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Differentiating wild and domesticated bananas using volcaniform phytolith morphology and dimensions: Evidence from Sri Lanka

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ABSTRACT

Identifying domesticated banana phytoliths from archaeological sites within the natural geographical range of the wild progenitors of domesticated bananas is very challenging. This is because of the considerable similarity between phytoliths of domesticated triploid and tetraploid banana plants and those of the diploid species *Musa acuminata* and *M. balbisiana* in the *Eumusa* section, from which the domesticated varieties ultimately derive. This paper presents evidence for separating phytoliths derived from diploid, triploid and tetraploid banana plants in the Sri Lankan context. 8649 volcaniform (cavate) phytoliths from domesticated (triploid/tetraploid) banana plants and 2592 volcaniform phytoliths from diploid cultiwild and wild banana plants underwent morphotypic analysis into Ball et al.'s eight classes and were measured for basal length and crater width. Although there is overlap, modern domesticated triploid/tetraploid and diploid banana plants in Sri Lanka can be discriminated on morphotypic variation and size-ranges of volcaniform phytoliths. In our sampling, triploid and tetraploid banana plants have higher percentages of V3 morphotypes and generally higher percentages of V4 and V6 morphotypes of volcaniform phytoliths relative to *M. acuminata* and *M. balbisiana*, while V2 and V7 morphotypes are restricted to triploid and tetraploid banana plants and are not present in *M. acuminata* and *M. balbisiana*. Further, V4 and V8 are found in *M. balbisiana*, but not in *M. acuminata*. In Sri Lanka, mean basal length and crater width of volcaniform phytoliths in triploid and tetraploid bananas are greater than in *M. acuminata* and *M. balbisiana*. The overlap of size-ranges between phytoliths of triploid/tetraploid and diploid banana taxa is problematical, but threshold values of basal length > 29.1 μm and crater width > 12.1 μm can be used to distinguish some of the larger volcaniform phytoliths from triploid and tetraploid banana plants from those from and *M. balbisiana*, which do not exceed these dimensions in Sri Lanka, while *M. acuminata* volcaniforms do not exceed basal length of 27.2 μm and crater width of 10.2 μm. The size distributions of *M. balbisiana* volcaniforms suggest that two populations of this species are present in Sri Lanka, conceivably with different histories.

1. Introduction

Domesticated bananas are one of the world's most extensively used crops. They have been used as a staple food in some tropical regions since prehistoric times (Castillo and Fuller, 2015). Genetic evidence suggests that domesticated bananas derive from the genus *Musa* in the *Eumusa* section of family Musaceae (Perrier et al., 2011; Li et al., 2013; Ball et al., 2016). In the archaeological context, volcaniform phytoliths (a more specific term than "cavate" ICPT, 2019 – under which these phytoliths might be classified in the terminology of ICPN 2.0) from banana leaves are one of the best means for identifying ancient banana plants (Ball et al., 2006, 2016; Mbida, et al., 2006; Lejju et al., 2006; Lentfer, 2009; Premathilake and Hunt, 2018). Taxonomic identification and classification of phytoliths relies on combining morphotypic and morphometrical characteristics of volcaniforms derived from samples of modern banana taxa. Identification of domesticated banana plants using phytoliths is, however, complicated because there are strong morphological similarities between phytoliths from wild and domesticated banana plants. The latter were produced from wild taxa through intra- and interspecific hybridization, polyploidization and somaclonal mutations (De Langhe et al., 2009).

Understanding the evidence for domesticated banana plants in the

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archaeological context is further complicated because of the taphonomic issues involved (Ball et al., 2016; Premathilake et al., 2022). It has therefore been argued that combined records of volcaniform phytolith morphological variation, taphonomy and other lines of evidence (e.g. archaeology, linguistics, botany and genetics) are crucial for understanding the appearance and spread of domesticated bananas (Mindzie et al., 2001; Lejju et al., 2006; De Langhe et al., 2009; Donohue and Denham, 2009; Fuller and Madella, 2009; Blench, 2009; Castillo and Fuller, 2015; Perrier et al., 2011; Perrier et al., 2009; Li et al., 2013; Premathilake and Hunt, 2018).

An archaeological site, Kuk Swamp in the highlands of Papua New Guinea, yielded the earliest archaeological and phytolith evidence for banana cultivation, dating to 6.9–6.4 ka BP (Denham et al., 2003). An early phase of banana domestication involving *Musa acuminata* ssp. *banksii* seems to have taken place in Papua New Guinea since genetic evidence indicates that *M. acuminata* ssp. *banksii*, most probably morphologically wild but cultivated specimens (cultiwild), associated with humans in Island Southeast Asia, were a key contributor to the development of domesticated *M. acuminata* diploid (AA) forms (Perrier et al., 2009; Perrier et al., 2011). Following the polyploidy and hybridization of diploid genomes, various triploid and tetraploid bananas have been generated. These are domesticated bananas/cultivars (De Langhe et al., 2009; Perrier et al., 2011; Castillo and Fuller, 2015; Kagy et al., 2016).

Kot Diji in Pakistan (Fuller and Madella, 2009) and Loteshwar in North Gujarat, India (García-Granero et al., 2015a,b) yielded banana plant phytoliths dating to 4.5–3.9 ka BP and 5.6–4.2 ka BP respectively. These are the earliest evidence for banana phytoliths derived from cultivation in South Asian sites (Castillo and Fuller, 2015). Phytolith evidence for banana cultivation at Munsa in Uganda dating to 4.5–4.0 ka BP (Lejju et al., 2005; Lejju et al., 2006) is regarded by Mindzie et al. (2001), Mbida et al. (2004, 2005, 2006), Vansina (2003), Eggert et al. (2006), Neumann and Hildebrand (2009) as problematic because (1) reliability of morphological criteria used to understand the phytoliths of domesticated bananas and (2) the lack of evaluation of the impact of sedimentary hiatuses (i.e. taphonomic impact) on the phytolith sequence studied there. Archaeological sediments at Nkang, Cameroon in West Africa yielded domesticated banana (triploid banana) leaf phytoliths at 2.7–2.3 ka BP. This suggests the dispersal of banana cultivars from Southeast Asia to West Africa had happened by that time (Mbida et al., 2001).

Two banana species (*M. acuminata* and *M. balbisiana*) occur in lowland and montane disturbed rainforests in southwestern Sri Lanka to ca. 2000 m above sea level (Simmonds, 1962). *M. acuminata* is found far from human habitation and known archaeological sites at high altitude in Sri Lanka and there seems little doubt that it is truly a native wild species (see also De Langhe et al., 2009). The status of *M. balbisiana* is less certain – Sri Lanka lies outside the range of this species shown by De Langhe et al. (2009) but it is found growing wild in disturbed forest in highland areas and local botanists regard it as a native species. Some *M. balbisiana* plants are found in garden cultivation, and would be classed as cultiwild; others grow in proximity to settlements and may possibly be regarded as naturalised if not wild. In South Asia, *Ensete superbum,* a closely related false banana species is restricted to the Central Indian and Western Ghats hill regions (Fuller and Madella, 2009).

Genetic studies suggest that hybrid genomes (e.g. domesticated triploid bananas) emerged when *M. balbisiana* (BB) and edible *M. acuminata* diploids (AA), came into contact during the period of primary domestication during the early-mid Holocene (Perrier et al., 2011; Perrier et al., 2009; Kagy et al., 2016). *M. balbisiana* and *M. acuminata* are known to have contributed towards the development of triploids (e.g. AAA, AAB and ABB) in New Guinea and other regions of Southeast Asia (Castillo and Fuller, 2015). As yet, there is no evidence to suggest this happened in Sri Lanka, but human-associated members of these two wild banana taxa or their fertile (cultiwild) derivatives may have been present since 6.5 ka BP (Perrier et al., 2011). Currently, multiproxy evidence seems to suggest that triploids were more likely dispersed *via* trade routes from Southeast Asia into Sri Lanka and further west after 4.5 ka BP (Bulbeck, 2008; Perrier et al., 2011).

Table 1
Genome types of diploid, triploid and tetraploid banana taxa and varieties and their local names used in Sri Lanka. With the exception of Alu kesel (ABB), all other banana cultivars are used as dessert bananas.

Genome Type		Name	Local name
AA		*Musa acuminata*	Unel
BB		***Musa balbasiana***	Ati-kehel
AAA		Gros michel	Anamalu
		Introduced	Ambun
AAA	Cavendish subgroup	Cavendish	Cavendish
		Dwarf Cavendish	Bin kesel
		Pisang masak hijau	Sapumal anamalu
		Introduced Cavendish	William hybrid
AAB		Pisank kelat	Suwandel
		Silk	Kolikuttu
		Mysore	Embul
		Pome	Puwalu
		Introduced	Muwanthi kesel
		—	Neithrapalam
		—	Udakombu
ABB		Bluggoe	Mondan
		Pisang awak	Seeni kesel
		Pey kunnan = Pisang awak	Alu kesel
		Monthan	Alu mondan
		—	Atamuru
AAAA		Introduced (Gros michel hybrid)	Golden banana (IC2)
AAAB		—	Kandula
AABB		—	Pulthalsi

Evidence suggesting domesticated banana phytoliths from the archaeological sequence at the FaHien Rockshelter in Sri Lanka, dated to 6.2–5.9 ka BP (Premathilake and Hunt, 2018), has been questioned by De Langhe et al. (2019) on the grounds of (1) the uncertainties of morphological criteria used to separate wild and domesticated banana phytoliths, (2) overlaps in volcaniform crater width and basal length among the phytoliths from wild and domesticated bananas, (3) the minimum number of phytoliths counted (n), and (4) equivocal and subjective descriptions given to volcaniform morphotypes.

Identification of phytoliths of domesticated banana plants in archaeological sites in the core area (De Langhe et al., 2009; Kennedy, 2009) where grow the wild progenitors of edible bananas in the *Eumusa* section, including *M. acuminata* and *M. balbisiana*, is a challenging issue for both morphotypic (Ball et al., 2006; Lentfer, 2009; Vrydaghs et al., 2009) and morphometric studies of volcaniform phytoliths (Ball et al., 2006; Mbida et al., 2001; Vrydaghs et al., 2009). This is because the volcaniform phytoliths produced by different wild, cultiwild, and domesticated *Musa* bananas have strong but so-far mostly unquantified morphological similarities. This issue poses a critical issue for identifying phytoliths of domesticated banana plants. To address these uncertainties (see also Neumann and Hildebrand (2009) and De Langhe et al. (2019)), the range of variation within the volcaniform phytoliths of extant banana plants must be established. Therefore, to enable confident discrimination of the phytoliths of wild and domesticated banana plants, we provide in this paper the results of a comprehensive study of volcaniform phytoliths – their dimensions and morphotypological variation – within 97 accessions of the two wild species and 21 domesticated banana cultivars from Sri Lanka. Genomes of banana cultivars and their local names in Sri Lanka are given in Table 1 and studied accessions and their ecology in Table 2 (following Simmonds, 1966; Valmayor et al., 2000). Ecological zones in Sri Lanka are shown in Fig. 1.

Table 2
The localities and ecology of the Sri Lankan banana cultivars and wild banana taxa accessioned for phytolith extraction. Reference numbers refer to the authenticated banana specimens deposited in the Laboratory for Palaeoecology, Postgraduate Institute of Archaeology, University of Kelaniya, Sri Lanka and Royal Botanic Garden, Kew, UK.

Variety name/ species	LaboratoryReference No. at PGIAR/Kew	Genome type	Part studied	Locality, Ecology	Climatic Zone (altitudes and rainfall)
Anamalu	Ni19	AAA	Leaf	Nittambuwa, Home Garden	Lowland areas (0–500 m asl) of Wet Zone (2,000–2,600 mm/yr)
Amban (Ambun)	Ko08	AAA	Leaf	Kolonnawa, Home Garden	
Binkesel	Ra07	AAA	Leaf	Rathmalana, Home Garden	
Cavendish	Ni17	AAA	Leaf	Nittambuwa, Home Garden	
William hybrid	Ma65	AAA	Leaf	Makandura, Cultivated land	
Embul	Ni20	AAB	Leaf	Nittambuwa, Home Garden	
Kolikuttu	Po36	AAB	Leaf	Polgahawela, Home Garden	
Suwandel	Ma64	AAB	Leaf	Makandura, Cultivated land	
Puwalu	Ma51	AAB	Leaf	Makandura, Cultivated land	
Muwanathi kesel	Ma54	AAB	Leaf	Makandura, Cultivated land	
Seeni kesel	Ka04	ABB	Leaf	Kandy, Home Garden	
Alu kesel	Ko09, 4 samples	ABB	Leaf	Kolonnawa, Home Garden	
Alu mondan	Ma69	ABB	Leaf	Makandura, Cultivated land	
Atamuru	Ma 60	ABB	Leaf	Makandura, Cultivated land	
Golden Banana (IC2)	Ma72, 2 samples	AAAA	Leaf	Makandura, Cultivated land	
Neithrapalam	Ma61	AAB	Leaf	Makandura, Cultivated land	
Pulathisi	Ma59	AABB	Leaf	Makandura, Cultivated land	
Kandula	Ma68, 3 samples	AAAB	Leaf	Makandura, Cultivated land	
Udakonbo	Ma52	AAB	Leaf	Makandura, Cultivated land	
Amban (Ambun)	Nu127	AAA	Leaf	Nuwara-eliya, Home Garden	Highland areas (2,000–2,350 m asl) of Wet Zone (2,000–2,100 mm/yr)
Embul	Nu128	AAB	Leaf	Nuwara-eliya, Home Garden	
Seeni kesel	Nu135	ABB	Leaf	Nuwara-eliya, Home Garden	
Anamalu	An124	AAA	Leaf	Anuradhapura, Cultivated land	Lowland areas (0–100 m asl) of Dry Zone (1,100—1,700 mm/yr)
Amban	Da27	AAA	Leaf	Dambulla, Cultivated land	
Cavendish	Da26	AAA	Leaf	Dambulla, Cultivated land	
Embul	An123	AAB	Leaf	Anuradhapura, Cultivated land	
Kolikuttu	Da23	AAB	Leaf	Dambulla, Cultivated land	
Suwandel	An122	AAB	Leaf	Anuradhapura, Cultivated land	
Puwalu	An118	AAB	Leaf	Anuradhapura, Cultivated land	
Embul (Tissue cultured)	Da21	AAB	Leaf	Dambulla, Cultivated land	
Seeni kesel	Da24	ABB	Leaf	Dambulla, Cultivated land	
Alu kesel	Da22	ABB	Leaf	Dambulla, Cultivated land	
Mondan	Da28	ABB	Leaf	Dambulla, Home Garden	
Pulathisi	Da25	AABB	Leaf	Dambulla, Cultivated land	
Anamalu	Ha134	AAA	Leaf	Hambanthota, Home Garden	
Amban	Ha38	AAA	Leaf	Hambanthota, Home Garden	
Binkesel	Ra07	AAA	Leaf	Hambanthota, Home Garden	
Embul	Ha40, 2 samples	AAB	Leaf	Hambanthota, Home Garden	
Kolikuttu	Ha39	AAB	Leaf	Hambanthota, Home Garden	
Suwandel	Ha133	AAB	Leaf	Hambanthota, Home Garden	
Puwalu	Ha43	AAB	Leaf	Hambanthota, Home Garden	
Embul (Tissue cultured)	Ha37	AAB	Leaf	Padalangala, Cultivated land	
Seeni kesel	Ha46	ABB	Leaf	Hambanthota, Home Garden	
Alu kesel	Ha41	ABB	Leaf	Hambanthota, Home Garden	
Kandula	Ha44, 2 samples	AAAB	Leaf	Hambanthota, Home Garden	
Anamalu	Ja101	AAA	Leaf	Jaffna, Cultivated land	
Amban	Ja98	AAA	Leaf	Jaffna, Cultivated land	
Cavendish	Ja96, 3 samples	AAA	Leaf	Jaffna, Cultivated land	
Embul	Ja99	AAB	Leaf	Jaffna, Cultivated land	
Kolikuttu	Ja95	AAB	Leaf	Jaffna, Cultivated land	
Seeni kesel	Ja136	ABB	Leaf	Jaffna, Cultivated land	
Mondan	Ja100	ABB	Leaf	Jaffna, Cultivated alnd	
Embul	Ba129	AAB	Leaf	Batticaloa, Home Garden	
Mondan	Ba131	ABB	Leaf	Batticaloa, Home Garden	
Anamalu	Me31	AAA	Leaf	Melsiripura, Home Garden	Lowland areas of Inter-mediate zone (150–250 m asl (1,700–2,200 mm/yr)
Amban	Me29	AAA	Leaf	Melsiripura, Home Garden	
Embul	Me32	AAB	Leaf	Melsiripura, Home Garden	
Seeni kesel	Me30	ABB	Leaf	Melsiripura, Home Garden	
Alu kesel	Ib34	ABB	Leaf	Ibbagamuwa, Home Garden	
Musa balbisiana	Ma 71	BB	Leaf	Makandura, Cultivated land	Lowland areas (0–500 m of Wet Zone (2,000–4,500 mm/yr)
Musa balbisiana	Av75a, Av75b (1+4 samples)	BB	Leaf	Avissawella, Disturbed forest	
Musa balbisiana	Av78a, Av78b (2+3 samples	BB	Leaf & Seeds	Avissawella, Disturbed forest	
Musa balbisiana	Av 81a, Av81b (1+1 samples)	BB	Leaf & Seeds	Avissawella, Cultivated land	
Musa balbisiana	Av 119 (2 samples)	BB	Leaf & Seeds	Avissawella, Semi-disturbed forest	

(*continued on next page*)

Table 2 (*continued*)

Variety name/ species	LaboratoryReference No. at PGIAR/Kew	Genome type	Part studied	Locality, Ecology	Climatic Zone (altitudes and rainfall)
Musa balbisiana	Ra125a, Ra125b (1+1 samples)	BB	Leaf & Seeds	Rathnapura, Disturbedforest	
Musa balbisiana	Ya 87 (2 samples)	BB	Leaf & Seeds	Yatiyanthota, Disturbed forest	
Musa balbisiana	Mu 90 (2 samples)	BB	Leaf & Seeds	Maskeliya, Disturbed forest	Highland areas (1,000–1,500 m asl) of Wet zone (2,500–4,500 mm/yr
Musa acuminata	Ri126 (1 samples) 0M.0014/91.34 (1 sample)	AA	Leaf & Seeds	Riversten, Disturbed forestIndia	
Musa acuminata	Mu 91, 2 samplesNo. D.2681953	AA	Leaf & Seeds	Maskeliya, Disturbed forestIndia/ Combatore	
Musa acuminata	Mu 92 (3 samples)	AA	Leaf & Seeds	Maskeliya, Disturbed forest India/Combatore	

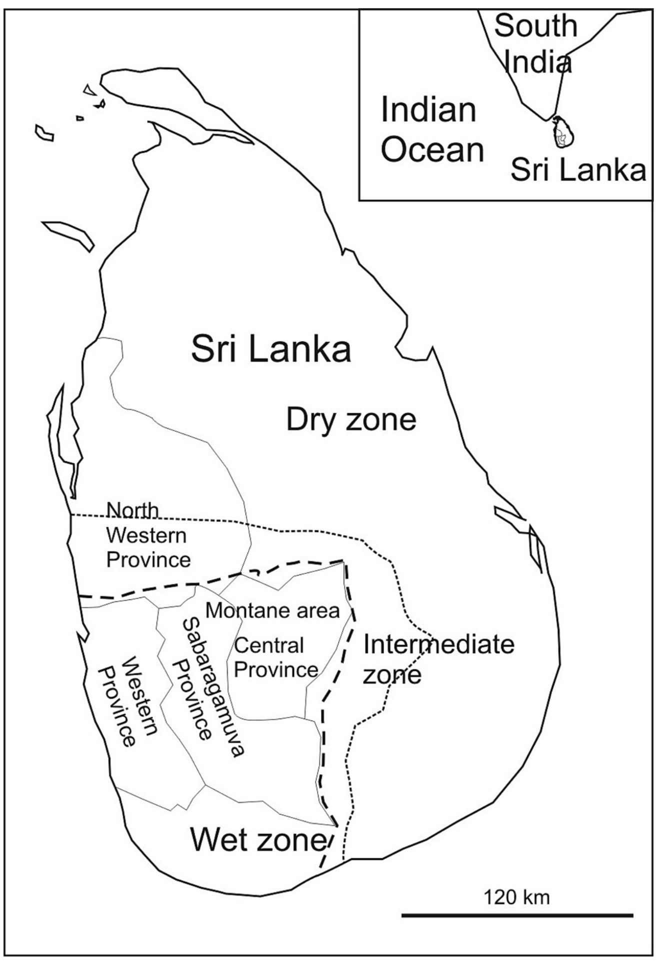


Fig. 1. Distribution of ecological zones with prevalence of *M. balbisiana* and *M. acuminata* in Sri Lanka. Both diploid bananas are primarily found in limited areas with a humid climate (i.e. lowland wet zone and wet montane zone). *M. balbisiana* populations are primarily found in the wet zone on human-used and abandoned land, where they are used for human consumption. *M acuminata* is restricted to the wet montane zone (ca. 2000 m above sea level). Domesticated triploid and tetraploid bananas are commonly grown in all ecological zones (wet zone, dry zone, intermediate zone and semi-arid zone). Samples were taken from banana plants growing in wet and dry zone areas with different anthropogenic pressures (human activities vary from very low to high). Bananas are grown by traditional cultivators, especially in the dry and wet regions of the country. The dry zone receives nearly 1800 mma^{-1} rainfall, and the wet zone receives more than 2500 mma^{-1}.

Table 3
Banana plant volcaniform phytolith morphotypes (after Ball et al. 2006, 2016; Vrydaghs et al. 2009).

Morphotype	Name	Base	Cone position	Cone sides
1	Volcaniform regular base central concave cone	Regular (square-ish to rectangular)	central	concave
2	Volcaniform irregular base central concave cone	irregular	central	concave
3	Volcaniform regular base eccentric concave cone	regular	eccentric	concave
4	Volcaniform irregular base eccentric concave cone	irregular	eccentric	concave
5	Volcaniform regular base central convex cone	regular	central	convex (dome-shaped)
6	Volcaniform regular base eccentric convex cone	regular	eccentric	convex
7	Volcaniform irregular base central convex cone	irregular	central	convex
8	Volcaniform irregular base eccentric convex cone	irregular	eccentric	convex

2. Materials and methods

2.1. Sampling

Ninety seven (97) samples of modern banana plants growing in four different ecological zones of Sri Lanka, namely the lowland wet zone, lowland dry zone, intermediate zone and humid montane zone, were collected for phytolith analysis (Table 2). Samples were all from well-matured leaves and (where present) seeds (Vrydaghs et al., 2009). Identification of banana taxa was based on the macro-morphological characters (e.g. leaf thickness, size, orientation, trunk color, leaf stem (petiole) structure, fruit stalk hairiness, shape and size of the male bud, scars left from falling flowers on the lower fruit stalk, and details of the male flowers) and genomic conditions described in Chandrarathna et al. (1951), Simmonds and Shepherd (1955), Simmonds (1962, 1966), Dassanayaka and Clayton (2000), Liyanage (2010), Perrier et al. (2011), Perera, (2017) and information from the Department of Agriculture, Sri

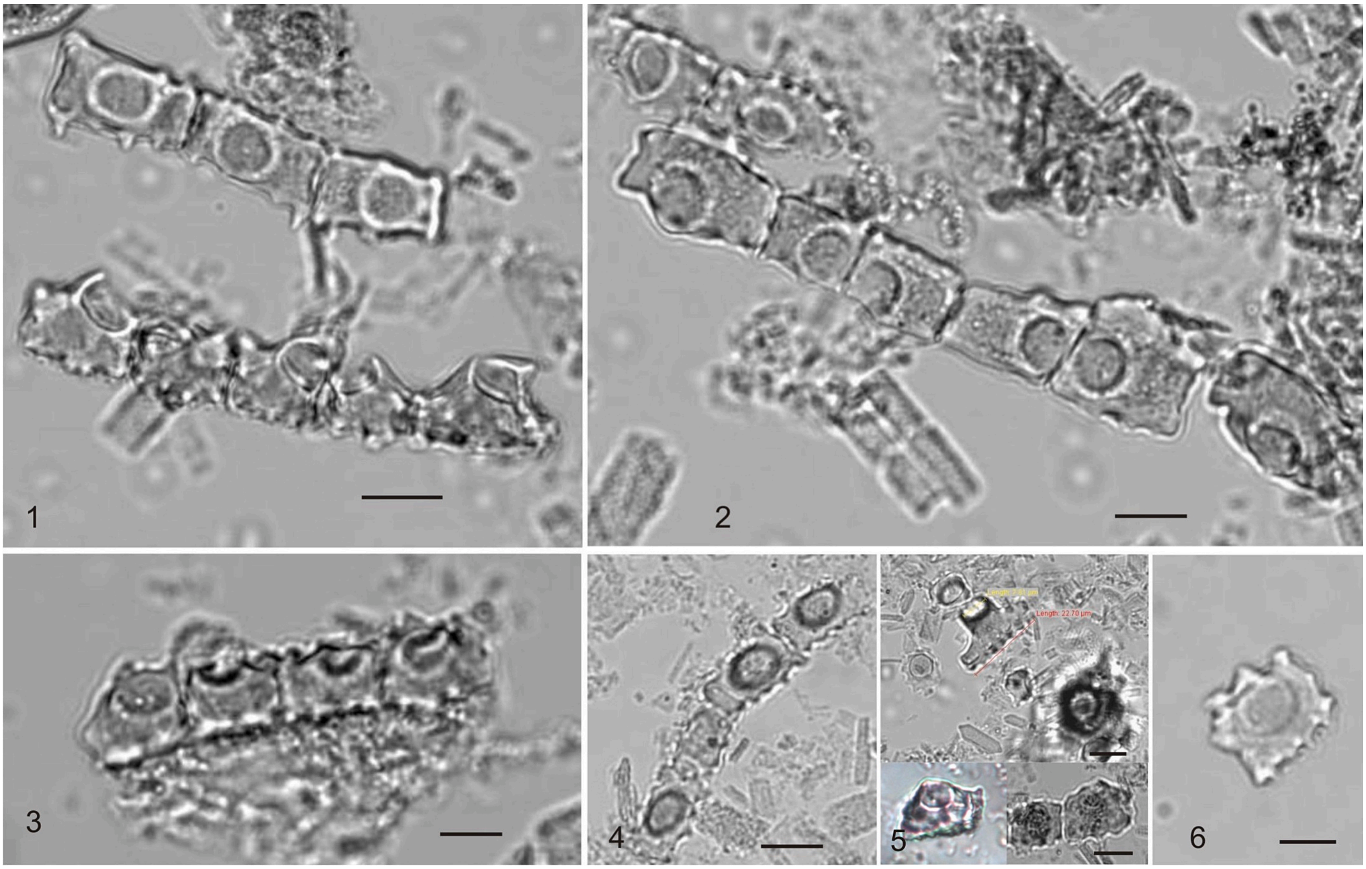


Fig. 2. Phytolith morphotypes from triploid banana cultivar leaves. Pey kunnan (Alukesel) ABB 1–3 and Ambun (Introduced) AAA (4–6). Scale bar = 10 μm.

Lanka (Table 2). Identification of wild banana samples was cross-checked with the available records of bananas in the herbaria of the Department of Ecology and Palynology, the French Institute, Pondicherry, India and the Royal Botanic Gardens, Kew, UK. A few additional samples from authenticated banana leaf and seed samples from southern India deposited in the above-mentioned herbaria were also used to extract phytoliths. Collected fresh samples were taken to the laboratory and were kept at 45° C for two days until the water content of the samples became minimized.

2.2. Phytolith extraction

Alconox was used to clean all the selected modern samples and they were then dried in a ceramic crucible at 50° C for five hours. Subsamples of 1 g of dry banana plant tissue were taken for chemical digestion (Carter, 2007). The materials were treated with concentrated H_2SO_4 at 80° C in a water bath for 4 h until the organic matter dissolved. The mixture was treated with 30 % H_2O_2 on a hotplate at 150° C for 2–3 h until it turned colourless. The residue was cleaned with distilled water, and the pellet was air-dried. Known dry residue weights were mounted separately in Canada balsam.

2.3. Phytolith morphotypology and dimensions

Care was taken to exclude all broken volcaniform phytoliths from our analysis. Broken volcaniform bases are recognizable because they lack the characteristic projections around some parts of their margin. The most common and diagnostic volcaniform phytolith morphotypes (Table 3, following Ball et al., 2006, 2016; Lentfer and Green, 2004; Lentfer, 2009; Horrocks et al., 2009; Vrydaghs et al., 2001, 2009; Perera, 2017) were recorded using Leitz Dialux 22, Olympus BX51 and Nikon phase contrast light microscopes at magnification of 1000 times. Morphotypic characterisation, measurement of basal length, crater width and photographic documentation were carried out at magnification of 1000 times using DP 72 view soft imaging and F-View Soft Imaging and Cool 5 Systems. In each sample, a minimum number of 100 phytoliths were recorded, except in a small number of samples where fewer complete phytoliths were present.

2.4. Statistical treatment

Data were logged and handled and the statistical measures computed in Excel. Percentage morphotypic data and dimensions of basal length and crater width were calculated for each species and domesticated variety and displayed as stacked histogram using Tilia (Grimm, 1991).

3. Results

3.1. Discriminating wild and domesticated modern banana plant phytoliths

Counts of the volcaniform morphotypes (Figs. 2-4; Table 3: V1-V8, following Ball et al., 2006, 2016) and measurements of these phytoliths were carried out on the sampled banana plant taxa (Table 2). Counts of the numbers of V1-V8 phytolith morphotypes were made from the 69 domesticated banana plant samples totaling 8949 specimens and from the 28 diploid banana plant samples totaling 2592 specimens. The numbers and percentage of each phytolith morphotype from the sampled genomes (AA, BB, AAA, AAB, ABB, AAAA, AABB and AAAB) are presented in Fig. 6, Table 4 and Supplementary Table 1. Basal length and crater width of 8949 volcaniform phytoliths from domesticated (triploid/tetraploid) and 2592 phytoliths from diploid banana plants are presented for morphometric analysis (Figs. 7-8 and Supplementary Table 2). Morphotypes of phytoliths of modern triploid and diploid

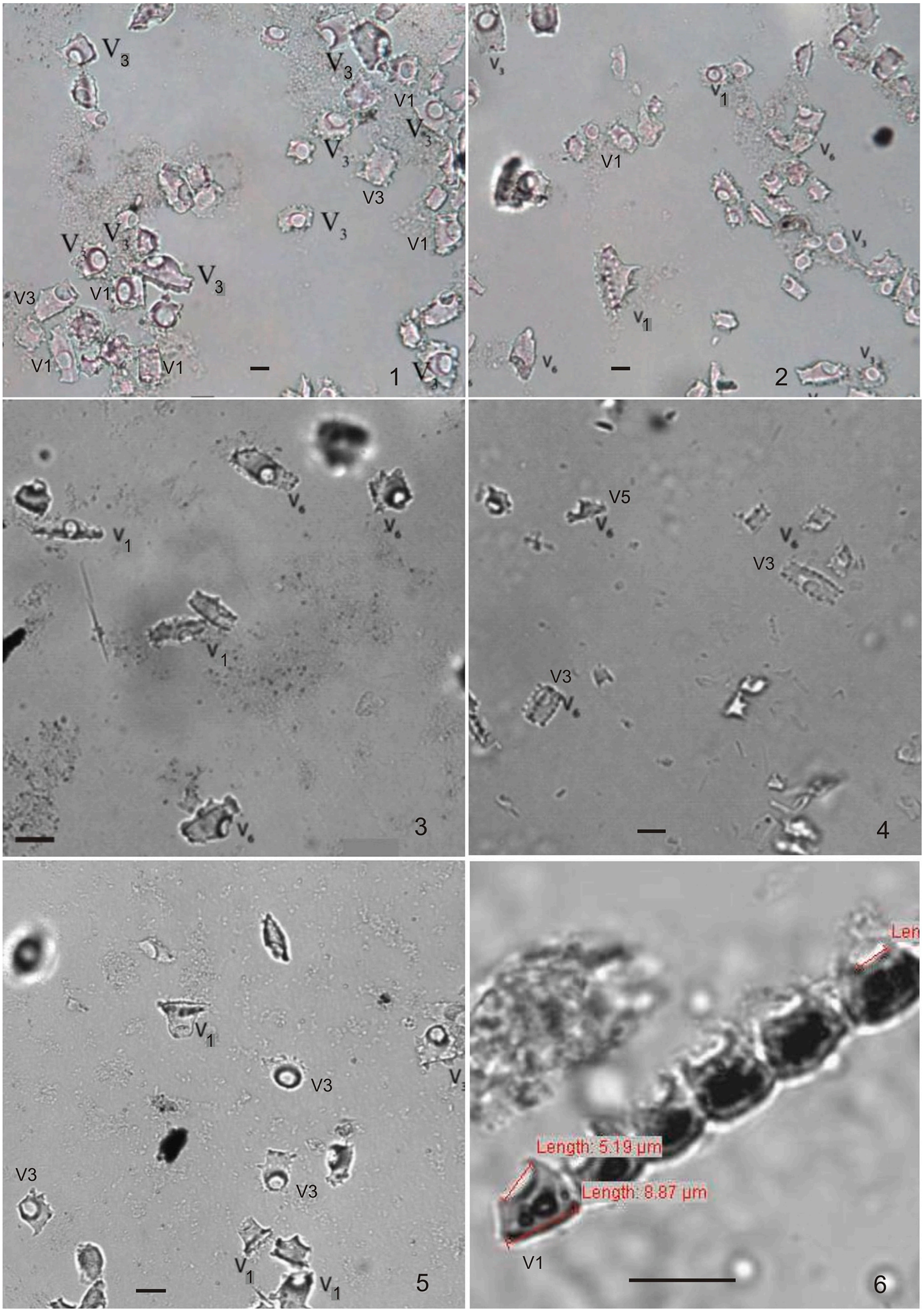


Fig. 3. Phytolith morphotypes from Pey kunnan (Alukesel) ABB banana cultivar (1–2), AA (*M. acuminata*) banana leaves (3–4) and BB (*M. balbisiana*) banana leaves (5–6). Scale bar = 10 µm.

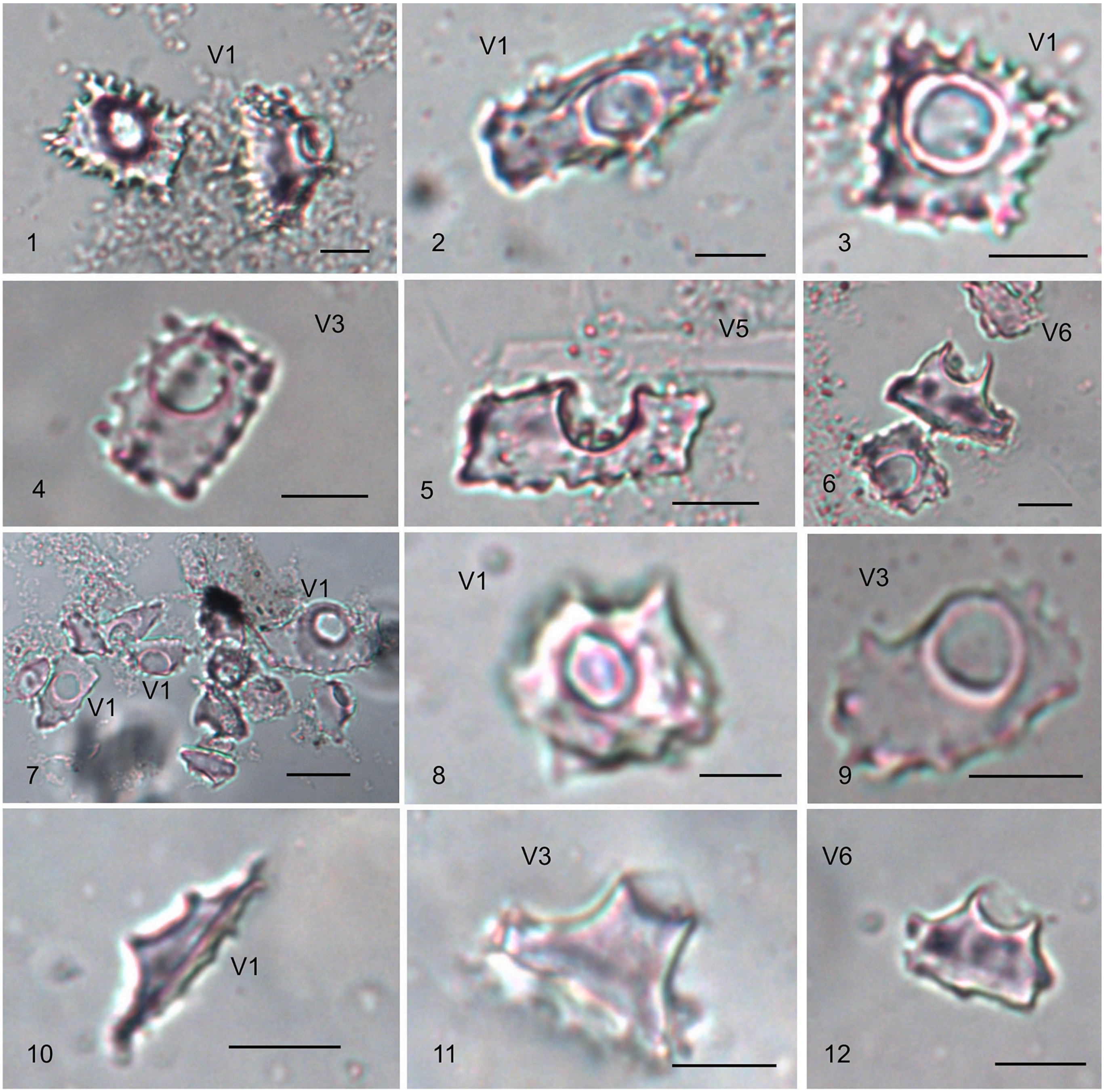


Fig. 4. Diversity of phytolith morphotypes of modern banana cultivars (1–12). Scale bar = 10 μm.

bananas are shown in Figs. 2-5.

3.2. Morphotypology

Morphotypic analyses are presented in Fig. 6, Table 4 and Supplementary Table 1. We observe that the data from the different accessions of any given taxon or variety, presented in Supplementary Table 1, are rather noisy, which is likely a function of the stochastic nature of counting entities under the microscope. The aggregated data for each taxon is likely to be more secure than that for individual accessions, simply because of the larger datasets after aggregation of accessions. For the same reasons, we have chosen to discuss the data mostly at the level of the genome, where data from different accessions and varieties are further aggregated, below.

The data provide evidence that in all the samples studied from all banana plants, the most common morphotypes are V1 and V3, with V1 noticeably more common than V3 (Fig. 6, Table 4, Supplementary Table 1). The percentage of V1 + V3 is higher for *M. acuminata* and *M. balbisiana* and for the triploid bananas than it is with most of the tetraploid bananas. The V3 percentage is lower in diploid banana plants (*M. acuminata* = 13.60 %; *M. balbisiana* = 18.08 %) than in triploid (AAA = 33.00 %; AAB = 28.20 %; ABB = 20.65 %) or tetraploid (AAAA = 21.54 %; AAAB = 22.40 %; AABB = 24.84 %) banana plants. Sri Lankan *M. acuminata* and *M. balbisiana* do not produce V2 and V7 morphotypes and these only occur, although in extremely low percentages, in some of the samples from domesticated banana plants (V2: Mysore AAB = 0.96 % and Neithrapalam AAB = 1 %; Golden Banana AAAA = 1.00 %; Kandula AAAB = 1.80 %; and V7: Ambun AAA = 0.13 %; Neithrapalam

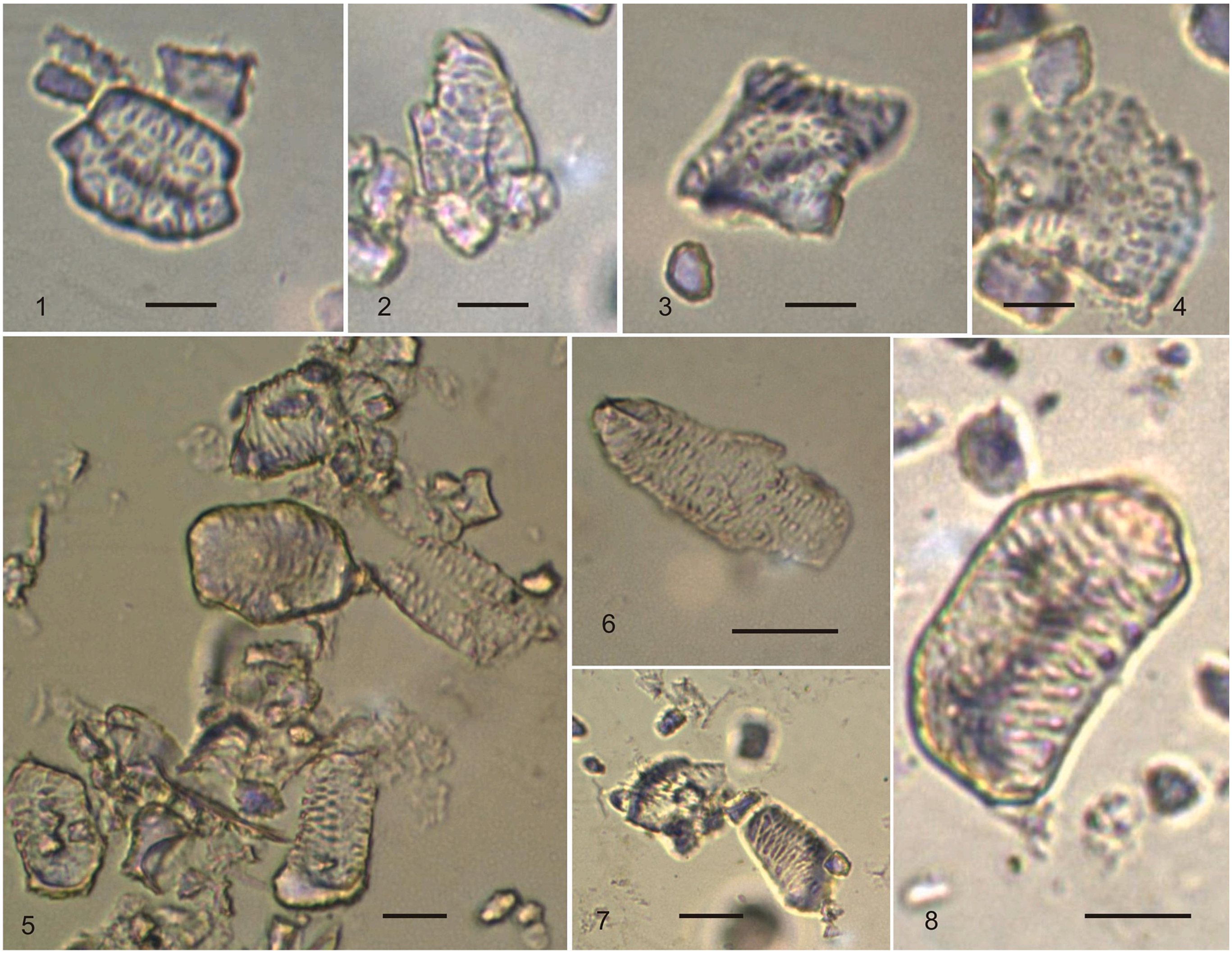


Fig. 5. Phytolith morphotypes from modern wild banana seeds. 1–4: morphology with irregular faceted and elongate with irregular short grooves from *M. acuminata*. 5–8: morphology with irregular facetate and with elongated well-defined regular long grooves from *M. balbisiana*.

AAB = 7; Pome AAB; 0.33 %; Udakonbo AAB = 6.48 %; Golden Banana AAAA = 1.50 %; Kandula AAAB = 0.73 %).

Sri Lankan *M. balbisiana* produce V4 and V8 volcaniforms, but these were not found in our study in *M. acuminata* (Fig. 6, Table 4, Supplementary Table 1). The diversity of V1-V8 morphotypes is low in the wild *M. acuminata*, which produce only V1, V3 V5 and V6, but similar or lower diversity is seen in some triploid banana plants, for instance Dwarf Cavendish (AAA), all the ABB triploids – Pisang Awak, Pey kunnan, Mondan Bluggoe and Atamuru – and two AAB triploids – Silk and Pisang kelat.

Percentages of other volcaniform morphotypes in diploid bananas are generally low with relatively high percentages of V5 and V6 (*M. acuminata*: V5 = 4.23 %, V6 = 1.10 %; *M. balbisiana*: V4 = 0.25 %, V5 = 6.52 %, V6 = 2.79 %, V8 = 1.25 %). Percentages of these other volcaniform morphotypes in triploid banana plants are also generally low with relatively high percentages from V5 and V6 (AAA: V4 = 0.64; V5 = 2.91; V6 = 4.40; V8 = 0.79; AAB: V4 = 0.57; V5 = 3.92; V6 = 4.16; V8 = 1.39; ABB V5 = 2.82; V6 = 1.59). Percentages of other volcaniform morphotypes in tetraploid banana plants are variable with fairly high percentages from V5 and V6 (AAAA: V4 = 1.50; V5 = 11.52; V6 = 6.51; V8 = 3.51; AAAB: V4 = 4.27., V5 = 5.67, V6 = 8.93, V8 = 2.93; AABB: V4 = 0.65, V5 = 11.76, V6 = 16.99; V8 = 0.33). There is no simple pattern whereby the triploid and tetraploid banana plants can be distinguished from *M. acuminata* and *M. balbisiana*, using percentages of V4, V5, V6 and V8, although higher percentages of V4 and V6 will separate the tetraploid banana plants from *M. acuminata* and *M. balbisiana* (Fig. 6, Supplementary Table 1).

3.3. Volcaniform basal length analyses

Volcaniform basal length appears to be highly variable, as shown in Fig. 7 and Tables 5-7; Supplementary Table 2). Basal length in *M. balbisiana* (BB genome) banana plants is between 3.2–29.1 μm with a mean of 14.05 μm, but this value is effectively meaningless because there are two groups of accessions (Table 5), one with small phytoliths (means of 6.97 μm [Ra125a], 7.36 μm [Av78a], 8.93 μm [Av75a] and 8.90 μm [Av81a] and a combined mean of 8.04 μm) and one with larger phytoliths (means of 13.91 μm [Ma71], 15.36 μm [Mu90], 15.56 μm [Av75b], 15.69 μm [Av78b], 16.11 μm [Av119], 16.29 μm [Ra125b], 16.36 μm [Ra126], 16.38 μm [Ya87], and 18.94 μm [Av81b] and a combined mean of 16.07 μm).

Basal length for *M. acuminata* (AA genome) banana plants is between 5.1–27.2 μm with a mean of 14.8 μm (Table 6). The lowest part of the basal length range (3.2–5.1 μm) observed in *M. balbisiana* volcaniforms is not observed in *M. acuminata*.

The basal lengths of volcaniforms from triploid (7.2–42.5 μm) and tetraploid (7.3–69.5 μm) banana plants overlap with the range of basal lengths of the diploid species, but critically extend to greater

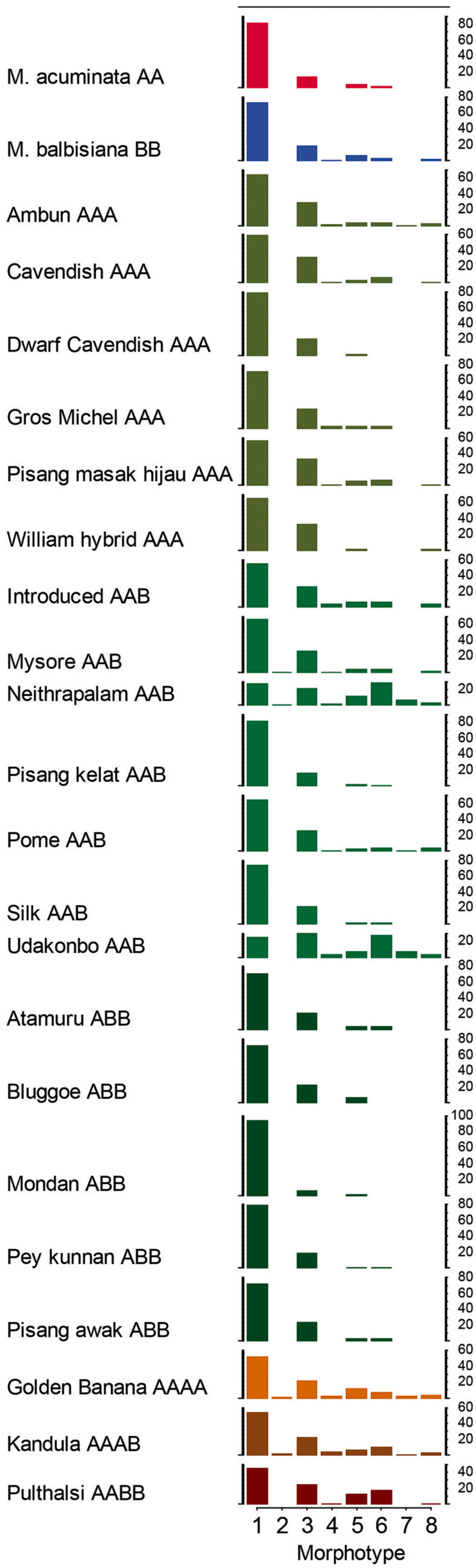


Fig. 6. Percentage morphotypic variation for diploid, triploid and tetraploid banana plant volcaniform phytoliths. Percentages are indicated in the vertical scales. The horizontal axis shows the eight morphotypic classes of Ball et al. (2006). Descriptions of these morphotypic classes are summarised in Table 3 and the counts are shown in Supplementary Table 1 and summarised in Table 4.

dimensions. Means vary between 14.59 and 21.58 μm with tetraploid banana phytoliths generally having larger mean basal lengths than phytoliths of triploid plants (Table 7). The threshold basal length value for separating *M. acuminata* from *M. balbisiana* is > 27.1 μm, while both diploids can be separated from triploid and tetraploid bananas with the maximum basal length of *M. balbisiana* of > 29.1 μm (Fig. 7 and Table 6). Only domesticated tetraploid and triploid banana plants have volcaniforms with longer basal lengths than this threshold in our samples from Sri Lanka, with only tetraploids having basal lengths over 42.5 μm (Fig. 7).

3.4. Volcaniform crater width analyses

Volcaniform crater width also seems highly variable, as shown in Fig. 8 and Tables 5-7; Supplementary Table 2). Crater width of *M. balbisiana* (BB genome) banana plants range between 1.62–12.1 μm with a mean of 6.38 μm, but this value is effectively meaningless because there are two groups of accessions (Fig. 8, Table 5), one with small phytoliths (means of 3.51 μm [Av81a], 3.60 μm [Av78a], 3.61 μm [Ra125a and Av75a] and a combined mean of 3.58 μm) and one with larger phytoliths (means of 6.91 μm [Mu90], 6.95 μm [Av119], 7.00 μm [Av75b], 7.06 μm[Ra125b], 7.11 μm [Ma71], 7.31 μm [Ya87], 7.36 μm [Av78b], 7.69 μm [Av81b], and 7.84 μm [Ra126], and a combined mean of 7.25 μm).

Crater widths in *M. acuminata* range between 5.1–10.2 μm with a mean of 7.06 μm. The lowest part of the range of crater width observed in *M. balbisiana* (1.62–5.0 μm) was not observed in *M. acuminata* (Fig. 8).

The crater width of triploid and tetraploid banana plants ranges between 4.1–18.6 μm with means of the different varieties between 7.94 and 10.91 μm (Table 7). Thus, the threshold crater width value for separating *M. balbisiana* from *M. acuminata* is > 10.5 μm and the threshold for separating both diploids from triploid and tetraploid banana plants is > 12.1 μm (Fig. 8, Table 7). Only triploid and tetraploid banana plants have volcaniforms with larger basal lengths than this threshold in our samples from Sri Lanka. Only tetraploid banana plants have crater widths over 16.1 μm (Fig. 8, Table 7).

4. Discussion

4.1. Phytolith morphotypology and the discrimination of banana taxa

Our morphological observation that the most common volcaniform morphotypes are V1 and V3 (Fig. 6, Table 4 and Supplementary Table 1) is broadly consistent with the findings of Ball et al., (2006); Vrydaghs et al., (2009) and Perera (2017). In our counts in Sri Lankan material V1 is nearly always more frequent than V3, as in the New Guinea, Philippine and Honduran material described in Ball et al. (2006), whereas in observations of Thai and Papua New Guinea accessions by Vrydaghs et al. (2009), V3 volcaniforms were more frequent than V1. We further note that the Vi + V3 discriminator which separates *M. acuminata* subspecies in Thailand and Papua New Guinea from edible taxa in the work of Vrydaghs et al. (2009) does not separate the Sri Lankan diploids from triploid or tetraploid edible bananas (Table 4, Supplementary Table 1). The percentage of V3 morphotypes in Sri Lankan *M. acuminata* and *M. balbisiana* is always lower, sometimes by as much as 10 %, than in the triploid and tetraploid accessions, and this provides us with a possible way to discriminate between wild diploid and domesticated triploids and tetraploids.

We did not find V2 and V7 volcaniforms in our Sri Lankan *M. acuminata* and *M. balbisiana*, but these were present occasionally in triploid and tetraploid accessions, always in very low numbers (Table 4, Supplementary Table 1). In the Sri Lankan context, these differences seem to enable discrimination of the diploids *M. acuminata* and *M. balbisiana* from triploids and tetraploids.

There seem to be other differences between the volcaniform morphotypes present in Sri Lankan *M. acuminata* and those present in this

Table 4
Summary of volcaniform morphotype occurrence in the studied genetic groups (see also Supplementary Table 1).

Volcaniform morphotype	V1	V2	V3	V4	V5	V6	V7	V8	V1 + V3
M. acuminata AA total	441		74		23	6			515
M. acuminata AA %	81.07		13.60		4.23	1.10			94.67
M. balbisiana BB total	1468		363	5	131	56		25	1831
M. balbisiana BB %	73.11		18.08	0.25	6.52	2.79		1.25	91.19
Ambun AAA total	505		224	8	21	22	1	12	729
Ambun AAA %	63.68		28.25	1.01	2.65	2.77	0.13	1.51	91.93
Cavendish AAA total	234		125	2	9	25		1	359
Cavendish AAA %	59.24		31.65	0.51	2.28	6.33		0.25	90.89
Dwarf Cavendish AAA total	79		20		1				99
Dwarf Cavendish AAA %	79.00		20.00		1.00				99.00
Gros Michel AAA total	212		72	1	8	7			284
Gros Michel AAA %	70.67		24.00	0.33	2.67	2.33			94.67
Pisang masak hijau AAA total	111		66	1	9	12		1	177
Pisang masak hijau AAA %	55.50		33.00	0.50	4.50	6.00		0.50	88.50
William hybrid total	65		33		1			1	98
William hybrid %	65.00		33.00		1.00			1.00	98.00
AAA total	1206		540	12	49	66	1	15	1746
AAA %	63.88		28.60	0.64	2.60	3.50	0.05	0.79	92.48
Introduced AAB total	55		25	4	6	6		4	80
Introduced AAB %	55.00		25.00	4.00	6.00	6.00		4.00	80.00
Mysore AAB total	697	2	274	1	33	29		7	971
Mysore AAB %	66.83	0.19	26.27	0.10	3.16	2.78		0.67	93.10
Neithrapalam AAB total	27	1	21	2	11	28	7	3	48
Neithrapalam AAB %	27	1	21	2	11	28	7	3	48
Pisang kelat AAB total	246		48		5	1			294
Pisang kelat AAB %	82.00		16.00		1.67	0.33			98
Pome AAB total	193		75	2	7	11	1	10	268
Pome AAB %	64.55		25.08	0.67	2.34	3.68	0.33	3.34	89.63
Silk AAB total	372		111		8	9			483
Silk AAB %	74.4		22.2		1.6	1.8			96.6
Udakonbo AAB total	27		32	3	7	29	7	3	59
Udakonbo %	25.00		29.63	2.78	6.48	26.85	6.48	2.78	54.63
AAB total	1617	3	586	12	77	113	15	27	2203
AAB %	66.00	0.12	23.92	0.49	3.14	4.61	0.61	1.10	89.92
Atamuru ABB total	71		21		4	4			92
Atamuru ABB %	71		21		4	4			92.00
Bluggoe ABB total	143		44		13				187
Bluggoe ABB %	71.50		22.00		6.50				93.50
Monthan ABB total	94		5		1				100
Monthan ABB %	94		5		1				99.00
Pey kunnan ABB total	394		96		6	4			490
Pey Kunnan ABB %	78.80		19.20		1.20	0.80			98.00
Pisang Awak ABB total	572		185		24	19			757
Pisang awak ABB %	71.50		23.13		3.00	2.38			94.63
ABB total	1274		351		48	27			1625
ABB %	74.94		20.65		2.82	1.59			95.59
Triploid total	4097	3	1477	24	174	206	16	42	5574
Triploid %	67.84	0.05	24.46	0.40	2.88	3.41	0.26	0.70	92.30
Golden Banana (IC2) AAAA total	103	2	43	3	23	13	3	7	146
Golden Banana (IC2) AAAA %	52.28	1.02	21.83	1.52	11.68	6.60	1.52	3.55	74.11
Kandula AAAB total	158	4	65	12	17	27	2	8	223
Kandula AAAB %	53.92	1.37	22.18	4.10	5.80	9.22	0.68	2.73	76.10
Pulathisi AABB total	139		76	2	36	52		1	215
Pulathisi AABB %	45.42		24.84	0.65	11.76	16.99		0.33	70.26
Tetraploid total	400	6	184	17	76	92	5	16	584
Tetraploid %	50.25	0.75	23.12	2.14	9.55	11.56	0.63	2.01	73.37

species and its subspecies in other countries. Thus Sri Lankan *M. acuminata* accessions did not contain V4 and V7 morphotypes, similar to the wild accession of *M. acuminata* ssp. *banksii* from Papua New Guinea reported in Ball et al. (2006) and Vrydaghs et al. (2009) although they are present in various Thai subspecies of *M. acuminata* (Vrydaghs et al. 2009).

Similarly, there seem to be differences in the phytoliths in *M. balbisiana* reported from different countries. Our *M. balbisiana* from Sri Lanka lack V2 and V7 but contain V8 volcaniforms, whereas Ball et al. (2006) show that V2 are present and V8 morphotypes are absent in the specimens from New Guinea and Honduras, and V7 is present in the *M. balbisiana* sample from New Guinea.

Our results thus suggest that in general the Sri Lankan diploid banana species can be discriminated from each other and from cultivated triploid and tetraploid banana plants using the volcaniform phytolith morphotypes (cf. Ball et al., 2006), although there are individual samples with very few morphotypes (only V1 and V3) among the different taxa and varieties that cannot be discriminated this way. Our results differ from those of researchers working on these species outside Sri Lanka (Ball et al. 2006; Vrydaghs et al., 2009; De Langhe et al. 2019) because *M. balbisiana* usually produces V4 and V8 in Sri Lanka; whereas Sri Lankan *M. acuminata* (Table 4, Supplementary Table 1) does not produce these morphotypes. This suggests that some members of these species had become isolated from their conspecifics in Southeast Asia and thus that at least parts of the Sri Lankan populations are of considerable antiquity. The occurrence of *M. acuminata* as isolated populations in very remote areas of Sri Lanka (e.g. hilltops, steep slopes of hilly areas) suggests that it may have a different genetic status relative

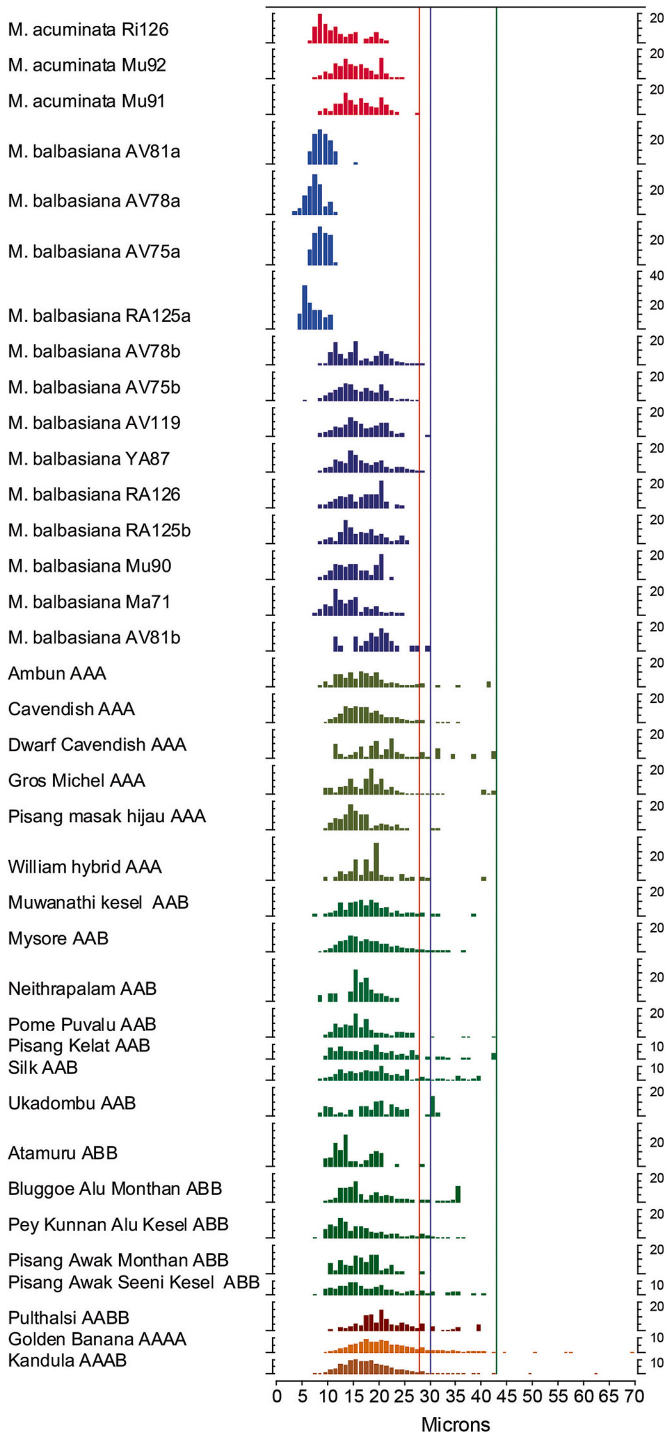


Fig. 7. Size histograms for basal lengths of diploid, triploid and tetraploid banana plant volcaniform phytoliths. Percentages are indicated in the vertical scales, and the horizontal axes show dimensions in 1 µm classes. The red vertical line indicates the maximum basal length of *M. acuminata* volcaniforms, the blue vertical line shows the maximum basal length of *M. balbisiana* volcaniforms, and the green vertical line indicates the maximum basal length of triploid volcaniforms. Multiple accessions of triploid and tetraploid taxa were fairly uniform and therefore averaged values for each variety are shown for these. Size histograms are shown for each accession of the diploid taxa. It is clear that two size-groups of *M. balbisiana* volcaniforms are present. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to *M. balbisiana* (Samarasinghe et al., 2010). It is possible that our observation in phytolith morphotypes seem to have a close relationship with lower genetic diversity in *M. acuminata* than in *M. balbisiana,* reported by Samarasinghe et al. (2010) and Jayaweera and Samarasinghe (2016).

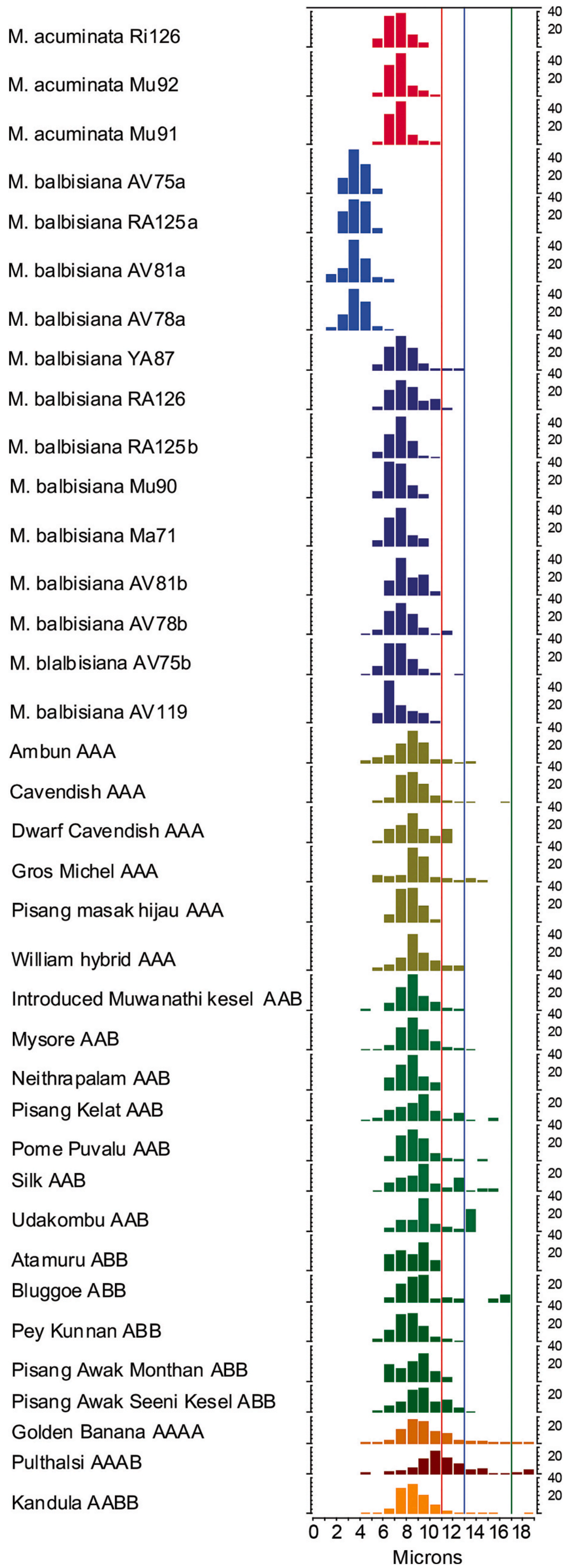
4.2. Phytolith dimensions and the discrimination of banana taxa

Ball et al. (2006) suggested that domesticated triploid bananas produce significantly larger phytoliths than *M. balbisiana* (BB) and *M. acuminata* (AA), which is in good agreement with our results (Figs. 7, 8, Tables 5-7). Ball et al. (2006) note that the mean basal length and mean aspect product allow for separating *M. balbisiana* phytoliths from those of *M. acuminata* subsp. *banksii*. There are, however, some significant differences between the volcaniform phytolith dimensions of Sri Lankan diploid bananas and those from the localities where Ball et al. (2006) sourced their samples (Tables 5, 6). The mean volcaniform basal length for Sri Lankan *M. balbisiana* (BB) that we observed was 13.83 µm, whereas the mean basal length for two accessions of this species in New Guinea was 19.6 and 20.2 µm (Table 5; see also Ball et al., 2006). We observed mean volcaniform basal length of 14.79 µm for wild *M. acuminata* (AA) whereas Ball et al. (2006) report mean volcaniform basal length for wild *M. acuminata* from New Guinea as 16.9 µm.

The mean crater width for *M. balbisiana* (BB) in our Sri Lankan populations is 6.30 µm, whereas it was recorded as 6.9 µm for wild *M. balbisiana* from New Guinea and 6.4 µm for specimens from Honduras (Ball et al. 2006). The mean crater width of wild *M. acuminata* (AA) varies slightly between the various subspecies but differences are not sufficient to allow distinction (Ball et al. 2006; Vrydaghs et al. 2009). Sri Lankan *M. acuminata* volcaniforms have a mean crater width of 7.06 µm, while the mean crater width of the same species from New Guinea is 6.0 µm (Ball et al. 2006). Other wild *M. acuminata* subspecies in Thailand have mean crater widths between 6.42 µm and 8.11 µm (Vrydaghs et al. 2009).

Volcaniform mean basal length and mean crater width, therefore, are not reliable ways to differentiate fully between *M. balbisiana* and *M. acuminata*. It may be observed, however, that a proportion of Sri Lankan *M. balbisiana* volcaniforms have basal lengths and crater widths smaller than any produced by *M. acuminata*, and thus in the Sri Lankan context, volcaniforms with basal lengths less than 5.9 µm and crater widths smaller than 5.1 µm can be fairly confidently attributed to *M. balbisiana* when discriminating between these species (Tables 4-6). Similarly, a small number of *M. balbisiana* volcaniforms have basal lengths and crater widths greater than *M. acuminata,* so volcaniforms over 27.2 µm in basal length and over 10.2 µm in crater width can be assigned to *M. balbisiana* where no other taxa are involved. Additionally, the differences between seed phytoliths derived from these two taxa (Fig. 5) and in some cases, phytolith morphotype occurrence also offer the possibility of secure differentiation of these two species. A detailed description of seed phytoliths is not included here because our main concern is in developing criteria for separating diploid, triploid and tetraploid banana volcaniform phytoliths. Seed morphotypes are not associated with the domesticated triploid and tetraploid seedless bananas.

Vrydaghs et al. (2009) suggests that the mean crater width from banana leaf samples of the northern (e.g. Thailand area), *M. acuminata* subspecies *malaccensis*, *burmannica-siamea* and *truncata* are 6.48–7.10 µm, 6.42–8.11 µm and 6.82 µm, respectively (Table 6). There is close correspondence of mean crater widths between ssp. *burmannica-siamea* reported by Vrydaghs et al. (2009) and the mean crater width (7.06 µm) in our samples from *M. acuminata*. Genetic studies suggest that Sri Lankan *M. acuminata* is not far removed from *M. acuminata* subsp. *burmanica* (Perrier et al., 2011). No significant banana cultivars (AA, AAA or AAB) have been identified that have descended from this subspecies (Perrier et al., 2011). The mean crater width (7.06 µm) of Sri Lankan *M. acuminata* and northern *M. acuminata* subsp. *burmannica-siamea*



(caption on next column)

Fig. 8. Size histograms for crater widths of diploid, triploid and tetraploid banana plant volcaniform phytoliths. Percentages are indicated in the vertical scales, and the horizontal axes show dimensions in 1 µm classes. The red vertical line indicates the maximum crater width of *M. acuminata* volcaniforms, the blue vertical line shows the maximum crater width of *M. balbisiana* volcaniforms, and the green vertical line indicates the maximum crater width of triploid volcaniforms. Multiple accessions of triploid and tetraploid taxa were fairly uniform and therefore averaged values for each variety are shown for these. Size histograms are shown for each accession of the diploid taxa. It is clear that two size-groups of *M. balbisiana* volcaniforms are present.

(~7.00 µm) is relatively larger than that of *M. acuminata* ssp. *banksii* (5.98–5.72 µm). The latter seems to have been a key contributor to developing edible *M. acuminata* diploids (AA) in the primary domestication that happened in the New Guinea area (cf. Vrydaghs et al., 2009; Perrier et al., 2011).

4.3. *Further Discussion*

As yet, there is no genetic evidence to support arguments that Sri Lanka was a source region for banana cultivars (Perrier et al., 2011). It was suggested that domesticated bananas in South Asia appeared after the dispersal of triploid AAB and ABB cultivars from Southeast Asia/ Indonesia–New Guinea through different routes (Lejju et al., 2006; Kagy et al., 2016; De Langhe, et al., 2019). It cannot be excluded, however, that the hybridization of AA and BB genomes, which seem to have occurred after introduction of AA diploid cultivars from Southeast Asia/ Indonesia-New Guinea, could also have occurred in Sri Lanka (Premathilake and Hunt, 2018). Additionally, some domesticated bananas in Sri Lanka could have originated from hybridization between an incoming triploid and a Sri Lankan *M. balbisiana* (cf. Ball et al., 2006: 1235). This hypothesis is tenable considering that triploid or tetraploid banana plants seem to have first appeared in premodern times in Sri Lanka, but cannot be substantiated given current lack of evidence.

Sri Lankan *M. balbisiana* has two distinct size groupings in basal length and crater width (Figs. 7, 8, Table 5). Overall in our samples of *M. balbisiana* has a mean crater width of 6.30 µm and mean basal length is 13.83 µm. There are, however, two apparent populations:

- small phytoliths with crater width minimum of 1.62 µm, mean of 3.58 µm and maximum of 6.0 µm; and basal length minimum of 3.20 µm, mean of 7.87 µm, maximum of 15.0 µm
- large phytoliths with crater width minimum of 4.2 µm, mean of 7.15 µm, maximum of 12.10 µm and basal length minimum of 5.0 µm, mean of 15.77 µm, maximum of 29.1 µm.

These populations cannot be separated morphotypically (Supplementary Table 1).

These data might suggest that *M. balbisiana* populations in Sri Lanka consist of two partially geographically-separated groups (Table 8, Fig. 1). This could be because of some sort of genetic divergence between native groups (cf. Samarasinghe et al., 2010; Jayaweera and Samarasinghe, 2016), or because one group is native to the island and the other was introduced. It is perhaps possible that the group that produces small phytoliths may be a key contributor to locally-originating triploid or tetraploid banana cultivars in Sri Lanka. Fuller and Madella (2009) indicate that in banana phytoliths at Kot Diji in Pakistan dating to 4.5–3.9 ka BP, the crater widths were between 11.4–15.7 µm and a single basal length was 34.2 µm, which fall with the triploid or tetraploid banana cultivars in our study (Table 4). However, it is still difficult to explain how these cultivars (likely triploids and diploids) were introduced from India to Sri Lanka or the reverse (Ball et al. 2006; De Langhe, et al., 2019) without having comparative studies of banana phytoliths, ethnoarchaeology and archaeology/history across a vast area extending from the New Guinea region where domesticated bananas seem to have mainly originated, across Southeast Asia, India,

Table 5
Basal length and crater width measurements of M. balbisiana banana plant volcaniform phytoliths in microns, showing the values for each Sri Lankan accession, the combined Sri Lankan values and comparative values from Honduras and New Guinea from Ball et al. (2006). Sri Lankan accessions with small phytoliths are indicated with (s).

Taxon & sample code	Description, genomics	Origin	Basal Length (μm)			Crater width (μm)			Author
			Min	Mean	Max	Min	Mean	Max	
M. balbisiana Av75a	Wild, BB (s)	Sri Lanka	6.1	8.93	15.0	2.0	3.61	5.5	This study
M. balbisiana Av78a	Wild, BB (s)	Sri Lanka	3.2	7.36	11.0	1.62	3.60	6.0	This study
M. balbisiana Av81a	Wild, BB (s)	Sri Lanka	6.74	8.90	15.0	1.62	3.52	6.0	This study
M. balbisiana Ra125a	Wild, BB (s)	Sri Lanka	4.24	6.97	11.54	2.0	3.61	5.55	This study
M. balbisiana Av75b	Wild, BB	Sri Lanka	5.0	15.56	27.1	4.0	7.00	12.1	This study
M. balbisiana Av78b	Wild, BB	Sri Lanka	8.1	15.69	28.5	4.2	7.36	11.0	This study
M. balbisiana Av81b	Wild, BB	Sri Lanka	12.0	18.94	29.0	6.1	7.69	10.1	This study
M. balbisiana Av119	Wild, BB	Sri Lanka	8.2	16.11	29.1	5.1	6.95	10.1	This study
M. balbisiana Ma71	Wild, BB	Sri Lanka	7.8	13.91	24.3	5.2	7.11	9.8	This study
M. balbisiana Mu90	Wild, BB	Sri Lanka	8.2	13.36	22.1	5.1	6.91	9.1	This study
M. balbisiana Ra125b	Wild, BB	Sri Lanka	8.3	16.29	25.0	5.1	7.06	10.1	This study
M. balbisiana Ra126	Wild, BB	Sri Lanka	8.1	16.36	24.0	5.5	7.84	11.2	This study
M. balbisiana Ya87	Wild, BB	Sri Lanka	8.1	16.37	28.1	5.1	7.31	12.1	This study
M. balbisiana (all data)	Wild, BB	Sri Lanka	3.2	13.83	29.1	1.62	6.30	12.1	This study
M. balbisiana	Wild, BB	Honduras	11.3	19.6	41.8	3.1	6.4	8.6	Ball et al., 2006
M. balbisiana	Wild, BB	New Guinea	10.4	20.2	37.7	3.1	6.9	10.2	Ball et al., 2006

Table 6
Basal length and crater width measurements in microns of M. acuminata banana plant volcaniform phytoliths, showing the values for each Sri Lankan accession, the combined Sri Lankan values and comparative values from New Guinea and Thailand from Vrydaghs et al. (2009) plus, for comparison, values for edible *M. acuminata* ssp. *banksii* after Ball et al. (2006).

Taxon Sample code	Description, genomics	Origin	Basal Length (μm)			Crater width (μm)			Author
			Min	Mean	Max	Min	Mean	Max	
M. acuminata M91	Wild, AA	Sri Lanka	8.10	15.75	27.2	5.1	7.08	10.2	This study
M. acuminata Mu92	Wild, AA	Sri Lanka	7.8	15.10	24.1	5.1	7.05	10.0	This study
M. acuminata Ri126	Wild, AA	Sri Lanka	5.97	11.71	21.2	5.22	7.03	9.2	This study
M. acuminata (all data)	Wild, AA	Sri Lanka	5.97	14.79	27.2	5.1	7.06	10.2	This study
M. acuminata ssp. *banksii*	Wild, AA	New Guinea	8.4	16.9	28.0	3.6	5.98	8.9	Ball et al. 2006; Vrydaghs et al. 2009
M. acuminata ssp. *truncata*	Wild, AA	Betong, Thailand	NA	NA	NA	4.2	6.82	10.0	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	Sri Lanka, Thailand	NA	NA	NA	4.8	7.10	10.5	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	Maesot, Thailand	NA	NA	NA	4.6	6.92	10.1	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	Kra, Thailand	NA	NA	NA	4.9	7.03	10.3	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	Namtok Thanto, Thailand	NA	NA	NA	4.6	6.86	9.8	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	HuaiYot,, Thailand	NA	NA	NA	3.9	6.53	11.8	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	Kapaang, Thailand	NA	NA	NA	4.5	6.62	10.9	Vrydaghs et al. 2009
M. acuminata ssp. *malaccensis*	Wild, AA	Namtok Phnomlook, Thailand	NA	NA	NA	4.7	6.48	9.8	Vrydaghs et al. 2009
M. acuminata ssp. *burmannica-siamea*	Wild, AA	PangSida, Thailand	NA	NA	NA	4.6	6.42	10.1	Vrydaghs et al. 2009
M. acuminata ssp. *burmannica-siamea*	Wild, AA	Khlung, Thailand	NA	NA	NA	3.8	7.08	14.0	Vrydaghs et al. 2009
M. acuminata ssp. *burmannica-siamea*	Wild, AA	Pala-U, Thailand	NA	NA	NA	4.2	6.53	10.1	Vrydaghs et al. 2009
M. acuminata ssp. *burmannica-siamea*	Wild, AA	Phrao, Thailand	NA	NA	NA	5.1	7.83	11.3	Vrydaghs et al. 2009
M. acuminata ssp. *burmannica-siamea*	Wild, AA	MaeWong, Thailand	NA	NA	NA	5.3	8.11	12.7	Vrydaghs et al. 2009
M. acuminata ssp. *burmannica-siamea*	Wild, AA	SaiYoke, Thailand	NA	NA	NA	4.1	7.17	10.3	Vrydaghs et al. 2009
M. acuminata ssp. *banksii*	Edible AA	Djum Tau, New Guinea	7.3	12.1	20.3	3.9	5.7	8.1	Ball et al. 2006
M. acuminata ssp. *banksii*	Edible AA	Uwati, New Guinea	11.3	16.1	35.4	3.7	5.9	10.0	Ball et al. 2006
M. acuminata ssp. *banksii*	Edible AA	Guyod, Philippines	7.6	15.0	30.8	3.7	6.0	8.4	Ball et al. 2006

and Africa (Perrier et al., 2011; Kagy et al., 2016). Work in other parts of this enormous region is urgently necessary.

All our data indicate the substantially larger size of the phytoliths from domesticated banana plants (AAA, AAB, ABB, AAAA, AAAB and AABB) sampled in this study, as evidenced by volcaniform basal lengths (means ranging from 14.58 to 21.58 μm) and crater width (means

Table 7
Minimum, mean and maximum dimensions in microns for volcaniform basal lengths and crater width of diploid, triploid and tetraploid banana plants. The two size morphs of phytoliths from *M. balbisiana* are summarised separately in this table.

Name	Genetic group	Basal length (μm)			Crater width (μm)		
		Minimum	Mean	Maximum	Minimum	Mean	Maximum
M. acuminata	AA	5.97	14.8	27.2	5.1	7.06	10.2
M. balbisiana (small)	BB	3.2	8.04	15.0	1.6	3.58	6.0
M. balbisiana (large)	BB	5.0	16.07	29.1	4.0	7.25	12.1
Ambun	AAA	8.1	17.45	41.2	4.1	8.07	13.1
Cavendish	AAA	9.5	17.09	36.1	5.1	8.23	16.1
Dwarf Cavendish	AAA	11.5	21.40	38.3	5.8	8.53	11.5
Gros Michel	AAA	9.1	18.20	42.2	5.1	8.68	14.0
Pisang masak hijau	AAA	9.5	15.57	32.2	6.1	9.72	10.2
William hybrid	AAA	9.8	18.33	39.1	5.1	8.67	12.6
Mysore	AAB	8.1	17.55	36.7	4.4	8.47	15.5
Neithrapalam	AAB	8.1	16.61	24.1	6.2	7.94	10.2
Pisang kelat	AAB	9.5	19.24	42.5	4.5	8.86	15.5
Introduced	AAB	7.0	17.77	38.1	4.8	8.31	12.0
Pome	AAB	9.1	16.81	42.2	6.1	8.34	14.5
Silk	AAB	8.0	19.95	39.1	5.1	9.36	15.1
Udakombu	AAB	8.9	19.90	31.0	6.1	9.87	13.7
Atamuru	ABB	9.2	14.59	28.5	6.0	8.15	10.1
Bluggoe	ABB	9.5	19.15	35.5	6.1	9.20	16.2
Pey kunnan	ABB	7.2	18.33	36.6	5.2	8.55	12.7
Mondan	ABB	9.0	19.66	36.1	5.2	8.55	12.8
Pisang Awak Seeni Kesel	ABB	7.2	18.61	40.0	5.6	8.95	13.2
Pisang Awak Monthan	ABB	10.0	16.37	28.0	6.0	8.22	11.0
Golden Banana	AAAA	9.5	21.07	69.5	4.2	9.33	18.5
Kandula	AAAB	7.3	17.72	62.8	4.5	8.40	18.0
Pulthalsi	AABB	10.0	21.58	39.2	4.2	10.91	18.6

Table 8
Number of accessions of *M. balbisiana* with large or small volcaniform phytoliths.

Sample codes	Locality/Province	Large Phytoliths	Small Phytoliths
Ma 71 1 sample	Makandura, North Western Province	1	0
Av 75a, 1 sample	Avissawella, Western Province	0	1
Av 75b, 4 samples	Avissawella, Western Province	4	0
Av 78a, 2 samples	Avissawella, Western Province	0	2
Av 78b, 3 samples	Avissawella, Western Province	3	0
Av 81a, 1 sample	Avissawella, Western Province	0	1
Av 81b, 1 sample	Avissawella, Western Province	1	0
Av 119, 2 samples	Avissawella, Western Province	2	0
Ya 87, 2 samples	Yatiyanthota, Sabaragamuwa Province	2	0
Ra 125a, 1 sample	Rathnapura, Sabaragamuwa Province	0	1
Mu 90, 2 samples	Maskeliya, Central Province	2	0
Ri 126, 1 sample 0M.0014/91.34, 1 sample	Riversten, Central Province	1	0
Ra125b, 1 sample	Rathnapura, Sabaragamuwa Province	1	0

ranging from 7.92 to 10.91 μm) compared with those of the observed Sri Lankan diploid species (*M. balbisiana* mean basal length 13.83 μm, mean crater width 6.30 μm and *M. acuminata* mean basal length 14.79 μm, mean crater width 7.06 μm). The use of basal length and crater width to distinguish volcaniform phytoliths from domesticated bananas is indeed challenging because of the considerable overlap of basal length and crater width among the banana taxa (Figs. 7-8). Separation of diploid and triploid/tetraploid banana phytoliths can be done using the threshold values of basal length > 29.1 μm and crater width > 12.1 μm for attested triploid and tetraploid banana plants, as shown in Figs. 7-8 and Table 7. Since there is no apparent difference in basal length and crater width in domesticated bananas grown under different environmental conditions in Sri Lanka (Perera, 2017), it cannot be argued that using these criteria will cause problems separating wild and domesticated banana phytoliths.

Anyone trying to identify ancient Sri Lankan banana plants should have a starting null hypothesis that all of the ancient phytoliths were from wild *M. acuminata* and/or *M. balbisiana*. Therefore, if all phytolith morphotypes in an ancient sample fall only within the zone of overlap (in morphotype occurrence and percentages; and in basal length and crater length) between current diploid taxa and domesticated triploid/tetraploid varieties, the conclusion has to be that only wild diploid taxa were present.

5. Conclusion

Understanding the appearance of domesticated *Musa* bananas in archaeological sites located within the natural geographical range of the wild progenitors of domesticated banana plants of the *Eumusa* section, including *M. acuminata* and *M. balbisiana,* has been a challenging issue using banana leaf volcaniform phytolith studies. This was especially the case because of the considerable overlap between volcaniform phytoliths of wild and domesticated bananas, morphotypically and in terms of their size. To understand this issue, we analysed large collections of volcaniform phytoliths from modern wild and domesticated banana taxa and varieties to ascertain patterns of morphology and size in volcaniform phytoliths at the present day.

In Sri Lanka, volcaniform phytoliths from domesticated (triploid and tetraploid) banana plants are characterized by relatively low percentages of V1 + V3 and relatively high percentages of V4, V5, V6 and V8 morphotypes compared with the percentages of these morphotypes in diploid species. The rarer V2 and V7 morphotypes are restricted to domesticated triploid/tetraploid bananas. Mean basal length (means of 14.58 to 21.58 μm) and crater width (means of 7.92 to 10.91 μm) in domesticated triploid/tetraploid bananas are somewhat larger than they are in diploid bananas (mean basal length for *M. balbisiana* 13.83 μm, for *M. acuminata* 14.79 μm; mean crater width for *M. balbisiana* 6.30 μm, for *M. acuminata* 7.06 μm). These size values of phytoliths cannot fully differentiate diploid and domesticated triploid/tetraploid banana plants due to overlapping size-ranges, but our work has identified threshold values of basal length > 29.1 μm and crater width > 12.1 μm, above which there are only volcaniform phytoliths from domesticated triploid and tetraploid banana plants in Sri Lanka. These larger phytoliths (above the thresholds) can therefore be taken as reliable evidence for the presence of domesticated triploid and tetraploid banana plants.

To address the antiquity of domesticated bananas in Sri Lanka, we will next renew our research on phytoliths found in archaeological stratigraphies in Sri Lanka, starting with the FaHien Rockshelter where our previous work suggested the likelihood of domesticated banana plant phytoliths in the mid Holocene (Premathilake and Hunt, 2018). We will compare the results of the new work with the modern banana phytolith dataset described in this paper.

Currently, our detailed size and morphological data is only for the banana volcaniform phytolith taxa present in Sri Lanka. Limited research has been published on volcaniform phytolith morphology and dimensions in other parts of the region (including South Asia, Southeast Asia and Australasia) where wild banana taxa are present, and this presents a barrier to full understanding of the origination and dispersal of this important food crop.

6. Statement

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CRediT authorship contribution statement

R. Premathilake: Writing – original draft, Methodology, Data curation, Conceptualization. **C.O. Hunt:** Conceptualization. **P.P.D.C. Perera:** Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Data availability

Data will be made available on request.

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