	16.1	13.8	1.7	5.3	0.7	11.6	1.1	7.3	10.2	19.4	25.3	5.0
Rectangular	12.6	2.2	0.6	1.0	1.5	0.8	3.3	2.8	1.5	5.0	1.3	0.0	5.1	1.1	10.4	8.5	1.3	4.0	0.0
Trapeziform short cell	1.1	2.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.7	0.0	0.4	1.1	3.1	1.1	1.8	2.0	5.0
Trapeziform bilobate/sinuate	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	1.1	0.6	0.7	0.0
Rondel	6.9	5.8	12.7	9.2	5.2	5.5	5.4	7.2	7.7	1.7	7.9	3.0	3.6	4.2	0.0	0.6	1.0	0.7	5.0
Collapsed saddle	1.1	0.4	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.7	1.3
Cuneiform bulliform	6.9	2.8	4.2	2.9	6.7	1.5	4.6	3.9	0.0	6.7	11.9	7.7	6.2	10.1	1.0	1.1	3.6	2.7	2.5
Elongate (psilate, echinate)	14.9	7.4	15.1	31.7	18.7	24.8	20.5	15.6	16.9	25.2	22.5	21.7	18.1	17.5	14.6	19.9	12.9	17.3	27.5
Conical rondel	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	8.5	0.5	0.0	0.0
Globular psilate	0.0	14.9	0.0	0.0	0.0	0.0	0.2	6.1	0.0	0.0	3.3	0.0	5.1	0.0	46.9	30.1	25.0	28.0	23.8

4.2. *Phytolith occurrence in lake sediments*

The most frequently occurring individual morphotypes in the sediment sequence in relation to the entire phytolith sum are bilobate-shaped (33%), oblong-shaped (16%), elongates (17%) and globular psilate (13%). The rest of the morphotypes did not occur as frequently; saddles (6%), rondels (4.3%), rectangular (2.6%), trapeziform short cells (1.4%), crosses (1%) and trapeziform sinuate/bilobate (0.7%). The bilobate-shaped phytoliths generally contribute 10–57% of the phytolith count in the individual samples and become more abundant in the samples in the top 25 cm of the core contributing mostly above 40%. They occur in the various forms known i.e. with convex ends, indented ends, flattened ends, scooped ends, long or short shanks, and slender or thick shanks (Fig. 5a.1–a.10) and were all grouped together as bilobates (Fig. 6).

Saddle-shaped types generally contribute less than 10% in most samples and are represented by mostly the short saddle type (Fig. 5b.1) and range generally from 1 to 14%, reaching 17% in one sample. Conical rondels were separated from other rondels that are more trapezoidal in outline during counting (Fig. 5c.1–c.6) and they consist of types with pointed or flat ends sometimes tapering to one side (Fig. 5c.7, c.8). All the rondel morphotypes combined (excluding the oblong shapes) occur in small numbers throughout the sequence and contribute between 0% and 13% in individual samples. The oblong shaped morphotypes vary between 1 and 44% and appear to be well represented. Their dominance in the samples varies with that of bilobate morphotypes throughout the sequence. The trapeziform short cells and trapeziform sinuate occur in small amounts and do not exceed 5%.

The globular psilates range from 4% to 56% in the samples and seem to be almost absent in the top 25 cm of the core ranging from 0 to 15%. They had a smooth surface (Fig. 5e.1) and sometimes the surface appeared slightly rough (Fig. 5e.2). The few morphotypes that appeared to have a more defined rough surface were difficult to recognise, as their surface appeared fuzzy and difficult to make sense of the features (Fig. 5f). The elongate phytoliths constitute those with smooth and echinate margins (Fig. 5g) and range between 8% and 32% in the samples analysed.

4.3. *Phytolith indices: Ic, Iph and D/P°*

Two vegetation indices were calculated from the grass short cell phytoliths from the phytolith assemblage i.e. Ic and Iph. Ic values range from 10% to 84% while Iph values range from 0% to 27% throughout the sequence. In the most recent sediments (top 24 cm), the Ic values range from 10% to 57% while the Iph values range from 11% to 26%.

5. Discussion

Our study provides new phytolith data from a high-altitude crater lake which does not conform to the general pattern of phytolith production known for high altitude grasses growing at this elevation (Tieszen et al., 1979; Livingstone and Clayton, 1980; Young and Young, 1983; Twiss, 1992; Bremond et al., 2008). We found in abundance bilobate morphotypes, which are known to decrease with increasing elevation in modern soils and nearly disappear at this elevation (Bremond et al., 2008), and the Panicoideae grasses that dominantly produce them are not known to occur at this elevation (Tieszen et al., 1979; Livingstone and Clayton, 1980; Young and Young, 1983). There is a strong decline of C_4 grasses and an increase of C_3 grasses with increasing elevation on African tropical mountains. Panicoideae grasses are said to never exceed 3700 m, while above 3600 m, C_3 cold climate grasses dominate, especially subfamily Pooideae grasses (Tieszen et al., 1979; Livingstone and Clayton, 1980; Young and Young, 1983; Street-Perrott et al., 1997). The C_4 Panicoideae sp. *Andropogon amethystinus* is dominant above treeline up to 3350 m on Mt. Muhavura (Snowden, 1933) and on Mt. Kenya, it occurs up to 3600 m (Wooller et al., 2001). In order to interpret the results from the phytolith analysis, the study site must be considered in its spatial context in terms of elevation i.e. location of the alpine lake, the vegetation around it and its relative distance from the treeline (the limit of rather closed forest with trees 6–8 m or taller, Carnelli

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Total
76.5	80.5	86.5	90.5	96.5	100.5	105.5	109.5	114.5	119.5	123.5	128.5	139.5	140.5	145.5	149.5	155.5	158.5	
40.0	7.7	11.5	42.9	17.3	29.1	31.6	47.0	17.1	26.8	35.6	47.6	9.5	19.1	24.9	23.6	20.9	8.0	3564
0.0	0.0	1.6	4.1	1.1	2.3	0.7	0.5	0.4	3.0	0.0	0.0	0.0	0.7	1.1	0.0	0.7	0.5	124
5.0	0.0	1.4	10.2	2.9	1.6	2.4	5.8	2.6	4.3	3.8	7.1	1.0	0.7	1.6	2.5	2.2	2.7	539
2.0	0.0	0.5	0.0	0.7	0.6	2.3	1.0	1.3	0.0	1.5	2.4	0.0	2.0	3.8	2.0	1.5	0.5	107
5.0	10.3	27.3	8.2	20.2	24.3	23.6	11.6	29.4	30.5	27.3	9.5	43.6	18.1	28.1	19.2	18.5	20.9	1758
1.0	17.9	1.4	0.0	3.1	2.6	1.1	1.5	7.9	1.2	1.5	2.4	4.5	9.9	2.2	0.5	2.1	5.9	286
0.0	0.0	3.3	2.0	2.0	1.3	0.9	0.8	0.4	0.6	1.5	0.0	4.3	2.3	5.4	3.9	2.5	2.1	155
3.0	0.0	1.6	2.0	0.4	0.3	1.7	0.3	1.8	3.0	3.0	2.4	0.2	1.0	2.2	1.5	0.7	1.1	73
4.0	0.0	1.4	2.0	0.7	1.9	1.6	3.5	3.9	2.4	2.3	2.4	3.1	4.3	4.3	0.0	1.2	2.1	409
0.0	0.0	0.3	0.0	0.0	0.3	0.4	0.0	0.0	0.6	0.8	0.0	0.2	2.0	1.1	0.0	0.9	1.1	33
5.0	0.0	3.3	2.0	2.2	5.5	5.5	5.0	4.4	4.9	6.1	0.0	1.7	2.6	3.2	2.0	4.2	4.3	440
26.0	7.7	13.4	6.1	11.2	17.5	19.3	15.9	13.6	13.4	11.4	19.0	12.4	26.6	8.6	19.7	16.0	22.5	1882
0.0	0.0	0.3	2.0	0.2	1.9	1.3	0.7	0.4	1.2	0.0	0.0	0.8	0.3	0.0	0.5	1.0	0.0	59
9.0	56.4	32.8	18.4	37.9	10.7	7.5	6.3	16.7	7.9	5.3	7.1	18.8	10.5	13.5	24.6	27.7	28.3	1421

et al. (2004) as an aid to determining the likely source vegetation of phytoliths into the lake.

5.1. Phytoliths in lake sediments: vegetation and the rationale

Of the 12 main phytolith morphotypes that we identified, ten were attributed to the grass family (Poaceae) and two were ubiquitous and treated as non-diagnostic (Table 2). We attribute all the 12 morphotypes to herbaceous taxa only. Of the ten morphotypes that are indicators of Poaceae, nine are GSSCs that are produced only in Poaceae (i.e. cross, bilobate, cylindrical polylobate, saddle, rondel, trapeziform short cell, trapeziform sinuate, rectangular, and oblong), and the other non-short cell type that is typical of Poaceae is the cuneiform bulliform cell (Twiss et al., 1969; Twiss, 1992). The assemblage therefore consists predominantly of phytoliths characteristic of grasses (70% of the total phytolith count). The two non-diagnostic phytoliths in our study are the elongates (Thorn, 2001, 2004) (Fig. 5g) and the globular psilate (Piperno, 1988, 2006; Mercader et al., 2009) (Fig. 5e.1, e.2) that we also observed in both the Poaceae and non-Poaceae species analysed. All the main phytolith morphotypes found in the sediment were found to be present in the Pooideae grasses we studied except the saddles and lobate morphortypes other than the flared saddle observed in *Agrostis* sp.

The phytolith record shows bilobates and oblong-shaped rondel morphotypes as the most well represented GSSCs and variations between them occur throughout the assemblage. The trapeziform short cells, trapeziform sinuate, rectangular and rondels seemed well represented in the C_3 modern grasses analysed but they do not appear to be as abundant in the sediment sequence (each less than 5%). Cordova (2013) found that short cells typical for C_3 Pooideae grasses rarely exceed 20% in the modern soils where these grasses are most abundant. Modern soils from the Alpine belt of Mt. Kenya where Pooideae grasses are dominant also seem to have similar low counts for these morphotypes (Bremond et al., 2008). For example, the modern soil samples show rondel phytoliths as the highest contributor reaching 57% while trapeziform polylobates/sinuates and trapeziform short cells have low numbers with a maximum of 13.5% and 1% respectively. Since all these morphotypes were observed in the subfamily Pooideae grasses we analysed, we attribute them to this subfamily and to some Danthonioideae/Arundinoideae grasses (Bremond et al., 2008) that may exist or have existed on this mountain. More so, rondels, trapeziform bilobates and trapeziform sinuates are said to be the only true markers of the Pooideae subfamily when they all occur in an assemblage (Barboni and Bremond, 2009). As aforementioned, conical rondels in the sediments were counted separately from other more trapezoidal rondels as many are similar to cones or 'hat-shaped' reported in Cypearaceae (sedges) (Ollendorf, 1992). These various forms of conical rondels were observed in the modern Pooideae grasses analysed (Fig. 4; a.1–a.3; b.6) and those in a.1 and a.2 are quite similar to those that are described in sedges (Ollendorf, 1992; Honaine et al., 2009). The conical rondel in Fig. 5c.8 has a hat-like shape but we do not recognize this very morphotype from micrographs in other studies. It is not readily clear from the literature if sedges occur around the crater lake but sedges have been confirmed by the pollen study at the same site (McGlynn et al., 2013).

From the literature, the amount of bilobates found in the lake sediments in our study exceeds the expected amount and the interpretation of the vegetation is not straightforward because of this bias. Modern soils on Mt. Kenya show a decrease of bilobate phytoliths with increasing elevation because of dominance of C_3 grasses at high elevations yielding only 3%–10% of bilobates in the Afroalpine zone (Bremond et al., 2008). Although not anywhere near abundant as the bilobates, saddle shapes that are typical of the subfamily Chloridoideae are also considered to be well represented given the elevation at which they have been found. This is because the Chloridoideae grasses are absent from the Alpine and Ericaceous belts on African mountains (Snowden, 1933; Livingstone and Clayton, 1980) and we assume from the literature that they are not likely to have existed there in the recent past either. These saddles occur in small amounts (0–3%) as expected in the modern soils of Mt. Kenya and are attributed to the C_3 grasses of Pooideae and Arundinoideae occurring at this elevation (Bremond et al., 2008). Lobates and saddle morphotypes are generally not produced in

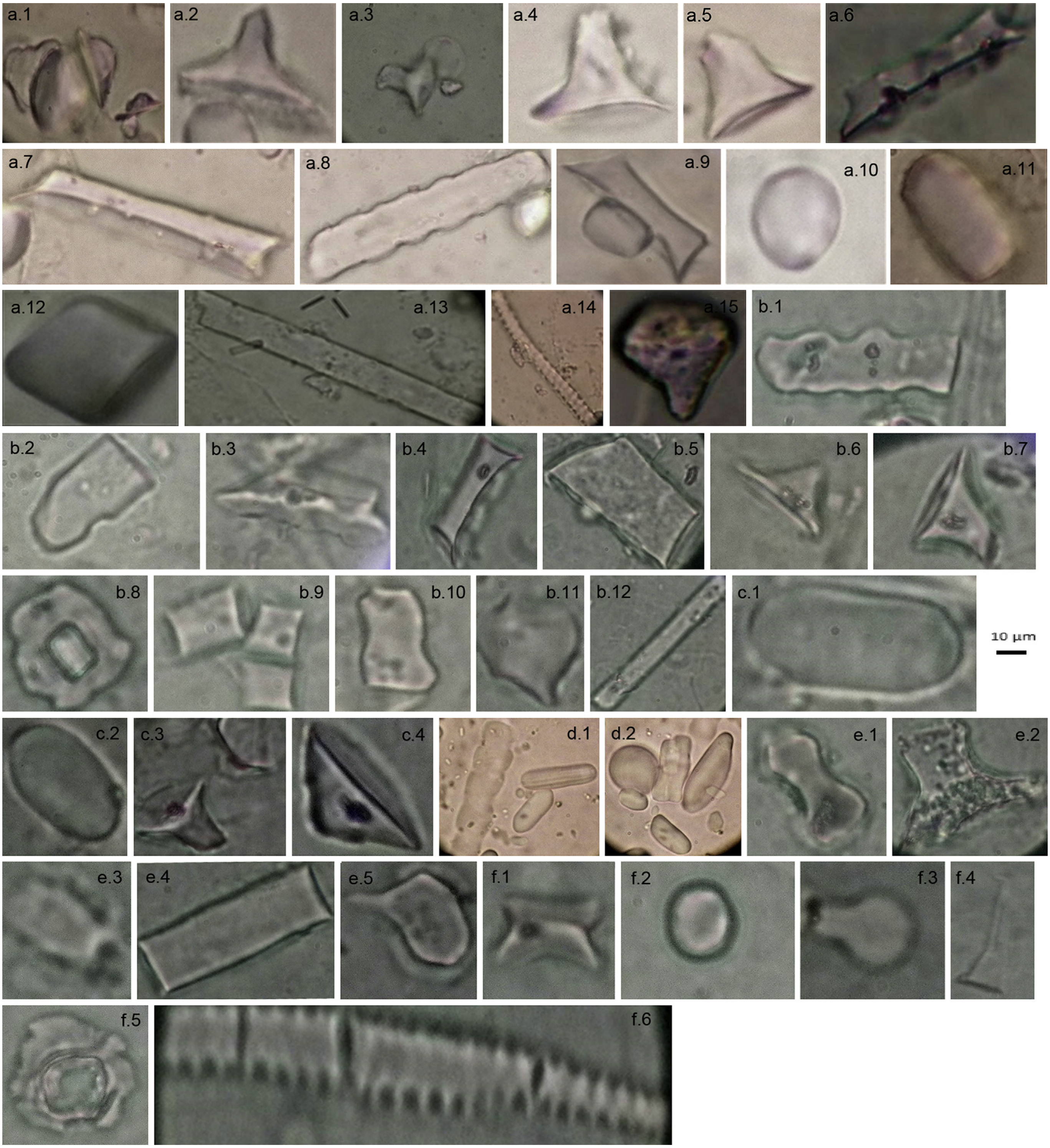

Fig. 4. Microphotographs of phytoliths from modern plants. A – Deschampsia flexuosa: a.1–a.4 conical rondels. a.5 rondel. a.6 trapeziform short cell/sinuate. a.7 trapeziform short cell. a.8 trapeziform sinuate. a.9 trapeziform short cell. a.10 globular psilate. a.11 rectangular. a.12 square. a.13 elongate psilate. a.14 elongate echinate. a.15 bulliform. B – Agrostis sp.: b.1 trapeziform sinuate. b.2 trapeziform sinuate – rectangular. b.3 trapeziform polylobate. b.4 trapeziform short cell. b.5 Trapeziform short cell. b.6 rondel – conical. b.7 rondel – conical. b.8 rondel – conical/papillae? b.9 squares. b.10 saddle-like. b.11 bulliform. b.12 elongate psilate. C – Festuca abyssinica: c.1 oblong. c.2 oblong. c.3 rondel – conical. c.4 rondel D – Poa anua: d.1 trapeziform sinuate. d.2 spherical and oblong. E – Luzula abyssinica: e.1 bilobate. e.2 hat like shape. e.3 saddle. e.4 elongate psilate. e.5 hair cell? F – Luzula johnstonii: f.1 rondel like. f.2 globular psilate. f.3 bulliform f.4 long conical shape – hair? f.5 unidentified f.6 elongate echinates.

Pooideae grasses (Twiss, 1992; Blinnikov, 1994; Carnelli et al., 2004; Mercader et al., 2010; this study). The modern reference collection here, though limited in scope, allows us to tentatively conclude that the major source of bilobate and saddle morphotypes is not Pooideae grasses. Bilobates and saddles are reported to be abundant in C_3 aquatic grasses of the subfamily Ehrhartoideae and some Arundinoideae grasses (Piperno, 2006; Rossouw, 2009; Mercader et al., 2010; Novello et al., 2012).

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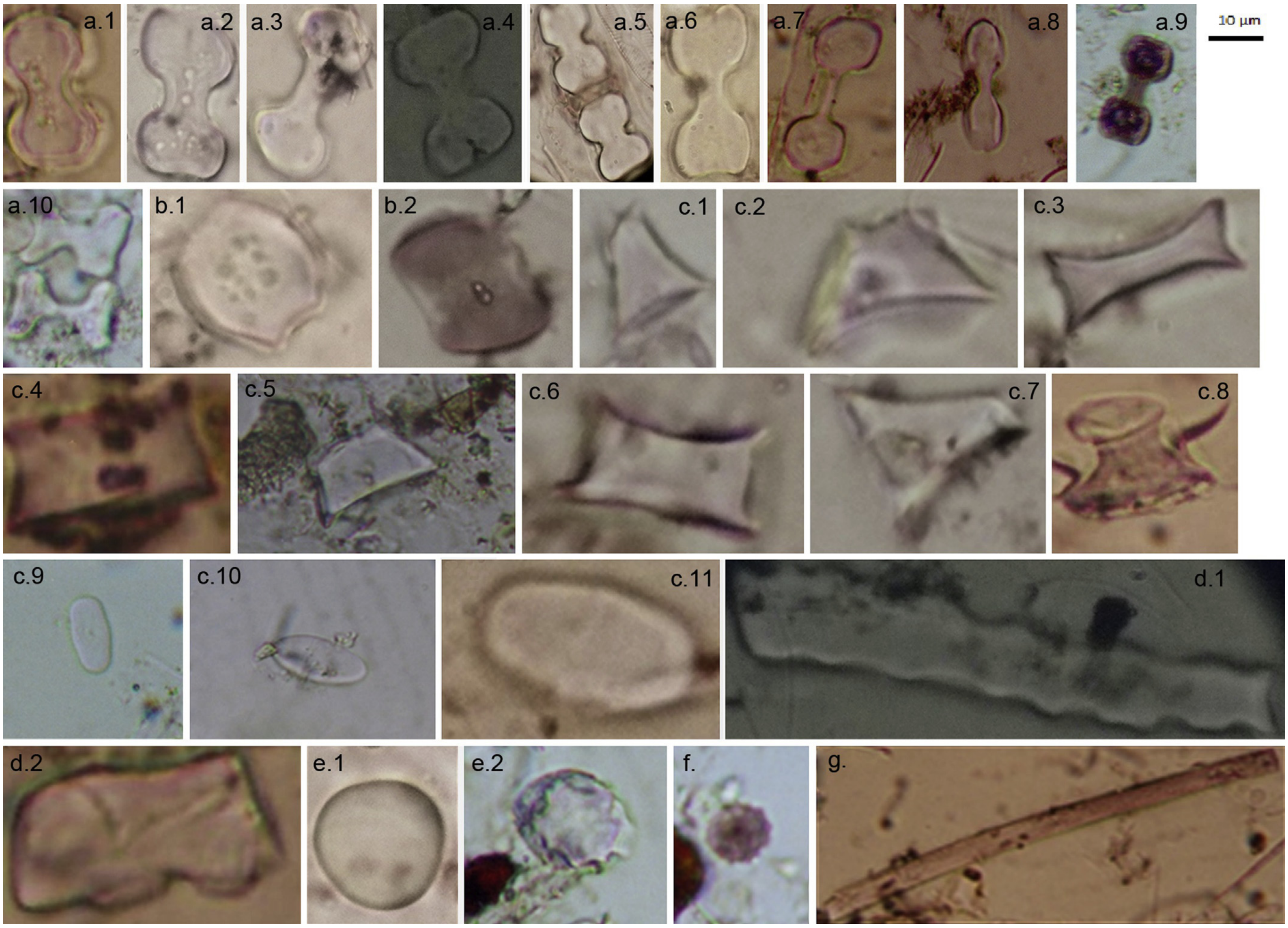

Fig. 5. Microphotographs of phytoliths from lake sediments. a.1 bilobate convex outer margin short shaft. a.2 bilobate flattened outer margin short shaft. a.3 bilobate convex outer margin long shaft. a.4 bilobate flattened outer margin short shaft. a.5 bilobate flattened outer margin short shaft. a.6 bilobate flared outer margin short shaft. a.7 bilobate convex outer margin long shaft. a.8 bilobate convex outer margin short shaft. a.9 bilobate flattened outer margin short shaft. a.10 bilobate flattened outer margin short shaft. b.1 saddle. b.2 saddle. c.1 rondel. c.2 rondel. c.3 rondel – oblong side view?. c.4 trapeziform. c.5 trapeziform. c.6 trapeziform. c.7 rondel – conical. c.8 rondel – conical/hat shape? c.9 rondel – oblong? c.10 rondel – oblong?. c.11 rondel – oblong. d.1 trapeziform sinuate. d.2 trapeziform sinuate – rectangular. e.1. globular psilate. e.2 globular psilate (slightly rough surface). f. globular echinate. g. elongate psilate.

Given what we know about phytolith production in grasses, it is likely that there are grass species close to the crater lake margin on Mt. Muhavura that are responsible for producing bilobates in such high numbers. According to Barboni et al. (2010), bilobate phytoliths are typical of moisture-loving grasses favouring mesic to hydric habitats. We attribute bilobates and saddles to the subfamilies Arundioideae/Danthonioideae and probably aquatic grasses of Ehrhartoideae if they occur on Mt. Muhavura or have occurred in the past. It has been shown that C_3 and C_4 grasses co-exist in areas where C_3 grasses are dominant as seasonal variations in temperature cause the C_3 grasses to flourish when the weather is moist and cool, and then C_4 grasses appear when the temperature increases during the summer or dry seasons (Twiss, 1992; Cordova, 2013). Because temperature is the most important environmental variable that controls the distribution of C_3 and C_4 grasses on tropical mountains (Livingstone and Clayton, 1980; Bremond et al., 2012), this is also a possibility for Mt. Muhavura.

Woody cover is not inferred in this study which is in agreement with Bremond et al. (2008). It has been suggested that woody dicotyledons on tropical mountains probably produce few or no phytoliths and that the D/P index can only be applied at lower elevations (Barboni et al., 2007; Bremond et al., 2008). Another plausible explanation for the lack of phytoliths typical of trees/shrubs in the record could be because the phytolith input in the lake is due to surface runoff and not wind deposition. In contrast, the pollen record would have its major input due to wind, covering longer distances along the mountain allowing for the reconstruction of the montane forest history (McGlynn et al., 2013). Cuticles from dicotyledons were also rarely encountered in the cores from Mt. Kenya (Wooller, 2002). However, D/P index values have also been found to be very low in forested lowlands in Africa resulting in an over representation of grasses (Neumann et al., 2009; Novello et al., 2012). Because both globular psilates and elongates were found to be ubiquitous in the reference collection (attributed to both monocots and dicots) in agreement with the literature, they are treated as non-diagnostic and are of no taxonomic importance (Piperno, 1988; Runge, 1999; Thorn, 2001; Piperno, 2006).

5.2. Implications for palaeoenvironmental reconstructions of grass subfamily dominance on mountains in East Africa

Our results suggest that even at high elevation, where the C_3 and C_4 distribution is better delineated and an overlap above a certain elevation is not expected, bilobate phytoliths may not be a good

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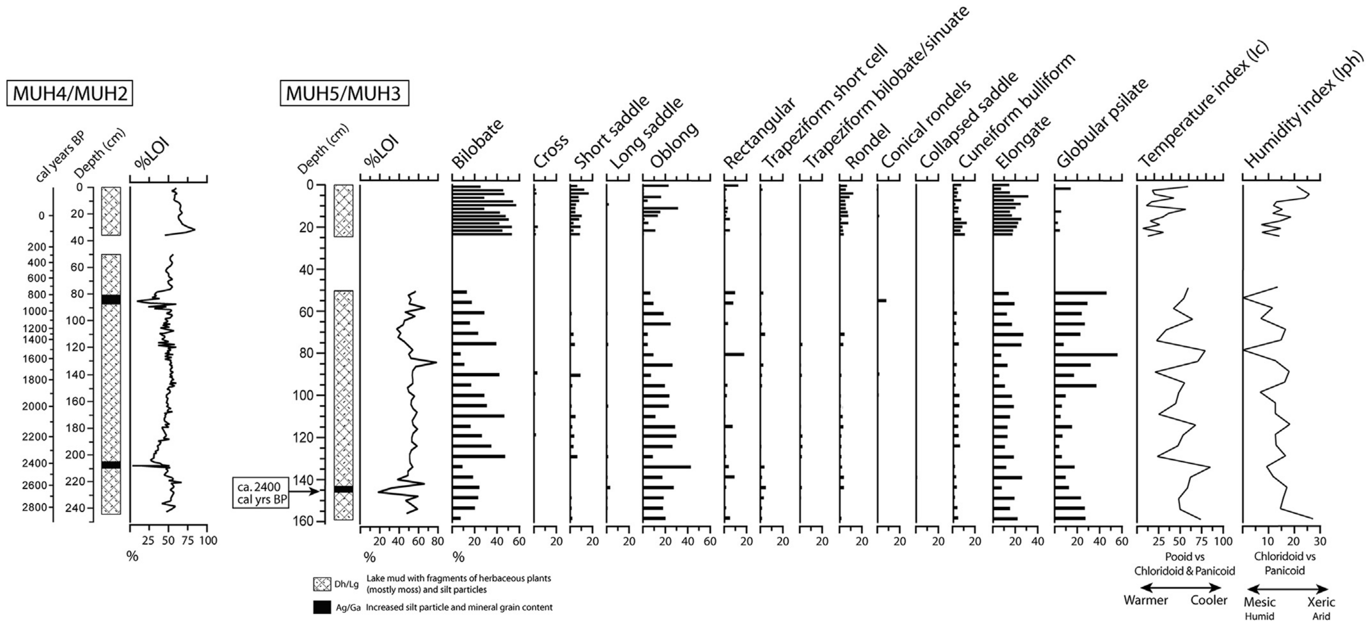

Fig. 6. Chronology, % LOI, and sediment stratigraphy of the sediment profiles from Mt. Muhavura for MUH2/MUH4 (McGlynn et al., 2013) and MUH5/MUH3 (this study) and the % phytolith morphotype abundance.

proxy to infer subfamily dominance in terms of the commonly inferred Panicoideae grasses when aquatic Ehrhartoideae grasses and Arundinoideae grasses are well represented in the fossil records. This is because the abundant bilobate phytoliths are likely to be misinterpreted as representative of C_4 Panicoideae. A study by Mercader et al. (2010) on modern grasses in Mozambique indicates that 60% of Arundinoideae species were statistically classified as Panicoideae because of the abundance of bilobates that they produce. However, it might be possible that phyoliths in the fossil assemblage at this elevation can be used to separate between grasses of the subfamily Arundionoideae or Danthonioideae and Pooideae that thrive in this environment. It may also present an opportunity to reconstruct local palaeotemperatures on the mountain if the percentage of Pooideae grasses can be estimated in the fossil record, and this can be done for the different vegetation belts if a fossil record is available (Livingstone and Clayton, 1980).

The Ic values in this study reach as low as 10% and do not exceed 84% throughout the sequence because of the strong presence of bilobate phytoliths. The Ic calculated from modern soils on Mt. Kenya gave the highest values in the Alpine belt between 80% and 97% because of the disappearance of Panicoideae grasses and dominance of Pooideae grasses (Bremond et al., 2008). The Ic does not reach 100% because of the presence of small amounts of saddle and lobate short cells that can be produced by some species of Pooideae and Arundinoideae that flourish at this altitude, illustrating the redundancy and multiplicity of phytolith production (Bremond et al., 2008). In our study, the top 20 cm of the sediment core that represent the most recent sediments give the lowest Ic values ranging from 10% to 57% because of the marked increase of bilobate phytoliths. The low values of the Ic calculated in our study suggest a strong presence of Panicoideae grasses which is not in agreement with known vegetation surveys and the modern soil phytolith analyses at this elevation. The Ic index calculated in this study should be treated with caution because it does not represent the taxonomic/ecological significance that it is meant to infer as Panicoideae grasses are most likely not the source of the bilobates used to calculate it. It is most likely that all the morphotypes used to calculate the Ic are all produced by C_3 subfamily high altitude grasses with no input from Panicoideae grasses that are known to occur at a lower elevation from the lake unless they may have existed at higher altitudes in the past. Iph values in this study were similar to those found by Bremond et al. (2008) in the Alpine belt of Mt. Kenya (0%–25%) and because it was not found to be taxonomically representative of the grasses for which it is meant, we do not discuss it any further. According to Strömberg (2009), count size is important for confident interpretation of vegetation index values and should be taken into account when making vegetation inferences. This study counted slides as whole slides and did not set out to standardise the counts for each slide to a set maximum or minimum.

The potential of the phytolith record to accurately reconstruct the past environment on this mountain is yet to be ascertained. Given the setting of the lake, the phytolith record is most likely local and only representative of the vegetation around the lake. Unlike the phytolith record, the pollen record from Mt. Muhavura allowed for the reconstruction of both local and regional vegetation and environmental conditions. It suggests an increase in aridity in the last 2000 years BP and human-induced vegetation change in the lower Forest Belt after 900 years BP. It records both high altitude and lower altitude vegetation on the mountain. Some studies have distinguished among the bilobate morphotypes based on their shank length and lobe shape as it can to some extent help to improve the identification of bilobates produced in a particular grass subfamily (e.g. Piperno, 2006; Mercader et al., 2010; Fahmy, 2007; Neumann et al., this issue). This study was not designed to separate the various bilobates although we acknowledge that it may have, to some extent aided the taxonomic interpretation of the result. However, the presence of the various bilobates described in all the main grass subfamilies in Piperno (2006) in the fossil record, further complicates this phytolith record. It is debatable to what extent these distinctions would have improved the discussion and highlights a bigger problem in the way bilobates have sometimes been interpreted in the fossil record in areas where aquatic or Arundinoideae grasses may have been prevalent.

Lastly, the abundant number of oblong and globular psilate phytolith morphotypes in the phytolith record is suspect. The globular psilate in modern soils on Mt. Kenya contribute only 1% (Bremond et al., 2008) while our study shows their over representation. For Mt. Muhavura, phytoliths typical of the subfamily Pooideae seem to be most well represented by rondel morphotypes that are oblong-shaped. Although rondels were also found to be most the abundant type in the Alpine belt of Mt. Kenya, in our study it is the oblong-shaped rondels that are well represented with the other rondels occurring in smaller amounts. It is possible that these shapes may have been overestimated as some of the shapes in the sediments may have been those of other siliceous elements. Diatoms were abundant in the samples studied and although they were obviously different from the phytoliths, other siliceous elements may have occurred because the oblong shapes seen in the sediments were not always exactly similar to those in the plants analysed although they had the same shape (see Fig. 4: c.1–c.2 and Fig. 5: c.9–c.11). Because of this, misidentification cannot be ruled out with certainty. Of the phytoliths that look similar in outline to those in grasses in the *Luzula* spp., it is the bilobate shape observed in *Luzula abyssinica* that is typically the same as those seen in grasses. Although the *Luzula* spp. produce interesting morphotypes, they are often seen only once under the microscope. Their influence on the fossil phytolith record when reconstructing past grasslands would be minimal. Phytolith production in the Juncaceae family is generally ambiguous (Pearsall, 2000; Piperno, 2006) and phytoliths were not observed in the four species of the *Juncus* genus analysed by Iriarte and Paz (2009).

6. Conclusions and future prospects

This study presents the first phytolith record from an Afroalpine lake at this altitude in Africa. Despite its limitations, it is a first attempt at testing the potential of phytoliths to reconstruct vegetation history in montane grasslands and contributes to the regional grassland reconstructions that are often taxonomically constrained. Our study is one of the few grassland studies at high altitude in East Africa that attempts to use phytoliths to give insights into past alpine grassland composition. The lack of comparable fossil phytolith data from a similar altitude was a major setback to drawing inferences. We are unable to provide a firm interpretation of the phytolith record in terms of the palaeoecological significance and we conclude that caution needs to be taken when using bilobate morphotypes and the phytolith index Ic as reliable indicators of the Panicoideae grass subfamily and palaeoenvironmental conditions on East African highlands where aquatic grasses might be well represented. It is likely that the phytoliths from aquatic grasses dilute the signal of terrestrial grasses that may be misinterpreted as terrestrial grasses. This study illustrates the inherent problem of phytolith redundancy even in areas where grass subfamily distribution is better delineated. Since the grasslands are open, the extent to which wind may move grass phytoliths from the subalpine belt into the lake needs to be investigated.

A wider and detailed analysis of living grasses in the alpine belt and the modern soil phytolith assemblages beneath them is necessary to determine the source of the abundant bilobate shaped phytolith input into the lake to determine if the morphotypes are firm indicators of taxonomic affiliation and determine the validity of this phytolith assemblage to reconstruct palaeoenvironments. Another logical step is to take sediment cores from swamps at lower elevation on this mountain for comparison with sediments from the summit to further draw well informed conclusions. More importantly, a more robust vegetation analysis along an elevation gradient is necessary to determine the C_3/C_4 grass distribution and their actual crossover point to improve our understanding of the fossil assemblage. This knowledge can also provide important information for conservation managers in biodiversity hotspots of global significance whose current conservation efforts in the Virunga Volcanoes largely target high-profile fauna such as the endemic mountain gorillas, with not much on how flora is responding to its natural environment. Until such a time, the results and interpretations made here are necessary tentative and should be treated as preliminary to further stimulate the discussion on the potential of phytoliths in alpine environments.

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