Evidence for opal phytolith preservation in the Langebaanweg 'E' Quarry Varswater Formation and its potential for palaeohabitat reconstruction

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At the end of the Miocene epoch, C_4 grasslands began to expand at the expense of tree-, shrub- and forb-dominated C_3 ecosystems. While C_4 grasses were spreading throughout most regions of the world, C_3 grasses may have been spreading along South Africa's southwest coast. Stable isotope analyses of hypsodont fossil ungulates from 'E' Quarry, a well-known Late Miocene/Early Pliocene fossil locality near the town of Langebaanweg, suggest that the local environment might have included a substantial C_3 grass component. Besides this indirect evidence, little is known about the evolution, nature and importance of grass in the 'E' Quarry biome. As a preliminary step towards addressing these questions, we initiated a trial investigation to assess whether sediments at the site are conducive to the preservation of phytoliths, an important tool in the reconstruction of palaeohabitats. Results indicate that fossil phytoliths are sufficiently well preserved to allow a comprehensive analysis of the 'E' Quarry phytolith assemblage.
Key words: phytoliths, grassland, habitat reconstruction, Langebaanweg, fynbos, hypsodonty

Introduction

The distribution of savannas and grasslands are associated with a range of climatic parameters and provide a link to past climate changes.[1] More specifically, grasses are potentially good indicators of past climates since the taxonomic composition of grass-dominated ecosystems indirectly reflect local climatic conditions.[2,3] This is because grasses are likely to adapt relatively quickly to environmental changes, including variation in atmospheric carbon dioxide, temperature and moisture availability.[4]

During the Late Miocene to Early Pliocene (7–5 Myr), a major vegetational shift occurred when C_4 grasslands expanded globally at the expense of tree-, shrub- and forb-dominated C_3 ecosystems.[5–8] The reason for this shift is not overtly clear. However, there is a suggestion that a drop in CO_2 concentrations at the time would have favoured plants using the C_4 photosynthetic pathway.[7,9–11] The shift towards grass-dominated biomes may in turn have driven many of the evolutionary changes seen in terminal Miocene faunal communities around the globe.[7] Faunal changes were particularly evident in Africa, where there was a proliferation in grazing ungulates and open-country adapted carnivores. Most significantly, some of the earliest known possible human ancestors also made their appearance.[12–14]

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At a time when C_4 grasses were spreading through most of Africa, C_3 grasses may have been spreading along South Africa's southwest coast. Stable isotope analyses of a variety of ungulate specimens from 'E' Quarry (32°58'S, 18°7'E), a well-known Late Miocene to Early Pliocene fossil locality near the town of Langebaanweg (Fig. 1), indicate that the local environment remained dominated by C_3 taxa.[15] While this might indicate a closed environment dominated by trees, shrubs and forbs, the occurrence of several species of high-crowned (hypsodont) ungulates in the 'E' Quarry faunal assemblage, hint at the presence of a substantial grass component. Despite this evidence, very little is known about the evolution, nature and importance of grass in the Langebaanweg 'E' Quarry biome. As a first step towards answering these questions, we initiated a trial investigation to assess whether sediments at the site are conducive to the preservation of phytoliths, an important tool in palaeohabitat reconstruction. Here we present the results of this preliminary study and elaborate on how we plan to take the research further.

Langebaanweg fossil deposits and geological sequence

Fossil deposits were first discovered close to the town of Langebaanweg during phosphate mining operations which initially began at Baard's Quarry in 1943 and later moved to 'C' and 'E' Quarries (Fig. 1). However, the importance of these and other fossil localities in the area was only recognised in the late 1950s and 1960s, once scientists commenced with formal fossil descriptions. The prolific bone beds of 'E' Quarry in particular, soon established this locality as a fossil site of great importance. From the late 1950s until the late 1980s, 'E' Quarry was a major focus of research at the South African Museum (now Iziko South African Museum). Museum palaeontologist, Brett Hendey, in particular, was a productive researcher and publisher on the geology and fauna of the Langebaanweg localities.[16–21]

All the 'E' Quarry fossils originate from the phosphatic sediments of the Mio-Pliocene Varswater Formation.[17,21,22] Four members are recognised in the most recent lithostratigraphic review of this formation—the Middle/Late Miocene Langeenheid Sandy Clay Member (LSCM) and Konings Vlei Gravel Member (KVGM), and the Late Miocene/Early Pliocene Langeberg Quartzose Sand Member (LQSM) and Muishond Fontein Pelletal Phosphate Member (MPPM)[22] (Fig. 2). The LQSM and the MPPM produced the majority of fossils (more than 230 vertebrate and invertebrate taxa). The former is construed as primarily a floodplain and salt marsh deposit, while the latter is interpreted as primarily a river channel deposit.[22,23] Two river channels, beds 3aS and 3aN, have been identified. Although the temporal relationship between these two beds remains unclarified, bed 3aS appears to be the earlier of the two.[24,25] In any event, both river channels reflect a progressive northward shift of the lower course of the proto-Berg River.

The 'E' Quarry palaeoenvironment

Pollen sequences from the LSCM point towards the presence of subtropical forests, palms and marshy vegetation in the region during the early Late Miocene. However, *Podocarpus* and grass pollens tend to dominate in subsequent members of the Varswater Formation.[26,27] There is also an increase in taxa which are characteristic of fynbos shrublands.[28,29]

As previously mentioned, stable carbon isotope analyses of tooth enamel carbonate of several ungulates from LQSM and MPPM, some with hypsodont dentition, provided values that remain within the C_3 range. The degree of hypsodonty in ungulates is used in palaeoenvironmental reconstruction as an

indicator of feeding preferences and habitat selection.[30–33] The feeding classification of living ungulates ranges from grazers to mixed browsers/grazers to browsers, with grazers usually having more hypsodont teeth compared to species not specialised in grass consumption.[34–37] An increase in tooth crown height represents an adaptation against tooth wear resulting from an abrasive diet consisting primarily of grasses with abundant phytoliths, and from the airborne grit and dust accumulated on the herbaceous plants of open environments.[38–40] The presence of hypsodont ungulates with C_3 stable carbon isotope values suggests that C_3 grasses were the prevalent grass type and also implies that the modern wet winter/dry summer climate regime was established by Late Miocene to Early Pliocene times.[15] Whereas fynbos vegetation today is characterised by an insignificant C_3 grass component,[41] the 'E' Quarry Late Miocene/Early Pliocene habitat may have included a substantial C_3 grass component along with riverine forests and fynbos shrublands.[42]

Phytolith analysis

Opal phytoliths are particles of hydrated silica that are produced in various parts of living plants.[43] Herbaceous plants, especially monocotyledonous plants, are prolific producers of phytoliths, particularly in the epidermal tissue of stems and leaves.[44] The morphology and rate of production of phytoliths are largely under genetic control and there is evidence for metabolic exclusion or preferential concentration of silica in some plants.[44] The grass family (Poaceae) in particular, produce abundant opaline silica bodies with diagnostic morphological features that permit identification to subfamily, or in some instances, lower taxonomic levels.[45–47]

Phytoliths preserve well in oxidising environments and have the potential to yield a record of past vegetation cover where there is no other information available.[43,48] The abundant production of opaline silica in grasses, for example, is reflected in post-depositional contexts, which facilitate quantitative applications of fossil grass phytolith assemblages.[49] This suggests that a predominance of any particular phytolith type in the soil is evidently a reflection of a locally-dominant group of plants. The predictive power of grass phytoliths also yields additional potential because the distribution of grasses in southern Africa is primarily linked to growing season temperature, which also accounts for the geographic distribution of C_3 and C_4 grasses.[2] Recently, a few preliminary studies of fossil grass phytolith assemblages from Pretoria Saltpan, the Free State Province and Lesotho, drew attention to the potential for grass phytolith analysis in palaeograssland research in South Africa.[50–52]

Methods

Eleven soil samples were collected from three different localities in 'E' Quarry. Sampling of the LSCM, the top of the KVGM and the LQSM was conducted in an old test pit, approximately half a kilometre southwest of the current fossil exhibition tunnel. Three samples were collected from the MPPM—two from previously excavated areas in the exhibition tunnel and one from a
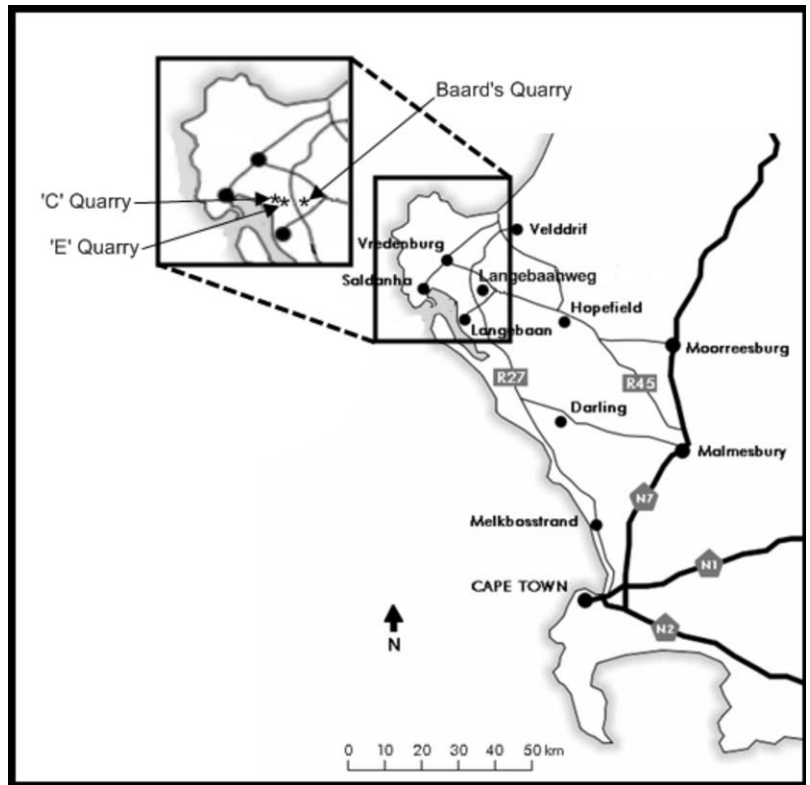

Fig. 1. The location of Baard's Quarry, 'C' Quarry and 'E' Quarry.

Fig. 2. Division of the geological members in the Varswater Formation (modified from Roberts[22]).

newly excavated area in the adjacent tunnel, which currently is closed to the public. An additional two samples were collected from fine-grained sandy deposits of the LQSM, in the latter tunnel.

The procedure for recovering phytoliths from sediment samples is based on published techniques.[53,54] Approximately 50 g of each sample was used for each phytolith extraction. Essential steps included deflocculation, removal of clays by means of sedimentation, and the elimination of carbonates using HCl in low concentration (10%). Phytolith extraction also involved mineral separation with a heavy liquid solution of sodium polytungstate (s.d. = 2.3). Fractions were mounted on microscope slides in glycerin jelly and scanned under a Nikon 50i polarising microscope at ×400 magnification. Morphological descriptions follow the guidelines provided by the International Code for Phytolith Nomenclature 1.0.[55] A modern phytolith comparative collection aided the identification of fossil phytoliths.

Results and conclusion

Preservational conditions for biogenic silica are generally favourable throughout the sequence despite comparatively low and more variable phytolith counts in the LQSM and MPPM samples (Table 1 and Fig. 3). The predominantly sandy matrix of the estuarine LQSM and fluviatile MPPM deposits most likely facilitated leaching of biogenic silica during waterlogged conditions, but more detailed analyses of phytoliths from the various depositional environments are needed to adequately interpret post-depositional processes.

Diagnostic grass phytolith morphotypes, as well as morphotypes produced by the monocot families Restionaceae (Cape reed grasses) (Figs 4e and 4r) and Arecaceae (palms) (Fig. 4f), were identified. Globular cavate phytoliths, analogous to silica bodies produced by the gymnospermous Encephalartoideae (cycad subfamily), were identified in the KVGM (Figs 4l and 4m). In addition, pennate diatoms, with surface markings at right angles to the long axis, are abundant in the LSCM (Fig. 4i).

Four grass short-cell phytolith types were recognised, namely bilobates, saddles, rondels and trapeziform morphotypes[43,46–48] (Figs 4a–d, 4k, 4o and 4p). Saddle-shaped grass phytoliths were absent in the KVGM, LQSM and MPPM samples. This is noteworthy and seems to support the suggestion that C_3 grasses prevailed during Late Miocene/Early Pliocene times at Langebaanweg. In contrast, saddle-shaped grass phytoliths were identified in the LSCM (Figs 4b and 4c), which is significant given that in the modern environment these phytoliths are almost exclusively found in the Chloridoideae, a grass subfamily that utilises the C_4 photosynthetic pathway.[3,56]

The results are very promising and show that fossil phytoliths are sufficiently preserved in terms of both quantity and variety (Table 2). The occurrence of palm and cycad-type phytoliths in the LSCM and KVGM supports previous work based on palynological indicators.[26] Except for the LQSM, grasses are well represented in the Varswater Formation—more than 50% of the total phytolith count in the LSCM and about 30% of the total phytolith count in the KVGM and MPPM (Fig. 5). A comparatively large proportion of restoid phytoliths in the LQSM and MPPM compliments earlier and more recent reconstructions,

suggesting that South Africa's southwest coast was becoming drier and more open during the Early Pliocene.[57,58] The presence of chloridoid-type grass phytoliths in the LSCM and subsequent lack in the KVGM, LQSM and MPPM further suggest that radical changes in grassland composition may have occurred towards the end of the Miocene when climate changed from subtropical to more temperate.[27,59] While intrigued, we are nevertheless reluctant to make firm inferences regarding the presence of C_3 or C_4 grasses in the 'E' Quarry Varswater sediments at this preliminary stage. Rather, we intend to proceed with a comprehensive quantitative study of grass phytoliths from the
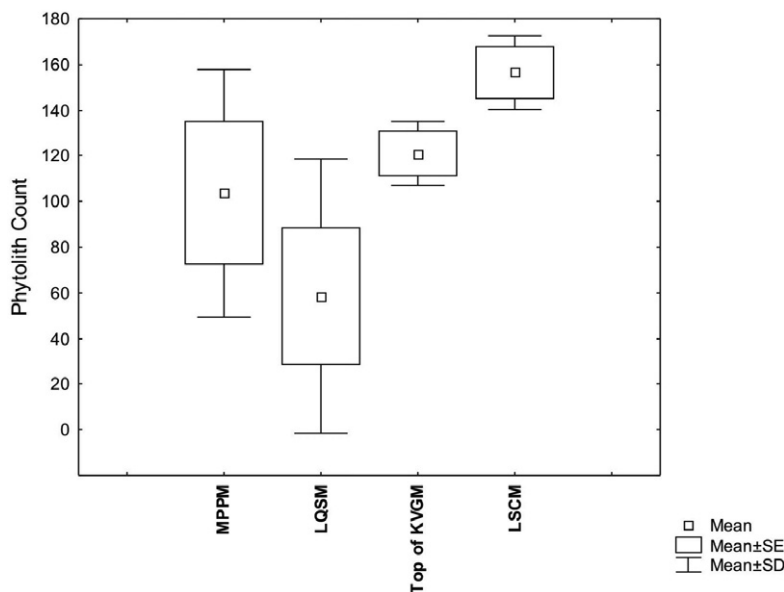

Fig. 3. Boxplot showing mean number of phytoliths counted per lithological unit: Muishond Fontein Pelletal Phosphate Member (MPPM); Langeberg Quartzose Sand Member (LQSM); Konings Vlei Gravel Member (KVGM); Langeenheid Sandy Clay Member (LSCM).

Table 1. Total number of phytoliths counted per sample.

Sample	Member	Weight (g)	Phytolith count
1	MPPM	50	47
2	MPPM	50	109
3	MPPM	50	155
4	LQSM	50	129
5	LQSM	50	88
6	LQSM	50	11
7	LQSM	50	6
8	Top of KVGM	50	111
9	Top of KVGM	50	131
10	LSCM	50	145
11	LSCM	50	168

Table 2. Number of phytoliths counted per sample according to each category.

Sample	Member	Poaceae	Restionaceae	Arecaceae	cf. Encephalartoideae	Unidentified phytoliths
1	MPPM	12	17	9	0	9
2	MPPM	29	35	16	0	20
3	MPPM	44	65	21	0	25
4	LQSM	26	33	18	0	52
5	LQSM	14	9	0	0	65
6	LQSM	0	3	0	0	8
7	LQSM	0	1	0	0	5
8	Top of KVGM	24	7	13	21	46
9	Top of KVGM	53	0	23	35	21
10	LSCM	84	4	9	0	48
11	LSCM	102	3	17	0	46
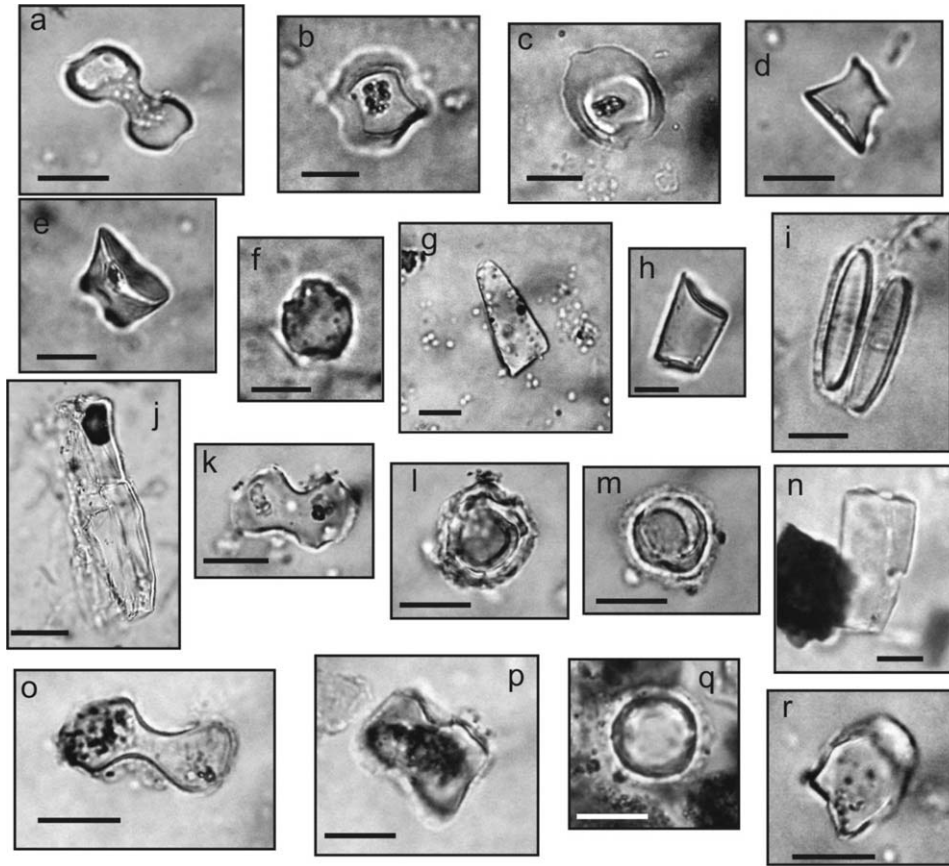
Fig. 4. Examples of distinctive phytolith types and other siliceous material identified in the Varswater Formation. A bilobate short cell (**a**), saddle short cell (**b**, **c**), rondel short cell (**d**), trapeziform phytolith (**e**), globular granulate phytolith (**f**), acicular phytolith (**g**), bulliform silica body (**h**) and bilaterally-symmetrical diatoms (**i**) from the LSCM. Unidentified, articulated and segmented silica bodies (**j**), bilobate short cell (**k**), and globular cavate phytoliths (**l**, **m**) from the top of the KVGM. A parallepipedal bulliform cell (**n**), bilobate short cell (**o**, **p**), globular sinuate phytolith (**q**), and a trapeziform silica body (**r**) from the MPPM. Scale bars = 10 µm.

Varswater Formation to ascertain the nature of Mio-Pliocene grass expansion in the southwestern Cape. This study will involve referencing modern plant material from the region, systematic soil sampling of the geological succession and evaluation of the fossil phytolith data through standard laboratory and analytical techniques.
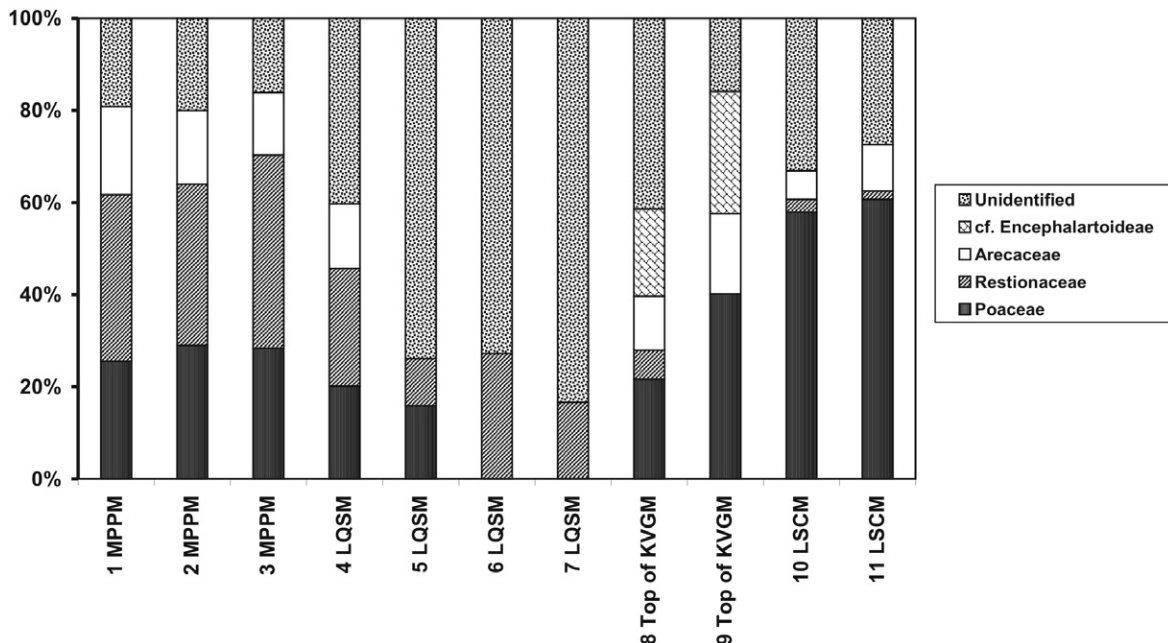
Fig. 5. Representation of phytoliths in a 100% stacked column. The graph compares the percentage each value contributes to the total across categories.

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