Earliest *Musa* banana from the late Quaternary sequence at Fahien Rock Shelter in Sri Lanka

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Abstract

The domestication and the time of arrival of bananas in South Asia and Africa are unresolved issues. We provide banana seed and leaf phytolith evidence from the archaeological sequence at Fahien Rock Shelter, located in southwest Sri Lanka, to help understand the geographical configuration of hybridization, dispersal, cultural association and chronology of banana domestication. Phytoliths from this sequence indicate that *Musa accuminata* subspecies and *M. balbisiana* existed in the south western lowland rainforest of Sri Lanka from 44,952-47,854 cal. BP., and rock shelter occupants exploited those taxa, possibly for starchy food. Edible diploid (AA) bananas may have introduced from elsewhere, possibly from Indonesia or PNG before 5,994-6,194 cal. BP. From this time onwards, phytoliths morphologically identical with those from triploid banana cultivars (AAB and ABB) appeared in the lowland rainforest of south western Sri Lanka. This precocity appears unique to Sri Lanka. Dispersal of these triploids to the east coast of Africa may have followed maritime trade networks in the Indian Ocean from the first half of the sixth millennium BP. Northward dispersal, e.g. to urban Harappan sites, happened in the middle of the fifth millennium BP. Sri Lanka's location in the Indian Ocean is thus important for understanding banana domestication and dispersal. This discovery shows the interconnection of prehistoric cultures and their engagement with the management of starchy staples in the lowland rainforests of Sri Lanka.

Key words: bananas, phytoliths, dispersal, maritime interaction, Sri Lanka.

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Introduction

Knowledge of *Musa* bananas (section: *Eumusa*) is important for understanding sustainable agriculture today, because domesticated bananas derived from *Eumusa* are globally the fourth most widely consumed crop used by humans after rice, wheat, and maize (Smith, 2010). Perrier et al., (2011) argue that understanding complex issues in the banana domestication process is essential in breeding programs and improving banana agriculture for the future. The earliest known domesticated banana cultivation (*Eumusa*) is at 6,950-6,660 cal. BP at Kuk Swamp in the Papua New Guinea (PNG) highlands (Denham, et al., 2003). The dispersal of domesticated bananas from PNG and their arrival in other regions in Asia and Africa on terrestrial (De Langhe, 2007) and maritime routes (De Langhe, 1995; Blench, 2009) are poorly documented, but the issue has recently been discussed using data from archaeology, phytoliths, genetics and linguistics (Perrier et al., 2011; Mindzie, et al., 2001; Lejju et al., 2006; Donohue and Denham, 2009; Fuller and Madella, 2009; Kennedy, 2008; Perrier, et al., 2009). Banana pytholiths are reported from Munsa, Uganda by 5,400-5,100 cal. BP (Lejju et al., 2005; 2006) and Kot Diji, Pakistan by 4,550-3,950 cal. BP (Fuller and Madella, 2009). The appearance of banana phytoliths at these early ages and their status as true *Musa* sp. cultivars have been questioned (Fuller and Madella, 2009; Neumann and Hildebrand, 2009). Banana phytoliths from Nkang, Cameroon, West Africa at 2,350-2,810 cal. BP (Blench, 2009; Mbida et al., 2000; 2004; 2005; 2006) have also been questioned (Neumann and Hildebrand, 2009). It seems that there is still dispute on chronological (Donohue and Denham, 2009; Neumann and Hildebrand, 2009), archaeological (Neer, 1990; Eggert, 2005; 2006; Mbida et al., 2001; Fuller et al., 2011) historical/linguistic (Blench, 2009; Vansina, 2003; Diamond and Bellwood, 2003) and archaeobotanical (Neumann and Hildebrand, 2009; Vrydaghs et al., 2003) grounds.

Identifying the exact appearance of domesticated bananas in archaeological contexts is challenging (Perrier et al., 2011; Donohue and Denham, 2009; Perrier et al., 2009; Vrydaghs et al., 2003; Ball et al., 2006; Lentfer, 2009; De Langhe, 2009a,b). The latter work suggested that banana seed and leaf phytoliths preserved in well-dated long archaeological sequences are the best proxies for understanding domestication process. Here, we address this issue by reporting the results of phytolith analysis from the deposits at Fahien Rock Shelter, Sri Lanka, which contains a sequence of cultural deposits from rainforest hunter-gatherers dating from 44,952-47,854 to 3,845-3,985 cal. BP.

Environment of the Fahien Rock Shelter

Fahien Rock Shelter (E 80° 12' 55" N 6° 38' 55" and 130 m above mean sea level) is situated in gneiss cliffs at Yatagampitiya Village, near Bulathsinhala in the Kalutara District in southwest Sri Lanka (**Fig. 1**). It is one of a complex of rock shelters (Cooray, 1984). Its mouth has a width of 30 m and an average height of 20 m. The interior is about 10 m deep and the floor slopes downward into the rock shelter. The regional climate is humid-tropical. Mean annual temperature is 27-29° C and rainfall is 5,016 mm, mostly from the South West Monsoon (SWM). This record is from the meteorological station in Sinharaja, in lowland rainforests, located some 10 km away from Fahien Rock Shelter (Zoysa and Raheem, 1987; Gunatillake et al., 2004). The surrounding landscape is today characterized by disturbed lowland rainforest. Paddy fields occur in the slightly incised valley system below the rock shelter.

Materials and methods

Litho-stratigraphy

Siran Deraniyagala first examined Fahien and excavated over several seasons between 1986 and 2012 under the direction of the Department of Archaeological Survey, Sri Lanka. This work led to the site being recognised as having, to date, the oldest archaeological sequence in Sri Lanka. The lithostratigraphy and archaeological contexts at Fahien were determined using a Harris Matrix, which is standard archaeological procedure (**Fig. 2; Table 1**). Excavations at two localities, named A (10 x10 m) and B (4 x 5 m), located respectively in the middle and east of the main chamber of the rock shelter, have shown potential for understanding the archaeological stratigraphy (Deraniyagala, 1992; Wijeyapala, 1997; Perera, 2010; Perera, 2015; Oshan, 2011). It is reported that historical human activity disturbed the lithostratigraphy at area A, but area B located ca. 2.40 m of *in-situ* well-stratified heterogeneous clast-rich loamy sediments with a relatively good chronology. The lithostratigraphic record comprises five major lithological layers, 10 archaeological phases and approximately 250 archaeological contexts. The lowest deposits (below layer 5), are yellowish brown consolidated clast-rich loam. Layer L5; is pinkish grey to greyish brown, moderately unconsolidated loam. L4 is dark grey to brown loam of medium compactness. L3 is light brown, moderately unconsolidated loam. L2 consists of yellowish brown, moderately unconsolidated loam. The top layer (L1) comprises brown to reddish brown loam (Table 1).

Biotic and archaeological remains

The sediments of L5 at area B contain shell beads, animal teeth (e.g. *Semnopithecus priam*, *Ratufa macroura*, *Parradoxurus* sp., *Trachypithecus vetulus* and *Macaca sinica*), human bones, burnt and unburnt shells (e.g. *Acavus* sp. and *Pila* sp.), charcoal, wild breadfruit (*Artocarpus nobilis*) epicarps, *Canarium* nuts, coprolites and stone artefacts. Human remains include several internments; some coated with red ochre, and are associated with the earliest microlithic and osseous technologies found anywhere in South Asia. The layer is dated on charcoal and charred materials to 39,850-35,750 cal. BP (**Table 2**). Phase VI in the sequence has been characterised as showing intensive human habitation, as indicated by the presence of a highly fragile and fragmentary human skeleton in a set position (Perera, 2010; 2015; Oshan, 2011; Perera, et al., 2011). This has recently been dated to around 12,000 cal. BP (Perera, 2015). The stratigraphy also contains palaeo-floors, postholes, excavated pits and preserved hearths (**Fig. 2; Table 1**).

Chrono-stratigraphy

Renewed excavations at Area B have yielded a secure chronology for the earliest evidence of human activity (Perera, 2010; 2015; Oshan, 2011; Kinnaird, 2011). Well preserved, *in-situ* charcoal, charred wood, shells and sediment samples were collected for ^{14}C and OSL dating (**Table 2; Fig. 2**). Radiocarbon dates were produced using Accelerator Mass Spectrometry at the ^{14}CHRONO centre, Queens University, Belfast and the Beta Analytic Laboratory in the USA. They were calibrated using Calib 6.11 (Reimer, et al., 2009).

The lowest habitation deposits (below L5) included relatively minor cultural content (e.g. a few fragments of microlithic flakes and human bone) compared with L5. From the lowest deposits (context 92), two sediment samples were OSL dated to 39.9 ± 2.5 ka (SUTL2327) and 22.0 ± 1.3 ka (SUTL2326) and one sample (context 92/91) was AMS dated on charred materials to 44,950-47,854 cal. BP indicating that Fahien Rock Shelter contains one of the earliest occurrences of anatomically modern humans in South Asia (Perera, 2015; Premathilake and Hunt 2017; **Table**

2). AMS dates obtained from charred materials, charcoal, *Canarium* cf. *zylanicum* nut and freshwater shells indicate that the deposits accumulated between 44,950-47,854 cal. BP. to 3,844-3,985 cal. BP. The most significant late Pleistocene archaeological evidence, which includes the oldest microlith toolkits known to South Asia, is associated with contexts 87 to 92; which are dated to between 44,950-47,854 and 27,860-29,089 cal. BP.

Sample selection, sediment processing and identification

Twelve 30x10x8 cm monoliths were taken from the southern profile of Fahien Rock Shelter Area B. These covered the five major layers (L1-L5) including the described archaeological phases (I-X) (Perera, 2010; 2015). Seventeen subsamples were selected from these monoliths for phytolith analysis (**Fig. 2**). In this procedure, eleven subsamples were extracted from the deposits of early to late Holocene age in part of a pit which was filled (C-86; C-68; C-53; C-52; C6), stratified (C-11; C-10; C-44) and re-worked (C-32; C-31; C-5). Six subsamples (C-92; C-91; C-89; C-88; C-87; C-81) were from the lowermost stratigraphic sediments of terminal to late Pleistocene age (**Fig. 2; Table 1; Table 2; Fig. 3**). Techniques and methods (e.g. Lentfer and Boyd, 1998; Jenkins, 2009; Geiss, 1973; Carter, 2007; Perera, 2017; Premathilake et al, 2017a,b) used for fossil (**SI1a)** and modern (**SI1b**) banana phytolith extraction, precise identification (**SI2a-b**) and microscopy (**SI1a**) are described separately in the Supplementary Information.

Results

Phytolith assemblages from the four different sample sets are shown in **Fig. 3**. Well-preserved phytoliths are variable in number, with counts ranging from 500 to 4000. Very few samples contained pitted phytoliths, or displayed few relatively large microchannels and mineralized microstructures. Broken phytoliths were rare. More than 54 morphotypes were identified. Note that this paper mainly considers detailed records of banana phytoliths, while the phytolith records of other taxa will be published separately.

Sample set 1: 44,952-47,854 to 11,936-12,239 cal. BP.

Phytolith counts decreased upwards through this sequence. High percentages of wild banana seed and leaf phytoliths, and disturbed-habitat lowland forest taxa (dicotyledonous and monocotyledonous) were found in all habitation deposits. Substantial quantities of burned phytoliths including *Musa* spp. occur. Freshwater diatom (e.g. *Navicula* cf. *contenta* and *Aulacoseria* spp.) counts increased upward through the sequence. A few brackish/marine diatoms (e.g. *Vanheurckia* cf. *lewisiana* and *Nitzschia cf. reinholdii*) were identified in three samples.

Sample set 3 (stratified sediments): 8,423-8,581 to 5,475-5,547 cal. BP.

Phytolith percentages of wild banana decrease while phytoliths from leaves of domesticated bananas appear in layer C-11 and above this level increased significantly. Phytoliths from monocotyledonous and dicotyledonous taxa occur commonly and blackened phytoliths are also common. Freshwater diatom counts relatively increased and a few marine diatoms were found.

Sample set 2 (pit fill): 5,475-5,547 to 3,845-3,985 cal. BP.

The samples from the pit fill probably reflect taphonomically-mixed material as the pit was excavated through stratified sediments of Sample set 3 (with an upper age of 5,475-5,547 cal. BP) but incorporate old carbon including the charred material dated to 7,817-8,019 cal. BP. Phytoliths from wild banana seeds and leaves decrease significantly in this material. The lowest phytolith counts occur in sample C-86; where wild banana seed phytoliths abruptly decrease. This coincides with the very first appearance in the pit fill of a few volcanifrom phytoliths derived from domesticated banana leaves. Phytoliths from monocotyledonous and dicotyledonous taxa increased. Samples C-68 and C-6 also contained a very few volcanifroms of domesticated bananas. Blackened phytoliths were common. The freshwater diatom count decreased. A few marine diatoms occur in two samples (C-68; C-6).

Sample set 4 (re-worked sediments) < 3,845-3,985 cal. BP.

There is a considerable decrease in phytoliths from leaves and seeds of wild bananas. Domesticated banana phytoliths occurred in one sample (C-5). Phytoliths from monocotyledonous and dicotyledonous taxa increase. Blackened phytoliths decrease significantly. Diatoms from fresh and marine/brackish water environments were present in varying frequencies.

Discussion

Formation of the rock shelter stratigraphy

Knowledge of the lithostratigraphy is imperative for interpreting rock shelter phytolith assemblages, although many challenges still lie ahead of investigators in terms of understanding how sediment stratigraphy can be developed (Stephens et al., 2005; Barker and Farr, 2016; Butzer, 2008; Friesem, 2016; Zurro et al., 2016). The sediments of Fahien Rock Shelter are heterogeneous. Geoarchaeological and archaeological analysis of the ca. 250 contexts suggests they result from very complex sedimentary processes (Perera, 2010; 2015; Oshan, 2011; Kourampas, 2009). The majority of dates are in good stratigraphic order from L5 to L1.

The chronology indicates that significant depositional hiatuses occur within the excavated sequence between the late Pleistocene and late Holocene (**Fig. 2; Table 2**). The oldest sample, from context 91/92; just above the date of 44,952-47,854 cal. BP. contains a very high number of phytoliths suggesting significant human activity (Premathilake and Hunt, 2017). A major hiatus extended from C-87 to C-81 (27,860-29,089 to 8,423-8,581 cal. BP) and is marked by the reduction of phytolith sums (**Fig. 3**).

The hiatuses can be explained by alternating periods of desiccation and erosion of the rock shelter sediments. The desiccation corresponds with several severe millennial to multi-century scale arid/semi-arid climatic cycles due to monsoon failures, identified from peat and sedimentary archives in southern Asia between 24,000 cal. BP and 8,100 cal. BP (Premathilake and Risberg, 2003; Premathilake and Gunathilaka, 2013). Multi-proxy studies (Premathilake and Risberg, 2003; Petraglia, 2009; Premathilake, 2006; 2012) indicate the prevalence of high rainfall events at 17-650-16,200; 13,700-12,800; 10,400-9,900; 9,200-8,800 cal. BP, caused by Inter-Tropical Convergence Zone-induced monsoon intensification. These may have caused severe erosional episodes affecting the rock shelter sediments (**Fig. 2**). The erosion episodes are contemporary with periods of increased landslide frequency in the landscape around the rock shelter (Kourampas, 2009) suggesting that the impact of climate and environment were the dominant factors forming the litho-stratigraphy through the late Pleistocene and early Holocene. Accumulation of clast-rich loams gradually resumed, caused by the combined effect of the increasingly semi-arid climate and human activities including biomass burning and foraging associated with lowland to upper montane rainforests after 8,800 cal. BP, (Perera et al., 2011; Kourampas, 2009; Premathilake, 2003; 2006). It seems that anthropogenic sedimentation, particularly accumulation of human habitation debris and sediment entrained by human action was prominent during the middle-late Holocene, but the accumulation rate varied very markedly between and within major layers throughout the sequence (**Fig. 2**). Detailed geo-archaeological research (soil micromorphology) with additional radiocarbon dates will provide more information that will further enhance and clarify the current understanding of the depositional history of the sequence (Friesem, 2016).

Phytolith taphonomy

Macrofloral remains including seeds, epicarps, charcoal, and wood, recovered from several rock shelter deposits in Southwestern Sri Lanka, were used to address archaeological issues such as subsistence models and in understanding depositional environments, although taphonomic processes may not have been considered in all cases (Deraniyagala, 1992; Perera, 2010; Perera et al., 2011; Kourampas, 2009; Roberts et al., 2015, 2017). Phytoliths, however, have not been discussed in detail. In the case of Fahien Rock Shelter, taphonomic investigation was essential to understand how phytoliths reached the site and how they were deposited and preserved. The presence of phytoliths in the rock shelter sediments may provide information about the depositional processes in several ways (1) plants living and decaying *in situ* (2) alluvial or colluvial re-deposition along with associated sediments (3) wind deposition and (4) cultural deposition through discarded plant materials used by rock shelter occupants for food and other cultural purposes (5) arrival of phytoliths through animal activity, for instance in dung.

The lack of living dicotyledonous and monocotyledonous plants and the lack of organic litter in the rock shelter (Premathilake and Hunt, 2017) suggests minimal deposition from plants living *in situ* or nearby. Abundant phytoliths from diverse dicotyledonous and monocotyledonous taxa in the samples suggest that alluvial and/or colluvial processes may have played a role in phytolith re-deposition, since many have no obvious cultural utility. The overhang prevents rainwater penetration into the rock shelter, but it is possible that surface flows originating outside the rock shelter could have carried phytoliths into the site. Wind deposition is rare today due to the particular geomorphology of the rock shelter in the humid tropical environment, and it was most likely rare in the past.

The main process, therefore, of phytolith deposition in the rock shelter is most likely to have been through human or animal vectors. Animals such as bats, birds, and insects, common in the vicinity of the rock shelter, are most unlikely to have played a role in phytolith deposition, however, since their lifestyle is inconsistent with them carring around quantities of leaf litter. The highly variable phytolith counts through the sequence (**Fig. 3**) and selective distribution of phytoliths from bananas used by rock shelter occupants suggest that most phytoliths were brought into the cave by people and remain *in-situ*. Hunt et al. (2016) suggested that similar strong patterning at Niah Cave was evidence for anthropogenic deposition. Thus, it is inferred that humans are the most likely agents for phytolith deposition – with materials from economically significant plants such as banana, breadfruit and palms from plants commonly growing in disturbed lowland rainforest near to the rock shelter (most likely within a few kilometers at most). Abundant phytoliths from monocotyledonous taxa - grasses and sedges - are identified as economically-useful taxa in this context. The significant occurrence of freshwater and brackish-marine diatom species throughout is not surprising in habitation deposits (Hunt et al. 2016) and is consistent with a number of human activities involving activity in wetlands ant the carrying of material encrusted with diatoms into the rock-shelter (Kanthilatha et al., 2017).

In the majority of samples, abundant banana seed and leaf phytoliths, together with the lack of taphonomic markers such as size sorting, breakage, corrosion, microchannels, dissolution pits, mineralized microstructures, cut marks and pitting, indicate excellent preservation conditions. This suggests high phytolith compositional fidelity in the samples. Excellent preservation conditions are further attested by the very common occurrence of variably durable phytoliths (e.g. globular echinates, volcaniforms, trichomes, elongate sinuous and bilobates) and very few phytoliths with isolated cavities, with occluded carbon. Those few phytoliths containing cavities, can perhaps be explained as the result of the natural silicification process, as evidenced by the modern phytolith collections. They are not related to taphonomic processes such as dissolution during fossilization.

Although they were directly subjected to the processes of diagenesis (i.e., physical and chemical impacts on phytoliths due to long-term burial and permanent incorporation into the stratigraphy), the well-preserved phytoliths suggest these impacts were minimal (Alexandre et al., 1997, 2015;

Behrensmeyer et al., 2000; Fredlund and Tieszen, 1997; Albert et al., 1999, 2006; Piperno, 2006; Farmer et al., 2005; Gérard, et al., 2008; Loucaides et al., 2008, 2010; Osterrieth, et al., 2009; Karkanas, 2010; Borrelli et al., 2010; Cabanes et al., 2011, 2012). Alkaline conditions are thought to contribute to phytolith dissolution processes (Loucaides et al., 2010; Cabanes et al., 2011; Fraysse et al., 2006, 2009) because of the increase in solubility of silica at pH > 7.8. In the iron-rich, fine-grained, Fahien sediments this was most likely limited, as indicated by pH measurements (6.5-7.3) in all the sediment samples studied (cf. Piperno, 1988). Facetate and sclereid phytoliths from woody dicotyledons (e.g. forest taxa) are rare in late Pleistocene and Holocene samples, possibly because of dissolution (Piperno, 2006), and/or minor incorporation of phytoliths from woody materials. We acknowledge that the production of facetate and sclereids from the modern forest plant species is relatively high, but they are very unlikely to be preserved in much older samples (Premathilake et al., 2017b).

Except in the very uppermost parts of the sequence, the absence of post-depositional disruption through root penetration, roof fall, vertical sediment cracks, human digging and animal burrowing and the lack of evidence for disruption within the clay- and silt-rich, highly-compacted and multi-layered sediments indicates likely very limited vertical movement of phytoliths (Perera, 2010; 2015). The distribution of the smallest phytoliths (e.g. small rectangles from wild banana seeds and globular nodules from Bombacaceae) and fine-grained sediments suggests the minimal impact of illuviation of clay minerals, reported as a common process in some rock shelter stratigraphies (Butzer 2008; Kourampas, 2009; Alexandre et al., 1997). All these minimized sources of bias indicate that spatial and temporal fidelity is relatively high in this rock shelter phytolith stratigraphy (Behrensmeyer et al., 2000). Therefore phytoliths buried in deep stratigraphic levels are likely to be securely *in-situ* and unaffected by bioturbation, suffusion, infiltration or corrosion.

Wild *Musa* banana exploitation

Today, more than 50 *Musa* species are recorded in tropical and subtropical regions (Fuller and Madella, 2009; Cheesman, 1947; Simmonds, 1956; 1962; Itino et al., 1991; Constantine, 1999-2008; Ge, et al., 2005; Häkkinen and Väre, 2008). In Sri Lanka, *M. acuminata* and *M. balbisiana*, the only two wild species, commonly grow in disturbed lowland rainforest from sea-level up to 900 m, and they are used for food and various cultural purposes by local peoples (Chandraratne and Nanayakkara, 1951; Perera, 2017). The Pali chronicle '*Mahavamsa*', written in the 5th century AD, reported the presence of wild banana (*attikehel*) with various uses. Ethnobotanical investigations indicate that immature and mature fruits with or without seeds, leaves, young leaf sheaths, the male inflorescence bud, male flowers, fruit peels, pseudostem, sucker/shoots, rhizome and ash of wild banana were widely used for purposes including plates, wrapping food, medicine, stimulants, textiles, clothing, packaging, paper-making, craft industry, ornaments and also ceremonial, magic and ritual activities in the countries of south and southeast Asia (Fuller and Madella, 2009; Simmonds, 1956, 1962; Albert et al., 2000; Kennedy, 2009).

High amounts of phytoliths of wild *Musa* banana seeds and leaves, and of other economic plants (Premathilake and Hunt, 2017) recovered from the samples, combined with cultural evidence including human bone, artifacts and hearths (**Table 1**) indicate that the rock shelter occupants exploited bananas from 44,952-47,850 cal. BP. The banana phytoliths in the late Pleistocene samples are identical to those found in modern *M. accuminata* and *M. balbisiana* populations in Sri Lanka (**Figs. 4a-b, SI1b, SI2a, Figs SI1-2; Table SI1; SI6-7; SI9; SI11**). This suggests that these two species existed as natural populations in association with open habitats amongst anthropogenically-affected lowland rainforest in Southwestern Sri Lanka while it was responding to changing climatic regimes through the latter part of the Last Glacial Period and early Holocene (Fuller and Madella, 2009; De Langhe, 2009b; Premathilake and Risberg, 2003; Premathilake, 2003, 2006, 2012; Roberts et al., 2015, 2017). This is consistent with the abundant phytoliths of wild banana seeds and relatively high number of monocotyledonous and burnt phytoliths and scarcity of phytoliths of woody dicotyledons, **(Fig. 3**). Charred seeds of the two species at Beli-lena rock shelter are of terminal Pleistocene age (Kajale, 1989).

Our phytolith results demonstrate that use of bananas, perhaps mainly for starchy food, was present from the beginning of rock shelter occupation from 44,952-47,850 cal. BP. Possibly, bananas were associated with a variety of ethnobotanical purposes, but this remains as an open question in the current work. The common occurrence of burnt (blackened) banana seed phytoliths associated with ashy deposits, charcoal and bone fragments from hearths (Perera, 2010; **Table 1**); suggests perhaps the roasting and inadvertent burning of banana fruits may have released blackened phytoliths, suggesting possible employment of food processing techniques (Heyne 1950; Perera, 2010; Kanthilatha et al., 2017). However, the available phytolith evidence is not enough to understand the relationship between the phytolith assemblages yielded by processing techniques and the phytoliths found in rock shelter floors (Kanthilatha et al., 2017). Such questions address the behavioural richness of the occupants in order to clarify the detailed archaeological picture at the rock shelter, in association with the use of shark vertebra, marine shells as beads and a shell pendant for ornamental purposes at 38,000 cal. BP (Perera, 2010; Perera et al., 2011; Roberts and Petraglia 2015). This is relatively younger than the late Pleistocene human rainforest occupation demonstrated in Sri Lanka, as well as the oldest multi-proxy evidence from the Niah Cave, Sarawak dating to 53,000 cal. BP (Barker, 2011; Barker and Farr, 2016; Hunt et al., 2016).

Appearance of domesticated banana in Sri Lanka

Currently, evidence for prehistoric banana cultivation in south Asia remains very sparse due to lack of systematic sampling and archaeobotanical - seed and phytolith - analysis in most archaeological excavations (Fuller and Madella, 2009). Banana seed and leaf phytoliths from the Fahien Rock Shelter open up the possibility of improving understanding of banana domestication, dispersal of early cultivars and the histories of the people involved (Vrydaghs et al., 2003, 2009; Ball et al., 2006; De Langhe, 2009b).

In the early Holocene sample (C-81), wild banana seed phytoliths are present in quantity suggesting use of seeded bananas. Low incidences of phytoliths of dicoteledonous plants suggest an open rainforest canopy, perhaps maintained by climatic activity but alternatively maintained as open by human activity (c.f. Hunt and Rabett, 2014; Roberts et al. 2017).

A relatively high number (5-20%) of *Musa* banana leaf phytoliths in samples C-86 C-68, C-6, C-11, C-10, C-44 and C-5 are identical to those found in modern domesticated banana plants, perhaps indicating the appearance and adoption of domesticated bananas during the mid Holocene, at 5,994-6,194 cal. BP (**Figs. 3; 5-6; Table 3; SI2b, Figs. SI1-2; Table SI2-5; 8; 10**). At the same time, the increase of phytoliths from woody dicotyledonous taxa suggests that the rainforest canopy closed (Roberts et al., 2015; 2017), consistent with a major climatic event or change in forest management practices. An increasing trend in the use of seedless bananas (domesticated) is attested by the remarkable decrease of banana seed phytoliths from wild plants. The domestication process ends in sterility, with seeds no longer produced. This pattern corresponds with the hypothesis of De Langhe (2009b), for tracking banana domestication in the archaeological context.

Morphometric records (e.g. crater length) suggest that phytoliths identical with those of domesticates in sample sets 2 and 3 derived from triploid AAB and ABB bananas (cf. Vrydaghs et al., 2009). Appearance of these triploids can be explained by the process of (a) domestication of *M. acuminata*, with the edible AA diploids, followed by (b) hybridization of the latter with either *M. acuminata* or *M. balbisiana*, leading to additional diploid AA and to AB hybrids and, *via* meiotic restitution, to triploid AAB and ABB. Edible AA diploids may have appeared before 5,994-6,194 cal. BP, at the onset of the wild-cultiwild-edible AA process in Sri Lanka (Fig. 3), or it is possible that this occurred elsewhere. However, it is difficult to distinguish wild from these edible diploids through comparative studies of leaf phytoliths, either by morphometric or morphological means (Ball et al., 2006; Vrydaghts et al., 2009). It seems that the domestication process leading to those hybrid triploids were not with *M. acuminata* ssp. *burmannica* (A-genome), that naturally covers the *acuminata* area centered on northeast India, Burma, southern China, Thailand and Sri Lanka as a wild ancestor, since this subspecies cannot evolve to domesticated edible AA diploids because lack of parthenocarpy potential (Perrier et al., 2009; 2011). Thus, we argue that edible AA parents were introduced from elsewhere; originally from the Indonesia-PNG zone where abundant edible AA diploid banana cultivars from subsp. *banksii* have been suggested to be the parents of several triploids, including some Indian AAB and ABB types (Simmonds and Shepherd, 1954; Denham et al., 2003; Bulbeck, 2008; Perrier et al., 2009; 2011). It seems that early appearance of edible AA diploids and the triploids was unique for Sri Lanka, and/or occurred elsewhere, but understanding these issues need additional investigations. Today, 29 modern banana cultivars include the AAB triploid (e.g. *Ambul*, *Kolikuttu*, *Suwandel* and *Puwalu*, in local langue) are commonly cultivated in Sri Lanka (Chandraratne and Nanayakkara, 1951; Perera, 2017) suggesting that triploid banana cultivars may have been generated as a direct consequence of the local geographical configuration of hybridization and dispersal during the Holocene, but the cultivars may not have been introduced into Sri Lanka from PNG or the Philippines at this antiquity (Perrier et al., 2009; 2011; Bulbeck, 2008).

Banana dispersal

Synthesized genetic, linguistic and archaeological records of banana dispersal indicate that domesticated diploid and triploid banana cultivars originated in at least three areas (Smith, 2010). This includes the South contact (between PNG region and Java), the East contact (between PNG and the Philippines and the North contact (among the Philippines, Borneo and mainland Southeast Asia) (Denham et al., 2003; Perrier et al., 2011). The available records suggest that anthropic translocation of banana cultivars was may have led to the establishment of South Asian and African banana cultivation through the middle to late Holocene (De Langhe, 2007; Perrier et al., 2009; 2011; Blench, 1996). The Fahien phytolith evidence provides new light on this dispersal including geographical occurrence, cultural associations and calibrating the relative chronology available.

The earliest banana phytoliths from the Harappan site of Kot Diji in Sindh (Pakistan) indicates that *Musa* banana were identified, based on their morphometry (crater width = 11.4-15.7 μm; basal length = 34.2μm), and these have been dated to the middle of third millennium BC (4,400 cal. BP, Madella, 2003; Fuller and Madella, 2009). The authors suggested that phytoliths in Kot Diji may have been derived from AAB and/or ABB cultivars. It was proposed that anthropic translocation of domesticated bananas (AA cultivar) began in the South contact area (between PNG region and Java) and dispersed first towards to mainland southeast Asia, where it contributed to towards producing the triploid, AAA, and then to India/Kot Diji area, where it came into contact with *M. balbisiana* to produce the AAB cultivar at 4,400 cal. BP. (Simmonds and Shepherd, 1954; Madella, 2003; Ball et al., 2006; De Langhe, 2007; Fuller and Madella, 2009; Perrier et al., 2011). From our results, it is suggested that domesticated banana cultivars (AAB) reached Kot Diji area from Sri Lanka where the long tradition of banana exploitation with their cultivars occurred earlier. This indicates exchange of cultural objects and performances including triploid banana cultivars occurred between Sri Lanka and India following maritime network connections (Gulf-India trade network) established through the northwestern part of the Indian Ocean, in the middle of fifth millennium BP, i.e. in Harappan urban time. This agrees with the archaeobotanical, archaeozoological, palaeoecological and genetic evidence (Fuller, 2003; Fuller et al., 2011; Fuller and Boivin, 2009; MacDonald, 2011; Prasad et al., 2014).

Very early phytolith evidence (crater width = 5-10 μm; basal length = 15-25 μm) dating to the first half of fourth millennium BC (5,492-5,100 cal. BP; Lejju et al., 2006) from Munsa, an archaeological site in Uganda, in the African continent suggests that AAB Plantains and AAA Highland cooking bananas were directly introduced from the East and South contact areas in southeast Asia to Africa across the Indian Ocean (Perrier et al., 2009; 2011). AAB cultivars are scarce and AAA are nonexistent in the entirety of mainland Asia and Sri Lanka. The Fahien phytolith evidence suggests that the introduction of AAB and ABB from India and Sri Lanka could be linked to the Arabian civilization and to colonial activity. This indicates that trade networks between the East coast of Africa and India across the north-western Indian Ocean were established earlier than previously thought from the archaeological evidence (Fuller et al., 2011; Blench, 1996; Fuller, 2003; Fuller and Boivin, 2009).

There has been discussion about the proposed mode of banana dispersal by terrestrial (De Langhe, 2007) and maritime routes (De Langhe, 1995; Blench, 2009) from South East Asia to South Asia and Africa (Perrier et al., 2009; 2011), but no conclusive evidence has been obtained. We argue that the rapidity of the dispersal is consistent with movement by sea. In this regard, Sri Lanka was a possible centre for early banana dispersal in the Indian Ocean, where an early movement of artifacts and staples occurred as early as the first half of the sixth millennium BP. However, understanding of the associated routes and of timing of banana dispersal is still disputed on chronological (Neumann and Hildebrand, 2009), archaeological (Fuller et al., 2011), historical and linguistic (Blench, 2009; Diamond and Bellwood, 2003) and archaeobotanical (Vrydaghs et al., 2003; Lentfer, 2009; Madella, 2003) grounds. The findings from this study may help to settle a long-standing debate about how early humans developed cultural interactions between South Asia and Africa. Phytolith investigations and radiocarbon dating from a number of archaeological sites in conjunction with linguistic research may provide essential data that would contribute towards a better understanding of complex issues of banana domestication and dispersal patterns.

Conclusion

Banana seed and leaf phytoliths preserved in the archaeological sequence at Fahien Rock Shelter, located in Yatagampitiya village near Bulathsinhala in the Kalutara District in southwest Sri Lanka provide new insights into the contexts associated with geographical configuration of hybridization, dispersal, human contacts, and the chronology of banana domestication. The geographical conjunction of *Musa accuminata* subspecies and *Musa balbisiana* were remarkably early in the south western lowland rainforest of Sri Lanka. These two species were present from the beginning of the rock shelter occupation from 44,952-47,854 cal. BP. Edible diploid (AA) bananas may have introduced from elsewhere, possibly from the Indonesia-PNG zone before 5,994-6,194 cal. BP. From this time, triploid banana cultivars (AAB and ABB) appeared in the human-influenced lowland rainforest of south western Sri Lanka. This early appearance seems to have been unique to Sri Lanka. The banana cultivar dispersal from Sri Lanka northwards to urban Harappan sites during the middle of the fifth millennium BP, and westwards to the east coast of Africa during the first half of the sixth millennium BP may have followed maritime trade networks through the Indian Ocean. The evidence suggests that Sri Lanka's location in the Indian Ocean is important for understanding banana domestication and dispersal.

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Figures

Fig. 1. A: Location of the Fahien rockshelter in Sri Lanka. Area marked by dark green color receives relatively high rainfall (>2,500 mm/yr) from the South West Monsoon while area marked by light green color receives relatively low (< 2,500 mm/yr) rainfall from the North East Monsoon. B: Contour map providing topographic context of the rock shelter.

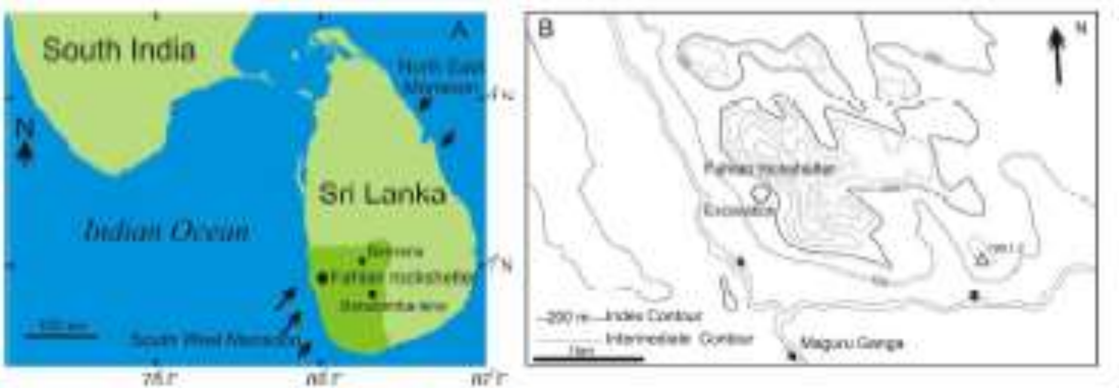


Fig. 2. X: Plan of the rock shelter with excavated areas (A and B). Y: Stratigraphy with the archaeological layers (L5-L1). Re-worked and pit fill sediments together with chronology of the sequence from the excavated area B are shown. Contexts are marked by numbers. Locations of the monoliths and subsamples taken for phytolith analysis are indicated.

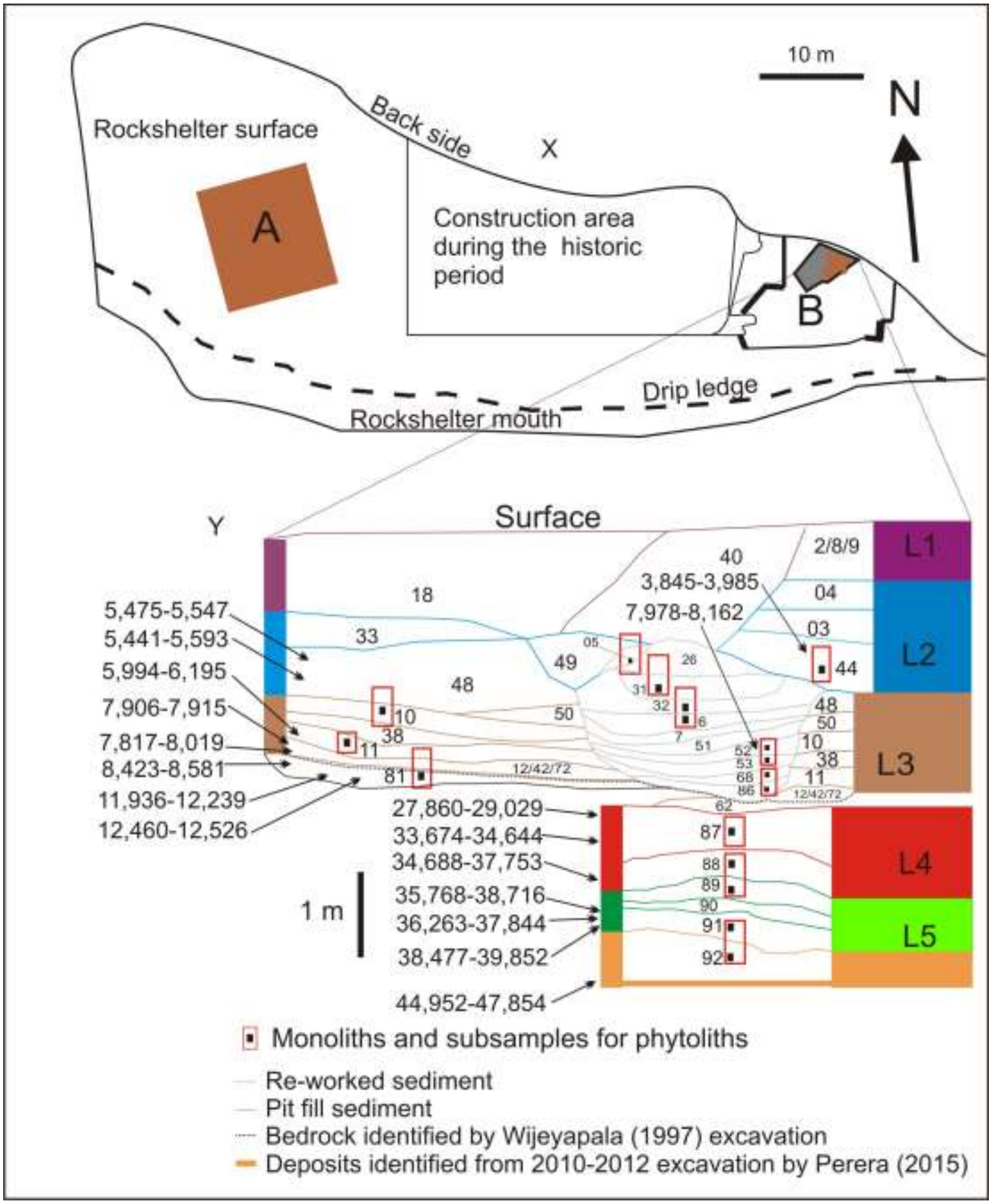


Fig. 3. Percentage summary phytolith diagram from the studied Fahien sequence in Excavation Area B.

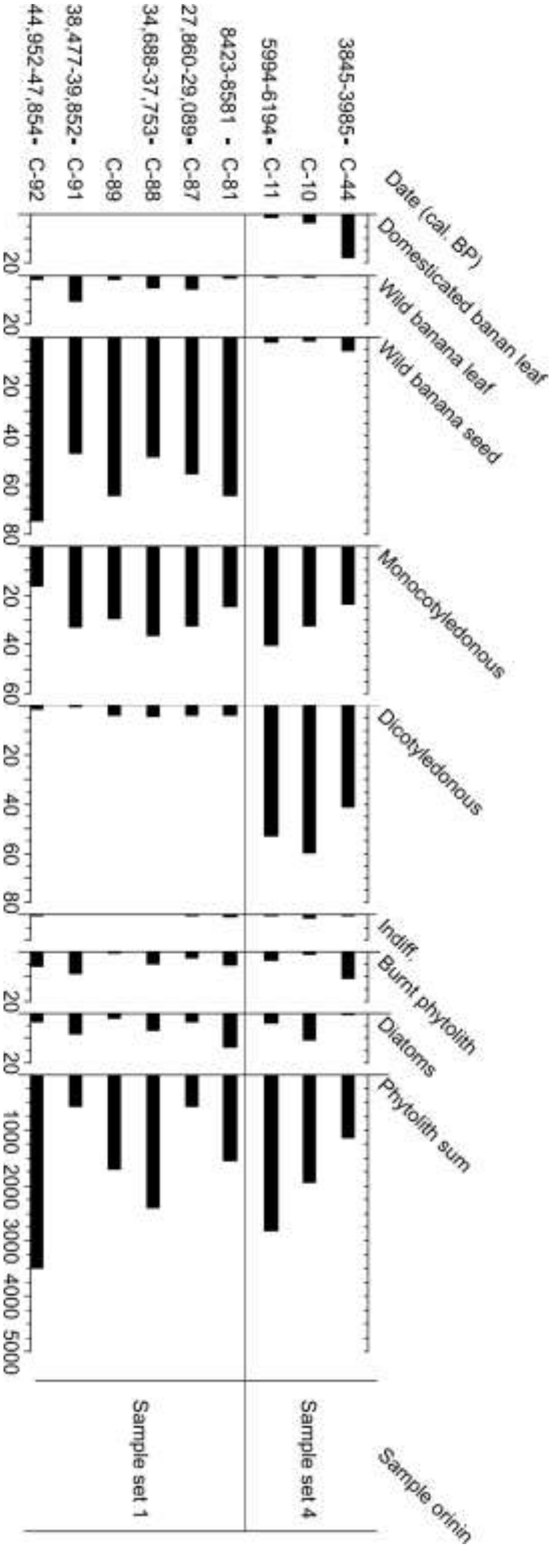


Fig. 4a. Phytolith morphotypes from the modern plants. Seed phytoliths of *Musa accuminata* (1-9): 1-2: volcaniforms which are characterized by rectangular and square base with few protuberances, 3-6: irregular faceted and elongate with irregular short grooves, 7-9: faceted with nodules. Seed phytoliths of *M. balbisiana* (10-17), 10-11: volcaniforms which are characterized by variable base with more protuberances. 12-15: irregular faceted with elongate well defined regular long grooves. 16-17: faceted with nodules. Volcaniform variants (V1-V8) from leaf of *M. accuminata* (18) and *M. balbisiana* (19). Crater, basal and protuberances of volcaniform are marked. Scale bar = 10 μm. (cf. Ball et al., 2006, Fig. SI1-2).

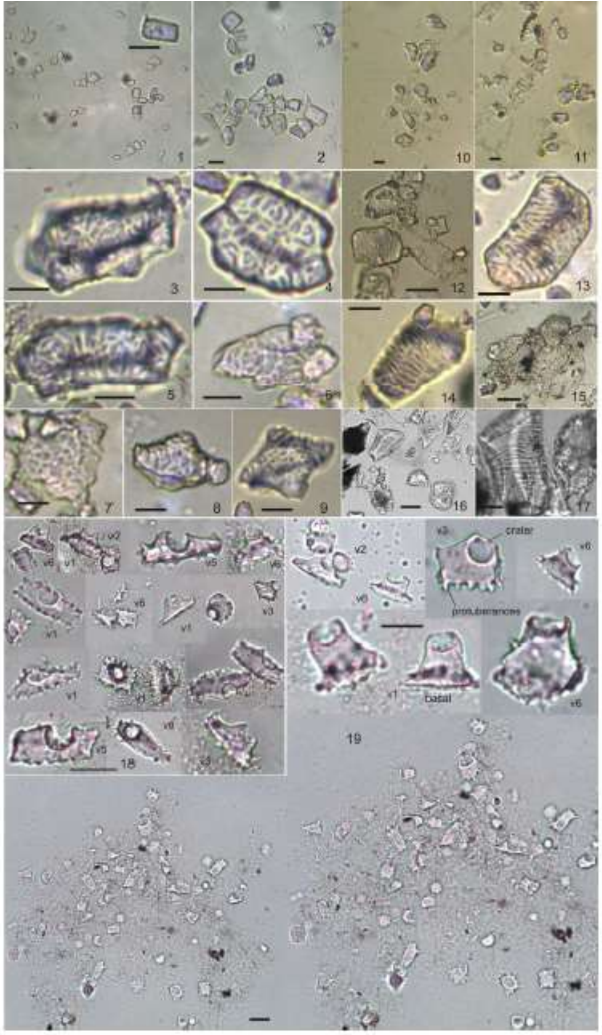


Fig. 4b. Wild banana phytoliths from Fahien rock shelter. 1-21: volcaniform variants (V1, V2, V3, V5 and V6) derived from wild banana leaves. 22-24: phytoliths from *M. balbisiana* seeds (cf. Fig. 5a). 25-26: phytoliths from *M. accuminata* seeds. 27-28: small volcaniform phytoliths derived from wild bananas seeds. (cf. Fig. 4a). Scale bar = 10 µm.

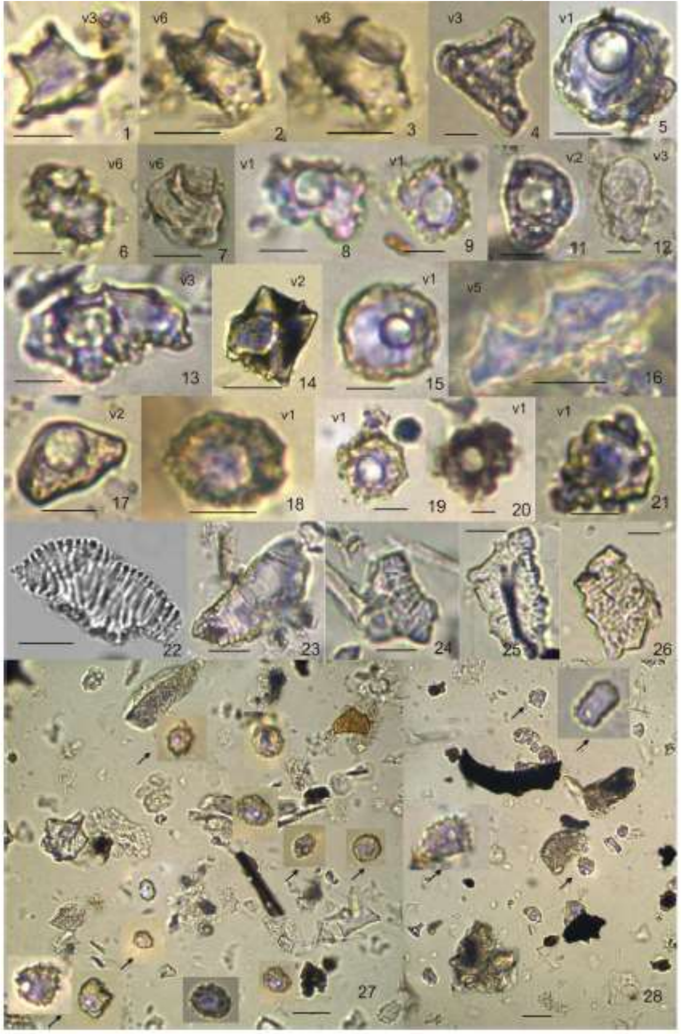


Fig. 5. Phytolith morphotypes from modern plants. Light micrograph (1-21) and scanning electron micrograph (22-25) of volcaniforms variants (V1-V8) from the leaf of domesticated bananas. The variants observed from domesticated banana samples are usually larger than wild banana species growing in Sri Lanka. V3 and V6 are the most common variants. V6 has a tendency to be higher in frequency among wild bananas than in domesticated bananas. V3 tended to be higher in frequency among domesticated bananas than in wild bananas (cf. Perera, 2016; Ball et al., 2006). Scale bar = 10 μm.

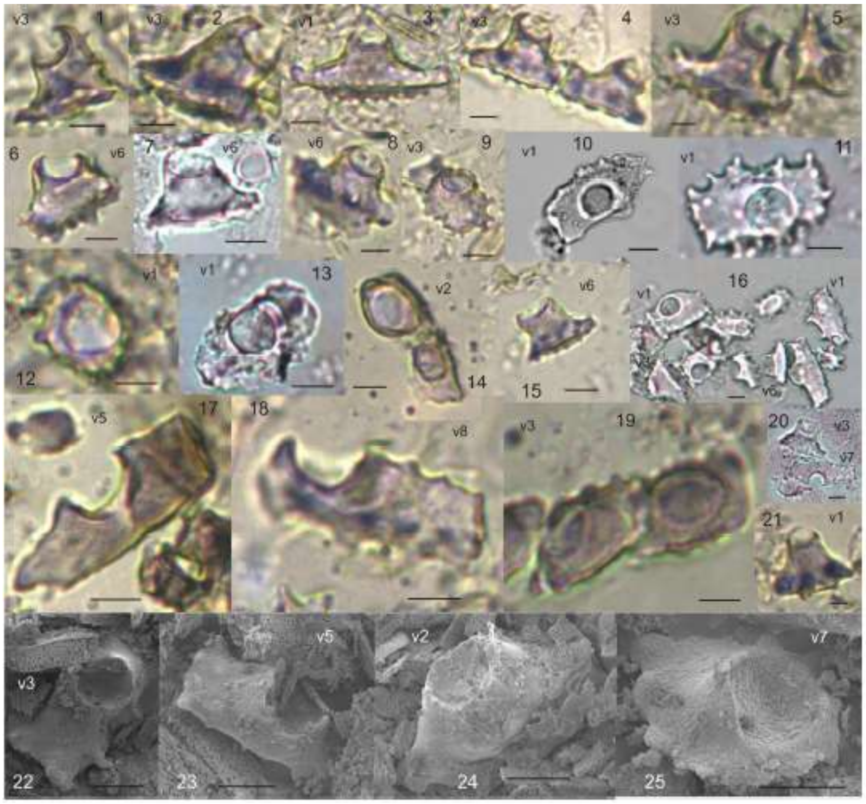
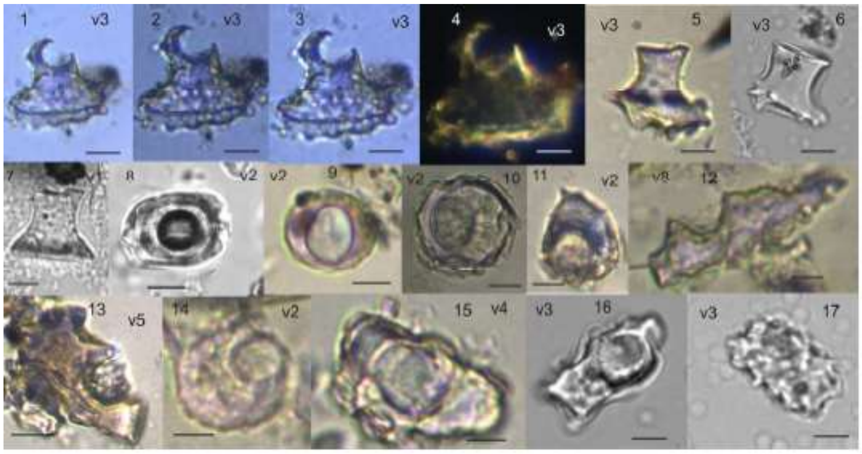


Fig. 6. 1-17: Domesticated banana phytoliths from Fahien rock shelter. 1-17: volcaniform variants (V1, V2, V3, V4, V5, and V8) derived from leaves. Microphotographs (1-4) of volcaniforms were taken under four different light conditions to indicate the granulate-verrucate surface pattern. V3 variant is the most common one. Scale bar = 10 µm.



Captions to Tables in the main text

Table 1. Summary of archaeology and stratigraphy described from the Fahien rock shelter. Bold font indicates the contexts sampled for phytolith analysis.

Table 2. Chronology of the Fahien rockshelter.

Table 3. Morphological differences of volcaniforms comparing wild and domesticated bananas.

Supplementary Online Figures

Fig. SI1. Morphology of a volcaniform phytoliths from banana leaves.

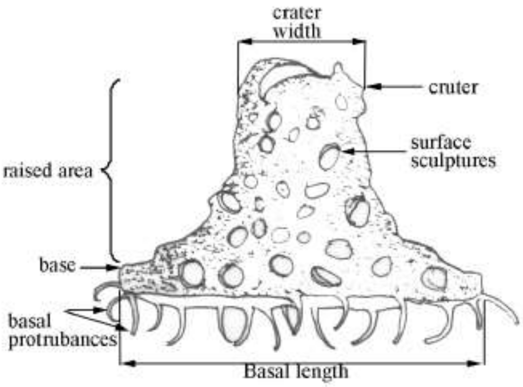
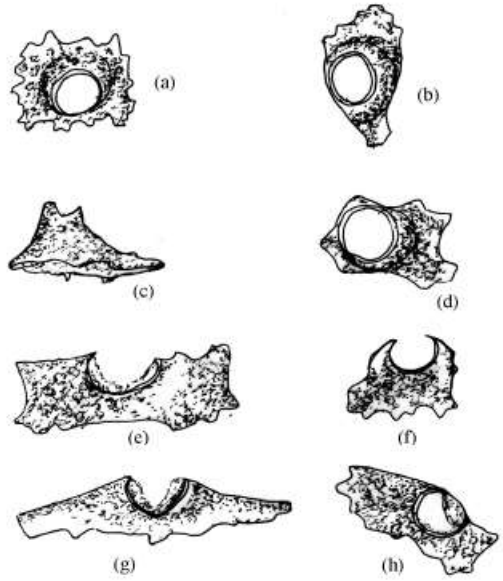


Fig. SI2. Morphology of 8 volcaniform variants (V1-V8) from banana leaves. (a) Variant 1 (V1):regular base, central concave cone, (b) variant 2 (V2): irregular base, central concave cone, (c) variant 3 (V3): regular base, acentric concave cone, (d) variant 4 (V4): irregular base, acentric concave cone, (e) variant 5 (V5): regular base, central convex cone, (f) variant 6 (V6): regular base, acentric convex cone, (g)- variant 7 (V7): irregular base, central convex cone, (h) variant 8 (V8): irregular base, acentric convex cone (adopted: Ball et al., 2006).



Supplementary Online Tables

Table SI1: Morphology of wild banana seed and leaf phytoliths.

Table. SI2. Variants of volcaniform phytoliths produced by cultivated banana samples collected from the wet zone (rainfall: 4000-2500 mm/yr). + indicates very minor occurrence. Freq. indicates the most common occurrence.

Table. SI3. Variants of volcaniform phytoliths produced by cultivated banana samples collected from the wet montane zone (rainfall: 4000-2500 mm/yr).

Table. SI4. Variants of volcaniform phytoliths produced by cultivated banana samples collected from the dry zone (rainfall: 1700-1100 mm/yr).

Table. SI5. Variants of volcaniform phytoliths produced by cultivated banana samples collected from the intermediate zone (rainfall: 2200-1700 mm/yr).

Table. SI6 Variants of volcaniform phytoliths produced by wild bananas samples collected from the wet zone.

Table. SI7. Variants of the volcaniform phytoliths produced by wild bananas samples from the wet montane zone

Table. SI8. Summary of Variant % from cultivated bananas. + indicates less than 5%.

Table. SI9. Summary of Variant % from wild bananas. + indicates less than 5%.

Table. SI10. Summary of morphometrics (BL: basal length and crater length: CW) of cultivated bananas.

Table. SI11. Summary of morphometrics (BL and CW) of wild bananas.