# Tracing Domestication and Cultivation of Bananas from Phytoliths: An update from Papua New Guinea

Carol J. Lentfer

## Research

## Abstract

There is now good evidence from current banana distributions and genetic analysis that Papua New Guinea and nearby regions have played a key role in the domestication of edible Eumusa and Australimusa bananas. Strong support for this also comes from phytoliths in the archaeobotanical record. Seeds have diagnostic phytoliths which can be used to discriminate between the two main sections of edible bananas, the giant banana, *Musa ingens*, and *Ensete*. Therefore, the presence of seed phytoliths and their subsequent disappearance from archaeological assemblages can be used to trace processes of domestication leading to parthenocarpy and sterility. Following loss of viable seeds, banana presence can still be documented from phytolith morphotypes from other plant parts, particularly the volcaniform morphotypes from leaves. Nevertheless, according to several pioneer studies, these are more difficult to differentiate unless they occur in regions where certain species or varieties of bananas are not endemic.

This paper reviews results from morphometric and morphotypic analyses of Musaceae phytoliths and briefly introduces the 'New Guinea Banana Project' which builds upon previous analyses. The morphometric database, combined with a comprehensive set of images, facilitates banana phytolith identification and is another step forward in solving the issues surrounding banana dispersal, cultivation and domestication, especially in the Pacific/New Guinea region.

## Introduction

*Musa* bananas (including plantains) constitute major food staples in the tropics and in terms of gross value of food production they are by far the most important world fruit crop. Furthermore, the banana plant is valued for more than just its fruit (Kennedy 2009): the stem, corm, bract (bell), seeds and flowers can also be eaten; the leaves are used for cooking, wrapping, serving food and for shelter from the sun and rain; fibers from the stem and petioles are used for making string, rope and other cordage for weaving; the sap is used for dye; and, the seeds are used as beads or money (Burkill 1935, Lentfer 2003a, b). Given this multitude of uses, even in their wild state and prior to the development of fleshy, seedless (or nearly seedless) fruit (Lentfer 2003a), it is likely that banana plants would have been recognized as a prized resource and exploited in the past in ways similar to the present. Indeed, this is the picture that is gradually emerging from a host of archaeobotanical, biogeographical, biomolecular and genetic evidence (e.g., Carreel *et al*. 2002, De Langue & de Maret 1999, Denham *et al*. 2003, Kennedy 2008, Mbida *et al*. 2001, Perrier *et al*. 2009, Vrydaghs *et al*. 2009). Complex origins and multiple dispersals for banana cultivars are indicated, but perhaps more striking is the significant role that the New Guinea region has played in the development of the domesticated banana. After a brief review of the evidence for the origins and spread of cultivated bananas, this paper outlines a current research project which expands current banana phy-

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tolith databases for further assessment of phytolith variation within and between wild and domesticated *Musa* bananas and *Ensete* in Papua New Guinea.

### *Origins and distributions of banana cultivars*

There are several wild species of *Musa* bananas and closely related *Ensete* species ranging from Africa (*Ensete* only) to India, Southeast Asia and as far east as New Guinea and the Solomon Islands (*Ensete* and *Musa*). Additionally, there are hundreds of diploid, triploid and polyploid cultivars derived from a few wild species from two sections of bananas (Eumusa and Australimusa) that are cultivated in tropical and subtropical regions worldwide (Argent 1976, Arnaud & Horry 1997, Daniells *et al*. 2001, De Langhe *et al*. 2009, Kennedy 2008, Lentfer 2003a, Pollefeys *et al*. 2004, Sharrock 1990, Simmonds 1959, 1962, Valmayor 2001, Wong *et al*. 2001). Phytogeography and genetic evidence shows that the domesticated Australimusa **Fe`i** banana almost certainly originated in the New Guinea region (Jarret *et al*. 1992, MacDaniels 1947, Simmonds 1959), but the origins of the more commonly known and widely marketed Eumusa cultivars have been more difficult to determine. Based on the distribution of diploid and triploid Eumusa bananas that contain an A genome derived from either *Musa acuminata* Colla subspecies *banksii* (F. Muell.) Simmonds or *errans* (Blanco) R.V. Valmayor or both (see summary in Table 6, Kennedy 2008:85), it appears that the primary center for the domestication of edible Eumusa section bananas was the Philippines/New Guinea region.

Significantly, a long history of banana manipulation by humans, particularly in the New Guinea region, is indicated by the presence of the *banksii* A genome in AAB plantains as far afield as Africa and the Pacific. Coupled with the proliferation of diploid AA cultivars in New Guinea, this points to the likelihood of an early dispersal from the New Guinea region in two directions, eastwards into the Pacific region and westwards through Island Southeast Asia, Malaysia and across to Africa (Kennedy 2008:85-86). The large number of diploid AA cultivars with both *banksii* and *errans* genomes, as well as the absence of the *errans* genome in the African AAB plantains but its presence together with the *banksii* genome in the Pacific AAB **Maia Maoli** plantains are interesting and imply complex species and subspecies interactions within the Philippines/New Guinea regions. This would have involved human diffusion of bananas, probably concurrent with the earliest transfer of the *banksii* A genome westwards into Island Southeast Asia, and then to mainland Asia and eventually Africa, and also subsequently over an extended period as people expanded eastwards into the Pacific (Kennedy 2008, Perrier *et al*. 2009).

### *Archaeobotanical records for bananas*

The archaeobotanical record for bananas is very sparse and is mostly derived from microfossil evidence, particularly phytoliths (reviewed in Denham & Donohue 2009 and Donohue & Denham 2009). Evidence from starch shows good promise of adding to this (Lentfer 2009), but currently there is only one confirmed record with a positive identification of banana starch associated with an archaeological deposit from Santa Cruz in the Solomon Islands (Crowther 2009). The only other record comes from the Yuku rock shelter site in the Western Highlands of Papua New Guinea, but this has not been confirmed as banana (Horrocks *et al*. 2008). Most phytolith records to date have been based on the identification of distinctive volcaniform morphotypes from Musaceae leaves. However, identification beyond the family level has not been successfully attempted in most studies because of the difficulties in discriminating between volcaniform morphotypes from different Musaceae genera, sections and species.

In his pioneering work at Kuk in the Western Highlands of Papua New Guinea, Wilson (1985) used morphometric analyses to discriminate between three sections of bananas and he also identified some Musaceae morphotypes in sediments dated to c. 10,000 cal B.P. as Australimusa. However, these identifications were problematic and inconclusive, partly due to the limited set of comparative reference material analyzed, but also due to the assumption that Eumusa section bananas were introduced into New Guinea from Southeast Asia during the mid-to-late Holocene (e.g., Spriggs 1996). More recently, Lentfer (2003a) found that the seeds from Australimusa, Eumusa, Ingentimusa and *Ensete* have diagnostic phytolith morphotypes (Figure 1), and was able to confirm the presence of *Musa ingens* Simmonds - the giant cold-tolerant banana belonging to Section Ingentimusa, *Ensete glaucum* (Roxb.) Cheesman, and Eumusa section bananas from seed phytolith morphotypes in a similar archaeological context at the Kuk Swamp site (Denham *et al*. 2003, Lentfer 2003b). The earliest records for Eumusa and Ingentimusa seed phytoliths recovered from palaeochannel fills in this analysis were dated at c. 10,000 cal B.P. Eumusa persisted to the top of the archaeological sequence dated at c. 2500 cal B.P. The earliest date for *Ensete* seed phytoliths recovered from palaeosurface feature fills was c. 7000-6500 cal B.P. Similar to Eumusa, these persisted to the top of the sequence. Volcaniform leaf phytoliths were also present but were not identified to any particular section or species.

In addition to the Kuk site, Lentfer also confirmed the presence of Eumusa section bananas from diagnostic seed phytoliths at the coastal Lapita site of SAC on Watom Island, East New Britain, Papua New Guinea (Lentfer & Green 2004), as well as *Ensete*, Eumusa and Australimusa section bananas at the archaeological site of FIF/4 at the Yombon airstrip in South West New Britain (Lentfer *et al*. 2008). As with Kuk, volcaniform leaf phytoliths were present in both assemblages but no attempt was made to identify them beyond the family level in the initial analyses.

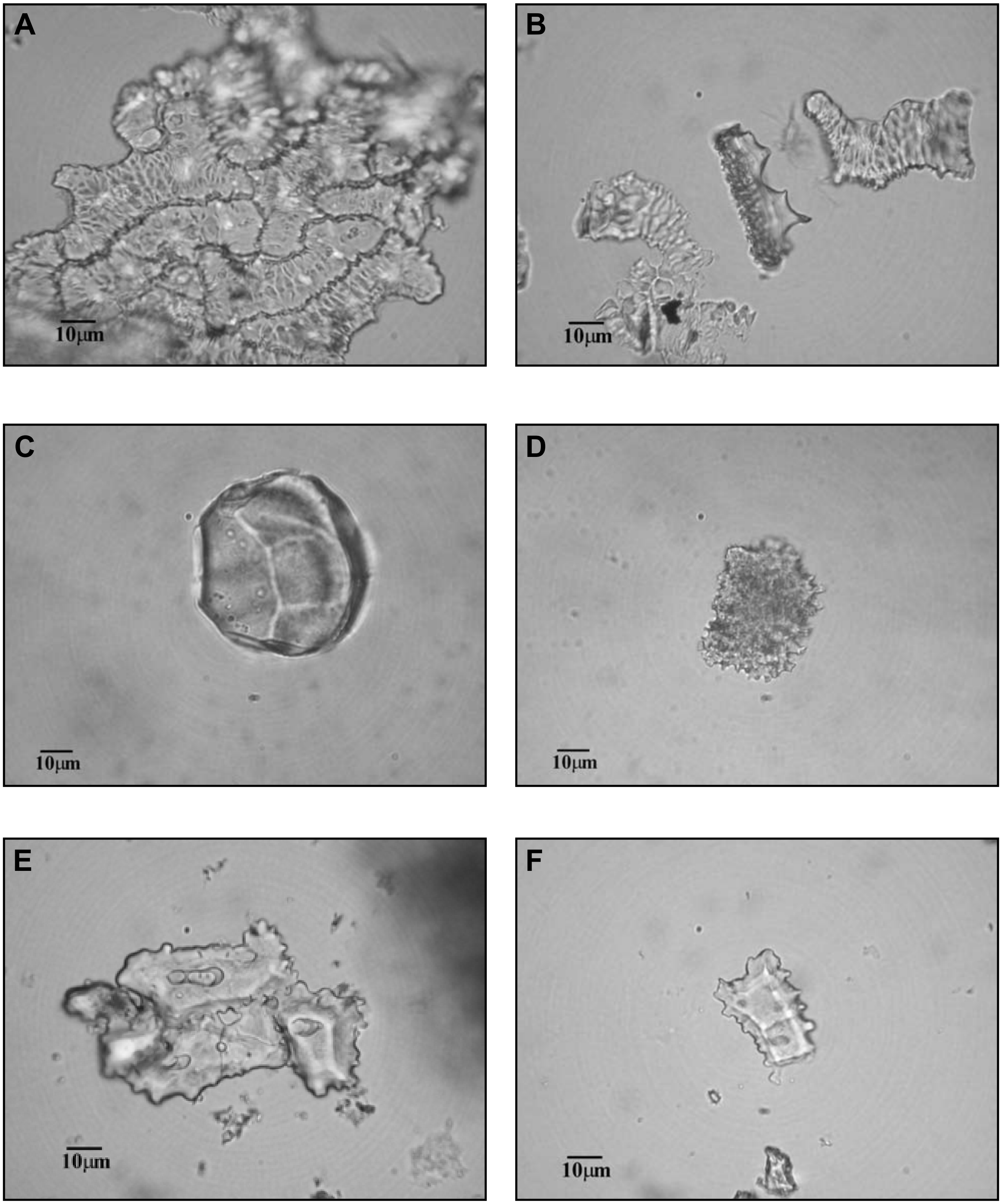


**Figure 1**. Diagnostic seed morphotypes of wild *Musa* bananas and *Ensete* from Papua New Guinea. **A**-**B**. *Ensete glaucum* (Accession No. QH28807); **C**-**D**. *Musa ingens*, Section Ingentimusa (Accession No. WH1); **E**-**F**. *Musa peekelii*, Section Australimusa (Accession No. WNB488).

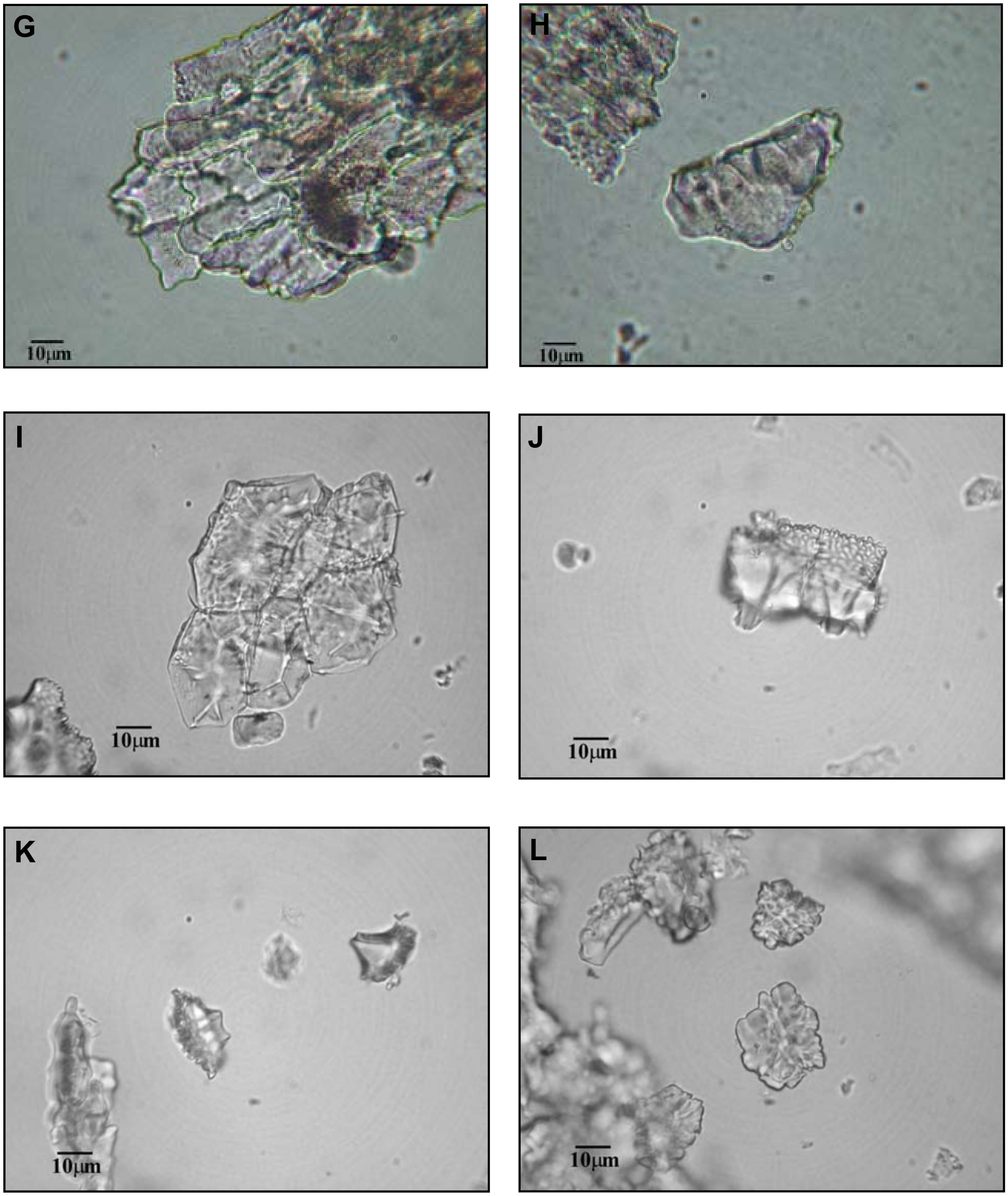


**Figure 1 cont**. Diagnostic seed morphotypes of wild *Musa* bananas and *Ensete* from Papua New Guinea. **G**-**H**. *Musa maclayi*, Section Australimusa (Accession No. MB6); **I**-**J**. *Musa acuminata* ssp.*banksii*, Section Eumusa (Accession No. QH067962); **K**-**L**. *Musa schizocarpa*, Section Eumusa (Accession No. NB489).

Apart from phytolith studies in New Guinea there are few other published accounts of banana identification beyond the family level with the exception of two African studies in Cameroon and Uganda. Volcaniform morphotypes recovered from refuse pits at an agricultural village site, Nkang in southern Cameroon dating to c. 2500 cal B.P. were identified to genus *Musa* (Mbida *et al*. 2001, 2004). Further to the east, at Munsa, Uganda, both *Musa* and *Ensete* phytoliths were identified from swamp sediment cores (Lejju *et al*. 2006). The oldest dates for these were c. 5200 cal B.P. (cf. Neumann & Hildebrand 2009). In contrast to New Guinea, no seed phytoliths were recorded from either African site, probably because *Musa* bananas were already seedless by the time they had been introduced into Africa.

### *The question of cultivation*

Banana plants in their natural state are light-demanding pioneer species of tropical environments. Growing naturally from seed and via suckers, bananas are adapted to opportunistic colonization of mostly well-drained open sites such as forest margins, forest gaps resulting from tree fall, and scree slopes associated with landslides and erosion (e.g., Argent 1976, MacDaniels 1947). Human selection, which eventually led to female sterility, loss of seeds and parthenocarpy, has produced hundreds of different land races and hybrids of Eumusa, Australimusa and Eumusa x Australimusa section bananas occurring in the Indo-Pacific region and Africa (see De Langhe *et al*. 2009) and implies a long history of somatic mutation and human manipulation involving cultivation.

Nevertheless, given the sparse record of prehistoric banana distribution, tracking evidence for cultivation and dispersal of cultivars is difficult. The record is derived mostly from two broad categories of evidence: ecological and geographical. This is mostly reliant on archaeobotanical finds showing presence of bananas: outside their natural range; in contexts with archaeological, sedimentary and ecofactual features indicative of cultivation; or, in association with other known domesticates and associated species, plants and/or animals. At Kuk, for instance, the altitude is exceptionally high (>1560 metres above sea level) for wild Eumusa section bananas and *Ensete* to occur naturally (see Argent 1976), but even if the early Holocene environment was warmer than it is today, the presence of stake holes, post holes and mounds, coupled with the relatively high proportions of Musaceae phytoliths in the phytolith assemblages, particularly following erosion and burning episodes, are strongly supportive of human influences and cultivation at least by about 7000-6500 cal B.P. (Denham *et al*. 2003).

Evidence for cultivation at the Watom site is equally strong. Banana phytoliths are found in black, humic rich soils typical of gardens. They are in association with phytoliths and macrobotanical remains from other cultivars including coconut, *Canarium*, Job's tears, possibly sugar cane, phytoliths derived from pioneer tree species and grasses that colonise gardens, and pig and chicken bones (Lentfer & Green 2004). All other evidence for cultivation primarily relies on bananas being outside their natural range of distribution. For instance, bananas are outside their natural range in the Pacific east of the Solomon Islands. Therefore, all records for bananas east of the Solomons are indicative of human translocation and cultivation including wild *M. acuminata* ssp. *banksii* found in Samoa (De Langhe 2009, MacDaniels 1947) and the *Musa* found associated with Lapita deposits in Vanuatu (Horrocks *et al*. in press). The same applies in Africa where only *Ensete* species are indigenous. *Musa* banana cultivation can be inferred at the Nkang site in Cameroon by 2500 cal B.P. from the presence of *Musa* phytoliths (Mbida *et al*. 2001, 2004) and pending the accuracy of dating and the morphotypic discrimination between *Musa* and *Ensete* volcaniform phytoliths (Neumann & Hildebrand 2009), it is possible that banana cultivation occurred in Uganda as early as c. 5200 cal B.P. (Lejju *et al*. 2006).

Identifying banana cultivation in areas where wild bananas grow naturally is perhaps the most difficult, especially in the absence of supportive archaeological and/or palaeobotanical evidence. At the Yombon airstrip locale, south West New Britain, Papua New Guinea, for instance, bananas appear in the early to middle Holocene. However, although this coincides with a major burning episode, there is no other evidence supportive of cultivation other than the presence of a few potential cultivars including *Saccharum* sp. and *Coix lachryma-jobi* L. In cases such as this, cultivation could only be confirmed if it could be proven that bananas were indeed seedless, and therefore cultivars.

## Identification of cultivars: morphometric and morphotypic analyses of phytoliths

Tracing the history of banana cultivation, domestication and dispersal could be greatly facilitated if phytoliths can be readily differentiated in archaeobotanical assemblages. However, the variation of phytoliths within and between Musaceae taxa and within and between plant parts (with the exception of banana seed phytoliths) has, until recently, been poorly understood. To address this shortfall and to expand previous morphotypic and morphometric analyses undertaken by Wilson (1985) and Mbida *et al*. (2001), phytolith researchers have commenced a series of rigorous morphometric analyses of banana phytoliths to determine their diagnostic value (e.g., Ball *et al*. 2006).

Lentfer (2003a) has undertaken preliminary studies to investigate the variation of phytoliths within and between species and also within and between plant parts. The first set of exploratory analyses examined seventeen acces-

**Table 1**. Banana accessions analysed by Lentfer (2003a, b).

| Section | Wild species | Accession code (plant parts*) |
|---|---|---|
| Eumusa | *Musa acuminata* ssp. *banksii* | QH325354 (lf,sd,sk,mrb,ped);<br>QH541190 (sd,br) |
| | *Musa schizocarpa* | 489 (lf,sd,sk);<br>QH356650 (lf) |
| Australimusa | *Musa peekelii* | QH067966 (lf,sd); 488 (lf;sd/fr); 489 (fr/sd);<br>QH067968 (sk) |
| | *Musa maclayi* | QH537000 (lf,br);<br>NB487 (lf,lfbs/st);<br>QH356648(mrb) |
| N/A | *Ensete glaucum* | QH28807 (sd,sk);<br>482 (lf,sk,sd);<br>QH356652 (lf) |
| | **Cultivars** | |
| Eumusa | *Musa acuminata* | QH438477 (lf) |
| | *Musa paradisiaca*? | QH4000037 (lf) |
| Australimusa | TT(**Fe`i**) | QH067969 (lf) |

*lf=leaf; sd=seed; fr=fruit; sk=skin; br=bract; mrb=mid rib; st=stem; lfbs=leaf base; ped=peduncle Note **Fe`i** is referred to as *M. fei* F. Muell. in figures.

sions consisting of *Ensete* and wild and cultivated Australimusa and Eumusa Section bananas (Table 1). Twenty-five phytoliths from a number of different plant parts including leaf blades, leaf mid-ribs, leaf bases, fruit and seed, skin, pseudostems, bracts and peduncles were analyzed separately. Only phytoliths with craters (i.e., spherical to sub-spherical to blocky morphotypes but not necessarily volcaniform morphotypes, see Figure 2) were included in the analysis. It did not include any of the clearly diagnostic seed morphotypes referred to previously and shown in Figure 1.

### *Analysis 1*

a) Differentiation of phytolith seed morphotypes from other plant parts: Long dimensions of phytolith bodies and craters were measured (see Figure 1, Vrydaghs *et al*., 2009) and ratios of body length to crater width were calculated. Results of the analysis using pooled data show that the ratio of mean body length to mean crater width is significantly different at $\alpha = 0.05$, differentiating between seed/fruit pulp morphotypes and morphotypes from other plant parts (Figure 3). Notably, body length and crater width scores by themselves were less helpful in this regard.

b) Differentiation of Eumusa, Australimusa seed morphotypes and *Ensete*: *Ensete glaucum* has distinctive

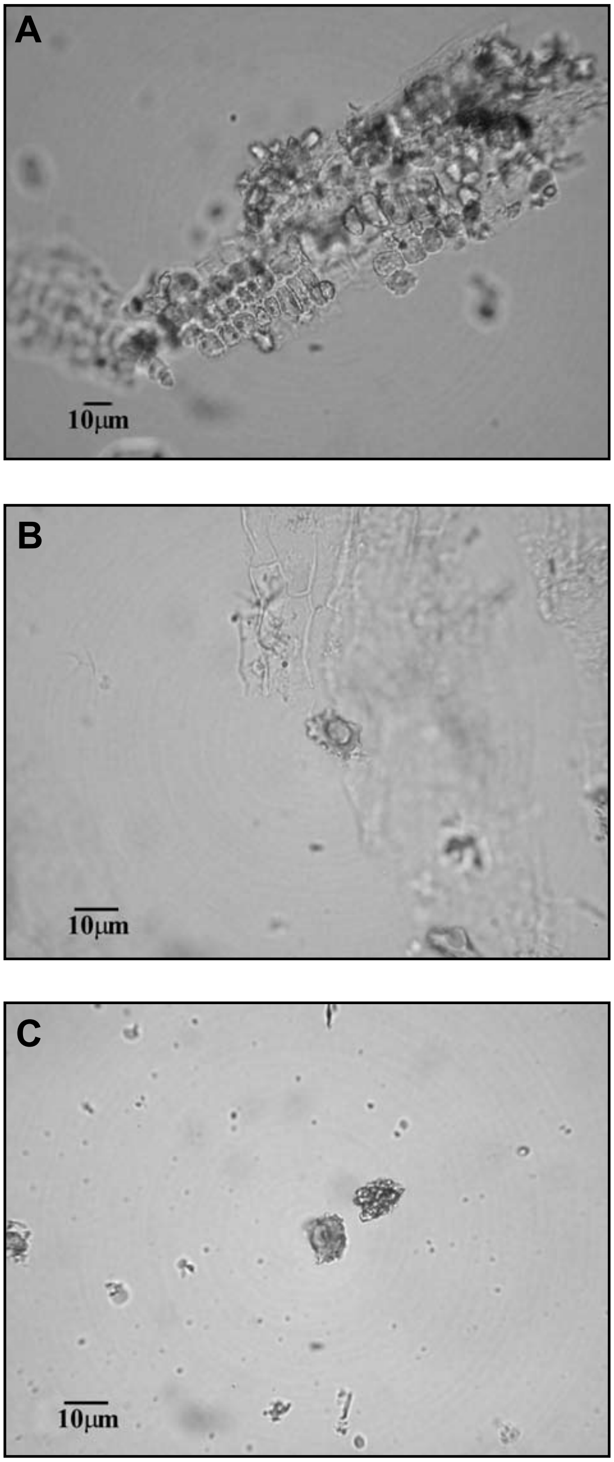
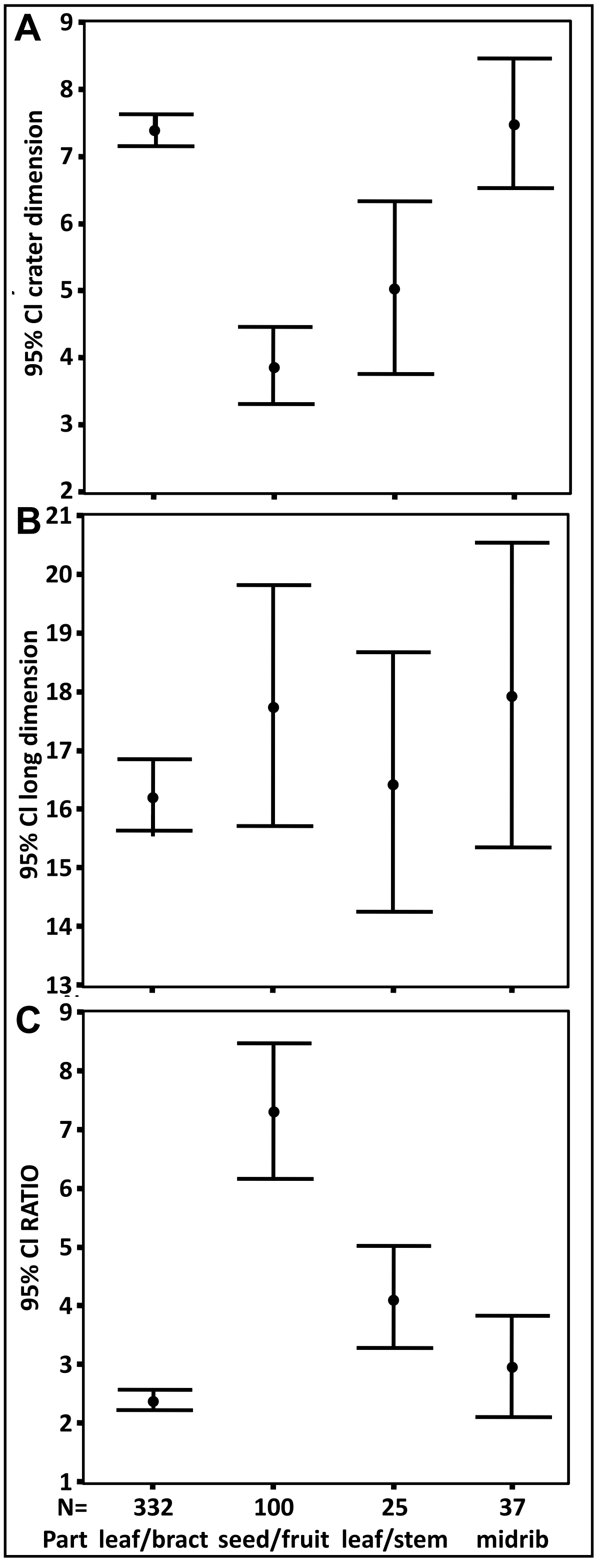


**Figure 2**. **A**. Sheet of polygonal and globular seed phytoliths from *Musa acuminata* ssp. *banksii*. These morphotypes have craters and were included in the analysis. The plant material was obtained from the Queensland Herbarium (Accession No. QH067962). **B**-**C**. Examples of volcaniform and globular leaf morphotypes from *Musa maclayi* (Accession No. NB487) examined in the analysis.



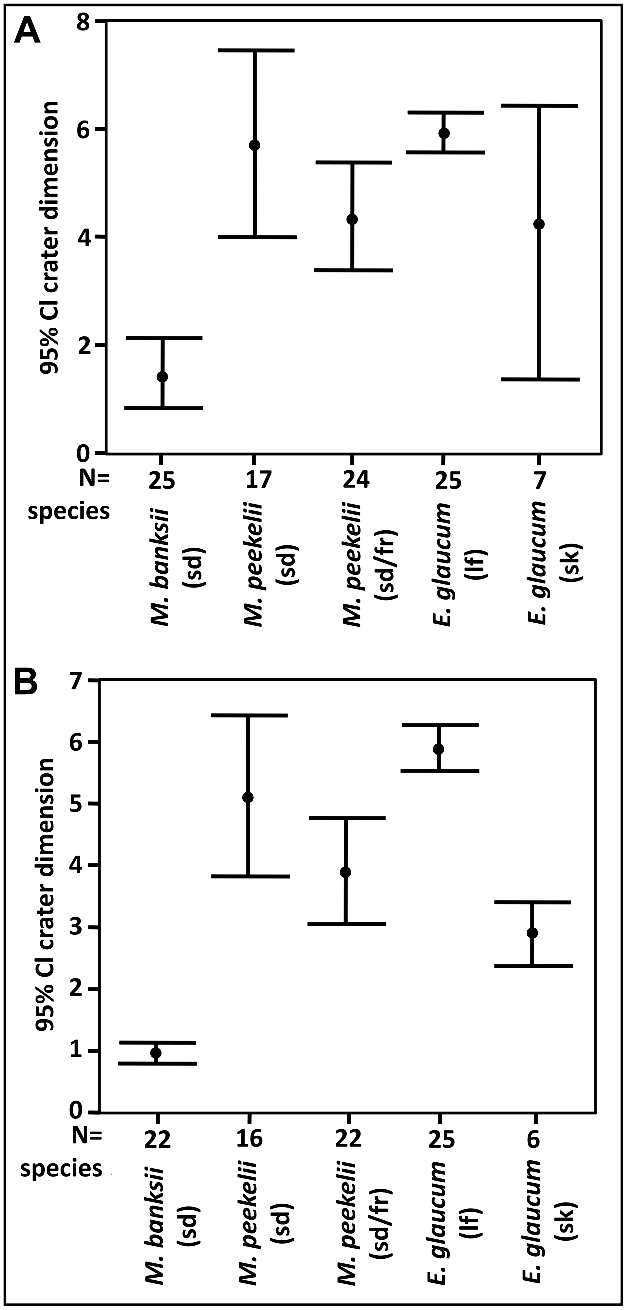


**Figure 4**. 95% confidence intervals for mean crater widths of *Musa* spp. seed and *Ensete* glaucum leaf and fruit-skin phytoliths based on full data set **A** and with outliers deleted **B** (sd = seed; fr = fruit; lf = leaf; sk = skin). *Musa acuminata* ssp. *banksii* is clearly differentiated at α = 0.05 when outliers are removed. The Australimusa species *M. peekelii* is not differentiated from *Ensete glaucum*.

**Figure 3**. 95% confidence intervals for mean crater widths **A**, mean long dimensions **B** and mean long dimension/ mean crater width ratios **C** of all phytoliths examined. Note that the leaf/stem sample consists of the base of leaf and pseudostem samples and the seed/fruit samples consist of: **A**) the fruit pulp attached to seeds, and **B**) seeds. Fruit pulp does not contain phytoliths and therefore phytoliths examined in the analysis are derived from seeds only. The ratio plot (**C**) shows that seed and seed/fruit phytoliths have significantly smaller craters compared to body length than leaf phytoliths and can be discriminated at α = 0.05 regardless of species derivation.

seed morphotypes (see Figure 1) that were not included in this analysis. However, the leaf and fruit skin phytolith morphotypes of *Ensete* have globular and polygonal morphotypes similar to *Musa* seed morphotypes. An analysis comparing mean body length and mean crater width of *M. acuminata* ssp. *banksii* and *Musa peekelii* Lauterb. seed morphotypes, and *E. glaucum* leaf and fruit skin morphotypes showed that the width of craters in *M. acuminata* ssp. *banksii* are significantly smaller than both *M. peekelii* and *Ensete* at α = 0.05 (Figure 4). *M. peekelii* and *E. glaucum* could not be differentiated according to crater width. However, mean body length of *M. peekelii* was significantly greater at α = 0.05 than *M. acuminata* ssp. *banksii* and *Ensete* (Figure 5).

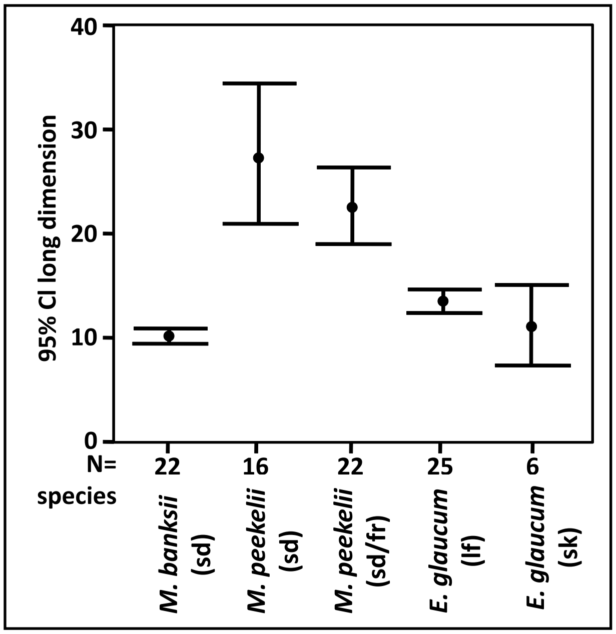


**Figure 5**. 95% confidence intervals for mean long dimensions of *Musa* spp. seed and *Ensete* leaf and fruit-skin phytoliths based on full data set (sd = seed; fr = fruit; lf = leaf; sk = skin). The Australimusa species, *M. peekelii* is differentiated from *Musa acuminata* ssp. *banksii* and *Ensete glaucum*.

### *Analysis 2*

This analysis was based on morphotypic analysis of the same set of leaf/bract volcaniform morphotypes used in the first analysis. Seven major categories of attributes (Table 2) were examined. Attributes within each category were given a score of 1 if present and 0 if absent and statistically tested using principal components analysis. Similar to the morphometric analysis, *Ensete glaucum* morphotypes were clearly differentiated by body texture and crater rim characteristics (Figure 6). Other taxa could not be clearly differentiated.

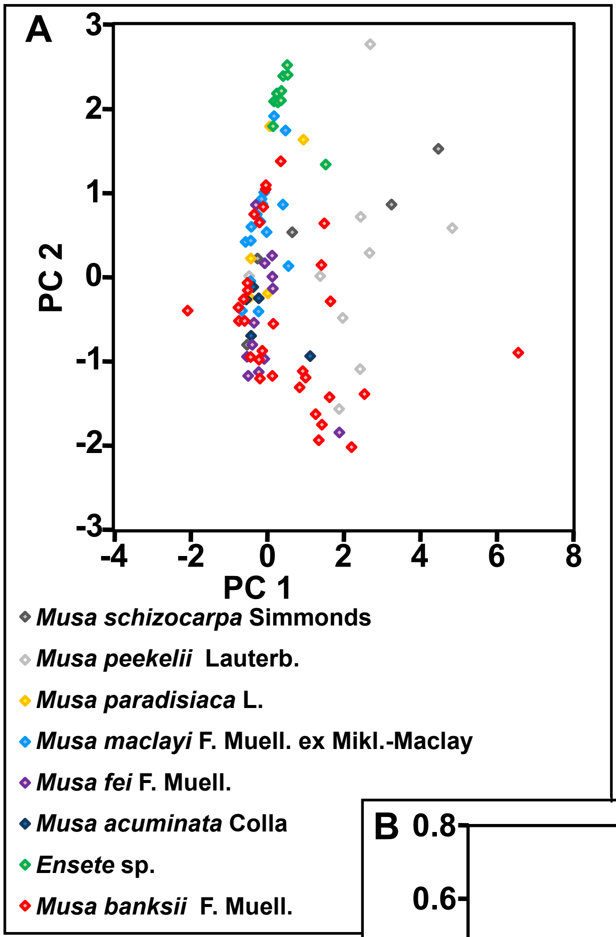
### *Analysis 3*

Additional morphometric analyses were undertaken to determine if leaf phytolith morphotypes could be further differentiated. Mean body length and mean crater width of leaf/bract volcaniform morphotypes from different taxa were compared (Figures 7 to 9). Crater width of *E. glaucum* morphotypes was significantly smaller at α = 0.05 than all other Eumusa and Australimusa bananas with the exception of the wild Australimusa species, *Musa maclayi* F. Muell. ex Mikl.-Maclay and the wild Eumusa species *Musa schizocarpa* Simmonds (Figure 7). Body length was significantly smaller than the two *M. acuminata* cultivars (listed as *M. acuminata* and *Musa paradisiaca* L.), *M. maclayi* and **Fe`i** (Figure 8). Crater length and body length of morphotypes from other bananas were more similar and consequently these taxa were found to be more difficult to differentiate (Figures 7 and 8). Crater width of the wild *M. maclayi* morphotypes were significantly different from the cultivated bananas, *M. acuminata* and **Fe`i** and the other wild Australimusa banana *M. peekelii*, but overlapped with the wild Eumusa species (*M. acuminata* ssp. *banksii* and *M. schizocarpa*). *Musa schizocarpa* could only be differentiated from the three cultivars (*M. acuminata*, *M. paradisiaca* and **Fe`i**), and the wild *M. acuminata* ssp. *banksii* was differentiated from only one of the Eumusa section cultivars, *M. acuminata*, not *M. paradisiaca*. Body length was a less helpful criterion for differentiating taxa than crater width. Interestingly, the only significant difference at α = 0.05 was between Australimusa section banan-

**Table 2**. Categories and attributes used in analysis of volcaniform leaf phytoliths (attributes shown in Figure 6B are the abbreviated forms shown in (…) and are equivalent terms from Madella *et al*. 2005).

| Categories | Attributes |
|---|---|
| Crater | round [r] (orbicular), oval [o], square [sqt], irregular [irrt] |
| Morphology | tabular [t], blocky [b], spherical [sph] (globose), platy [pl] (planar) |
| Base shape | square [squb], rectangular [rb], quadrilateral [qb], triangular [tb], boat [bb] (oblong), round [cb] (orbicular), other [ob] |
| Height | short [fh] (h<1/3 length), medium [mh] (h=1/3 to 1/2 length), tall [th] (h≥1/2 length) |
| Texture | psilate [stx], rough [rtx] verrucate, granulate [grx], dimpled [dtx] |
| Rim | present [rp]/absent [ra], regular [regr]/irregular [irrr] |
| Ornamentation | absent [no], short [sho], medium [mo], long [lo], lobed [lbo] |

as. Body lengths of *M. maclayi* and **Fe`i** bananas were significantly greater than *M. peekelii*. Finally the ratio of mean body length to crater width differentiated *M. maclayi* from all other samples with the exception of *M. schizocarpa* (Figure 9). *Musa schizocarpa* exhibited the greatest variability and could not be differentiated from any other taxon.



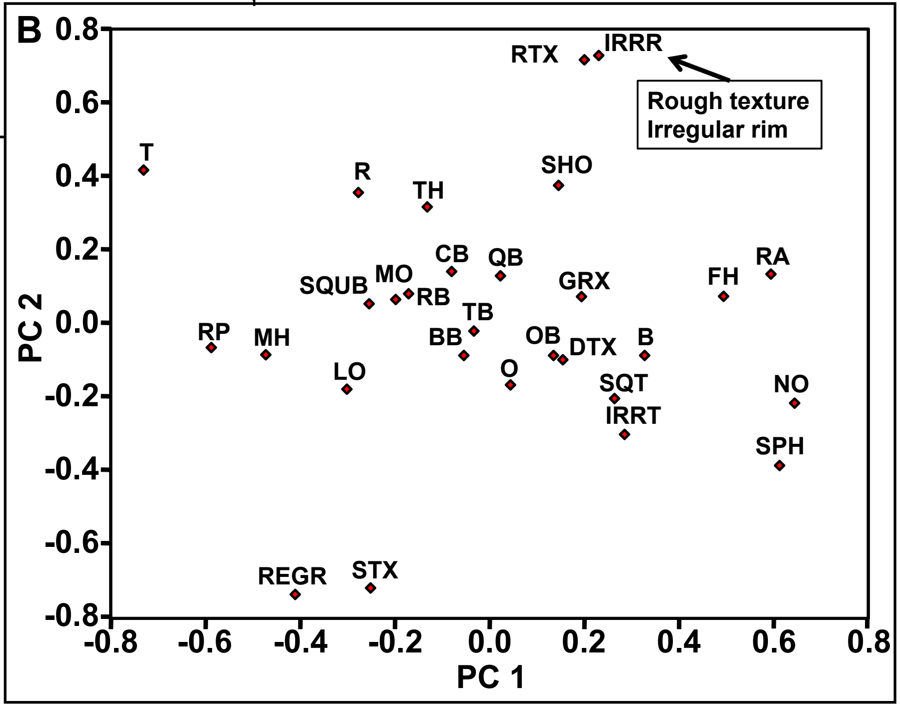


**Figure 6**. Biplot of principal components analysis of banana leaf phytolith attribute data. The sample plot A shows that *Ensete glaucum* is differentiated from other bananas. The main attributes separating it from other bananas are the irregular rim and the rough texture and to a lesser extent, short ornamentation (SHO). See the distribution of attributes in the vector plot B. (see abbreviations in Table 2)

Lentfer's findings broadly concur with those of Ball *et al*. (2006) and Vrydaghs *et al*. (2009), which have been confined to the distinctive volcaniform leaf phytoliths from a different set of Musaceae accessions including *M. acuminata*, *Musa balbisiana* Colla and various cultivar groups. A combination of morphometric (base length and crater width) and morphotypic analyses (base shape, crater position and cone shape) (Ball *et al*. 2006:3) can help to discriminate between certain taxa. Notably, wild diploid *M. balbisiana* (BB) volcaniform morphotypes were found to be significantly larger than both wild and edible diploid *M. acuminata* (AA) morphotypes (Ball *et al*. 2006:7), but edible AA could not be differentiated from wild AA. Subsequent studies analyzing AA, AAA, AAB and ABB have found a very complex pattern of phytolith variation. Continuing analyses with additional samples are further investigating the variation in crater width, particularly the role of *banksii* alleles in its expression (Vrydaghs *et al*. 2009).

## Implications for future research

The presence of seeded bananas in archaeobotanical assemblages can be identified from seed phytolith morphotypes. Distinctive morphotypes shown in Figure 1 are diagnostic at the section level. Other globular and polygonal morphotypes can be differentiated from other plant parts by body length/crater width ratios. Additionally, preliminary studies indicate that Eumusa bananas (*M. acuminata* ssp. *banksii*) can be differentiated from Australimusa bananas (*M. peekelii*) on the basis of crater width and body length. Although further comparative studies are needed to include a range of other species from either section, current results suggest the outlook is very promising for tracking the complex history of Musaceae in the archaeobotanical record. Phytoliths can be used to identify natural distributions of *Musa* and *Ensete*, differentiate wild populations from fully domesticated (seedless) populations and trace patterns of dispersal. However, based on this premise, mixed populations of wild and cultivated bananas (a common occurrence in Papua New Guinea; Lentfer 2003b; Jean Kennedy pers. comm.) and partially domesticated populations prior to the complete loss of seed – for some diploid cultivars commonly produce seed – cannot be differentiated. In these circumstances it is only the presence of Musaceae species outside their natural ranges that might imply human transmission and confirm evidence for cultivation.

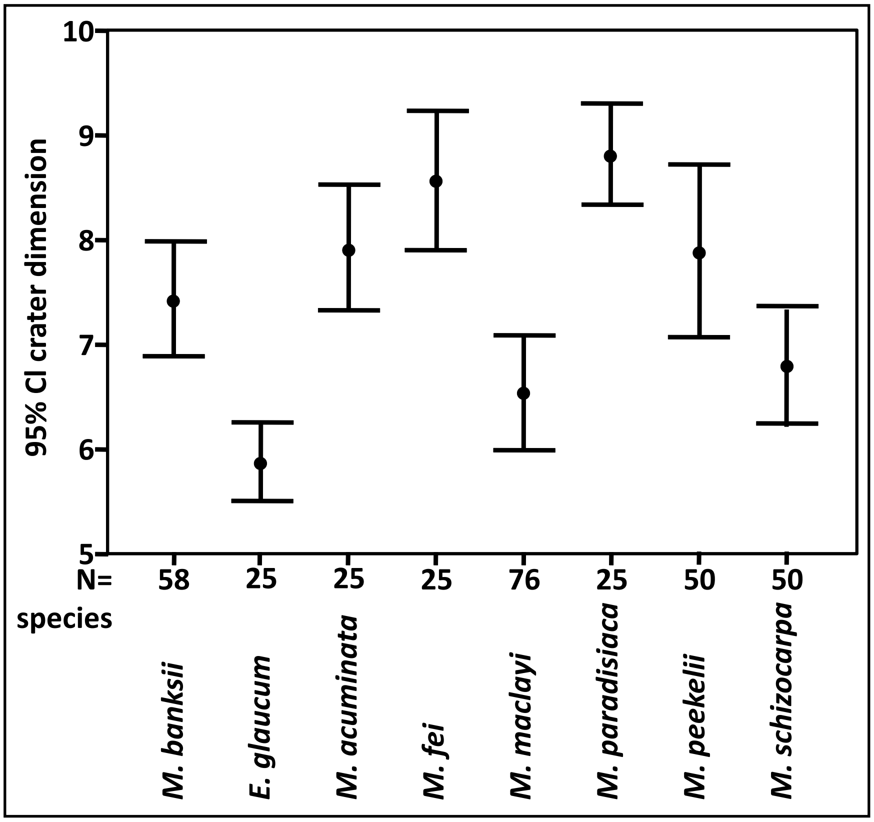


**Figure 7**. 95% confidence intervals for mean crater widths of leaf phytoliths differentiating *Ensete glaucum* from all other bananas except *Musa maclayi* and *Musa schizocarpa*.

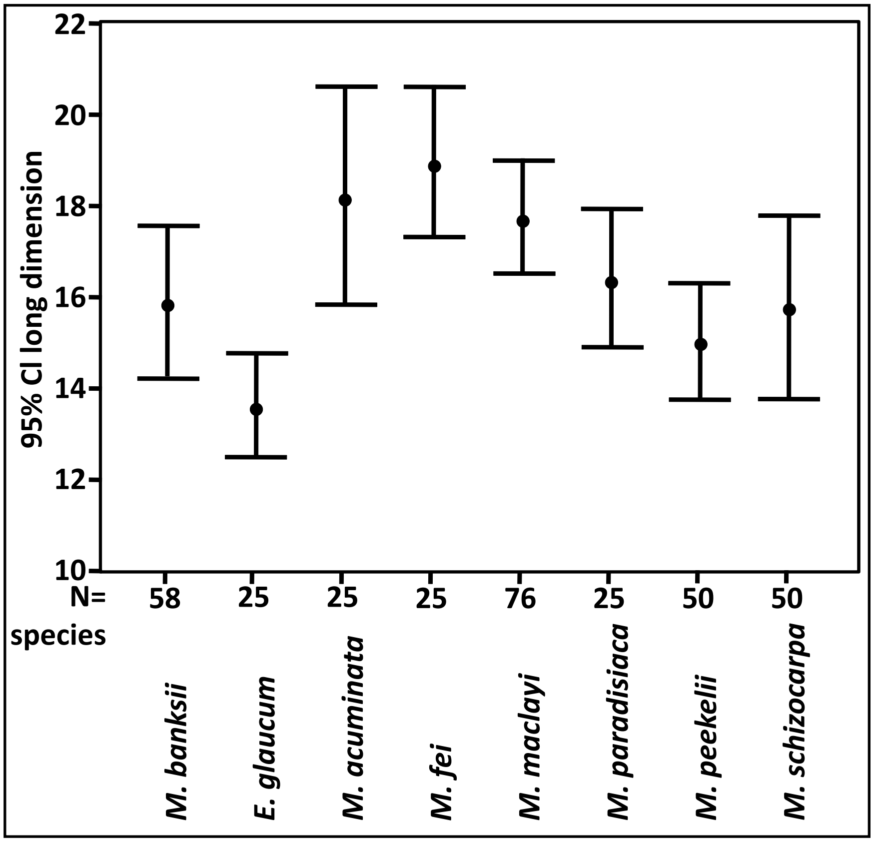


**Figure 8**. 95% confidence intervals for mean long dimensions of leaf phytoliths differentiating *Ensete glaucum* from four other bananas.

Where seed is absent from archaeobotanical assemblages, the problem of identification becomes more difficult and is reliant on differentiation of the distinctive volcaniform morphotypes. From the results of several studies (Lentfer et al. 2003b, Mbida *et al*. 2001) it is well-established that *Ensete* species can be readily differentiated from wild and domesticated diploid and triploid *Musa* bananas by morphotypic and morphometric means. However, differentiation between *Musa* species is more complex and would be reliant on a large sample size for any given archaeobotanical assemblage. Since triploid banana phytoliths are generally larger than diploids (Vrydaghs *et al*. 2009), there could be scope for differentiating domesticated triploid populations from wild and cultivated diploid populations by simply measuring crater widths of archaeological assemblages. Therefore, there is potential for tracking banana introductions and domestication. Nevertheless, results show that Eumusa and Australimusa section bananas cannot be differentiated at a general level and this is problematic in regions where bananas from both sections occur, either wild or cultivated. Indications are, however, that some species and/or cultivars within sections can be differentiated. Most importantly, wild and domesticated Eumusa bananas, *M. acuminata* (AA) and *M. balbisiana* (BB), can be differentiated and there might be potential for tracking the introduction of *Musa acuminata* bananas in mainland Southeast Asia west of the Philippines where *M. balbisiana* dominates native banana populations. A similar potential for discrimination is indicated for Australimusa; *M. maclayi* and *M. peekelii* could not only be differentiated from each other but also from the Australimusa domesticate **Fe`i**. Therefore, there may be good potential for tracking Australimusa banana dispersals and patterns of domestication for the near Oceania region, east of Papua New Guinea, where Australimusa bananas have dominated wild and cultivated populations.

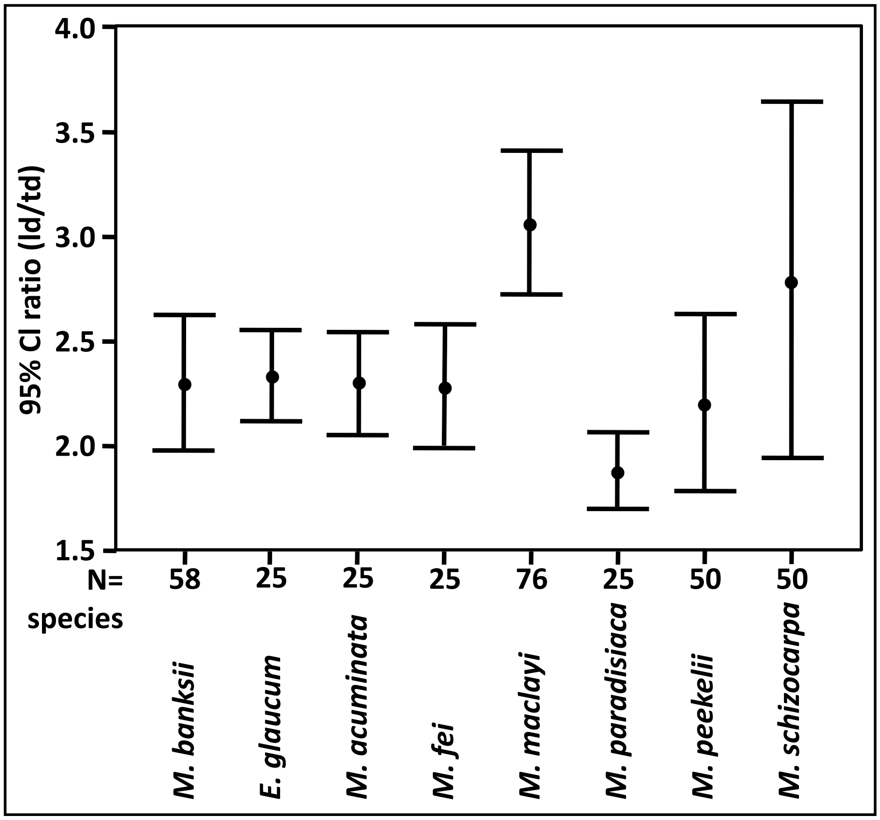


**Figure 9**. 95% confidence intervals for mean long dimension (ld)/crater width (td) ratios of leaf phytoliths differentiating *Musa maclayi* from all other bananas except *Musa schizocarpa*.

## The 'New Guinea Banana Project'

Good potential for differentiating between banana phytoliths is indicated from morphometric and morphotypic analyses. Nevertheless, preliminary studies point to a wide variation of morphotypes and additional study of a larger sample incorporating additional species and cultivars is required to determine the extent of this variation and further explore the potential for a more definitive set of criteria for differentiation. The 'New Guinea Banana Project' commenced in 2002 with collection of more than 100 wild and cultivated bananas from mainland Papua New Guinea, New Britain and New Ireland (Table 3). Volcaniform leaf phytoliths from 58 accessions were selected for a more rigorous analysis (Table 4) than previously undertaken, describing more morphological features (Table 5). Digital images and measurements and morphometric details from 50 phytoliths per accession have been recorded and saved on a readily accessible database. This in itself is useful for identification of morphotypes during routine analysis. Statistical analyses have yet to be completed. Firstly, data will be lumped according to the same criteria as Ball *et al*. (2006) and examined using the same statistical procedure as Ball *et al*. (2006) and Vrydaghs *et al*. (2009) for direct comparison. Subsequently, the analysis will be re-run to incorporate the full set of morphotypic attributes and morphometries.

## Conclusions

Recent research (Denham *et al*. 2003, Lebot 1999, Perrier *et al*. 2009) shows that the New Guinea region has played a key role in the development of the domesticated banana, and complex origins and multiple dispersals for banana cultivars within the southeast Asian/Pacific region are indicated (Kennedy 2008). Phytoliths hold the key to tracing the history of banana cultivation and domestication in the archaeobotanical record, and morphometric and morphotypic analyses show good potential for differentiation of phytoliths. Seed phytoliths can be readily dif-

**Table 3**. List of banana accessions collected from Papua New Guinea in 2002 for the 'New Guinea Banana Project', with associated ethnobotanical observations.

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| Nari 1047 | ABB | Cape Gloucester | Lowlands | | | ? | | |
| Nari 146 | AAB | ENB | Lowlands | | | **Luba** | | |
| Nari 186 | AAT | Madang | Lowlands | | | **Sar** | Amele | |
| Nari NBI 10 | ABB | ? | Lowlands | | | ? | | |
| Nari 168 | AAB | Central Province | Lowlands | | | ? | | |
| Nari NBL 20 | ABB | Bougainville | Lowlands | | | ? | | |
| Nari OBB 5 | AAA | Madang | Lowlands | | | **Lakem** | | |
| Nari 171 | ABB | Madang (orig. Milne Bay) | Lowlands | | | ? | | |
| Nari 142 | AA | ENB | Lowlands | | | **Tagomor** | | |
| Nari NB9 11 | ABB | Morobe | Lowlands | | | **Gana sumdu** | | |
| Nari NBI 18 | AAB | Chimbu | Highlands | | | **Kunambo** | | |
| Nari 206 | AAB | Western Highlands | Highlands | | | **Rukumamb tamby** | | |
| Nari 164 | AA | Madang | Lowlands | | | **Sihir** | | |
| Nari OBN 14 | AAA | ENB | Lowlands | | | **Towberne** | | |
| Nari 064 | AA | East Sepik | Lowlands | | | ? | | |
| WNB1 | *Ensete glaucum* (Roxb.) Cheesman | Tamare Village | Lowlands | 5°27'0.4'' | 150°5'3.6'' | **Tapupu** | Bakovi | Seeds used for making beads. |
| WNB2 | AA? | Tamare Village | Lowlands | 5°27'0.4'' | 150°5'3.6'' | **Kikiyou** | Bakovi | Cooked and also eaten ripe. |
| WNB3 | ABB | Tamare Village | Lowlands | 5°27'0.4'' | 150°5'3.6'' | **Tukuru** | Bakovi | Cooked and also eaten ripe. |
| WNB4 | ABB? | Tamare Village | Lowlands | 5°27'0.4'' | 150°5'3.6'' | **Tamane buro** | Bakovi | Cooked and also eaten ripe. |
| WNB5 | AA? | Tamare Village | Lowlands | 5°27'0.4'' | 150°5'3.6'' | **Maya** | Bakovi | Cooking banana. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| WNB6 | *Musa textilis* Née | Tamare Village | Lowlands | 5°27'0.4" | 150°5'3.6" | **Tuain** | Pisin | Pseudostem & sheath used for making rope. Suckers sold to villagers by agricultural supply stores. Used as cash crop. |
| WNB7 | ? | Tamare Village | Lowlands | 5°27'0.4" | 150°5'3.6" | **Hale vudi** | Bakovi | Ornamental banana with red leaves. |
| WNB8 | AA? | Tamare Village | Lowlands | 5°27'0.4" | 150°5'3.6" | **Karuke vudi** (**Karuke** =crab's hand) or Mrs. banana | Bakovi | Eaten ripe. |
| WNB9 | AA? | Tamare Village | Lowlands | 5°27'0.4" | 150°5'3.6" | sausage banana | English | Cooked and also eaten ripe. |
| WNB10 | *Musa acuminata* ssp. *banksii* (Ridl.) Kiew. | Garu plantation | Lowlands | 5°31'12.9" | 149°58'29.4" | Wil banana | Pisin | Wild banana growing along margins of swamp. |
| WNB11 | *E. glaucum* | Tabairikau | Lowlands | 5°28'25.2" | 150°27'27.2" | **Vudu vudu** | Kuanua | Collected from forest and grown in garden with other bananas. Necklaces made from seed. Sap red. |
| ENB1 | ABB | Tavui No.2 | Lowlands | 4°08'47.0" | 152°10'02.4" | **Yawa** | Kuanua | Large seeds often present. Fruit cooked and also eaten ripe. Fruit also fed to pigs. Stems and leaves used for **mumu**. Fruit used for making an alcoholic beverage. The ripe fruit is placed in drum and after heating to release juices the liquid is fermented. It is distilled into a clean drum and put into small bottles. The process takes two weeks. |
| ENB2 | ABB | Tavui No. 2 | Lowlands | 4°08'47.0" | 152°10'02.4" | **Kalapua** | Kuanua | Cooked and also eaten ripe. Fruit fed to pigs. Stems and leaves used for **mumu**. |
| ENB3 | ABB | Tavui No. 2 | Lowlands | 4°08'58.9" | 152°10'27.1" | **Tukuru** | Kuanua | Fruit cooked. Male bud is also eaten. |
| ENB4 | ? | Tavui No. 2 | Lowlands | 4°13'26.3" | 152°10'27.1" | **Kudukudu** | Kuanua | Eaten ripe and cooked. |
| ENB5 | ? | Malaguna | Lowlands | 4°08'58.9" | 152°08'59.0" | **Kakatur** | Kuanua | Eaten ripe. |
| ENB6 | ? | Gela Gela | Lowlands | 4°24'38.0" | 152°14'48.6" | **Pok pok** | Kuanua | Cooking banana. Leaves easily torn and unsuitable for cooking and wrapping. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| ENB7 | ? | Gela Gela | Lowlands | 4°24′36.7″ | 152°14′51.6″ | **Makau** | Kuanua | Cooking banana. Leaves easily torn and unsuitable for cooking and wrapping. |
| ENB8 | AAA | Gela Gela | Lowlands | 4°24′36.1″ | 152°14′49.1″ | **Katur** | Kuanua | Cooking banana. Leaves used for **mumu**. |
| ENB9 | AA | Gela Gela | Lowlands | 4°24′36.1″ | 152°14′49.1″ | **Pitu** | Kuanua | Cooking banana. Leaves easily torn and unsuitable for cooking and wrapping. |
| ENB10 | ABB | Takabua Mission Station | Lowlands | 4°22′29.8″ | 152°13′3.1″ | **Makala tukuru** | Kuanua | Eaten ripe. Leaves used for **mumu**. |
| ENB11 | ABB | Malakuna No. 4 | Lowlands | 4°23′6.0″ | 152°12′18.3″ | **Yawa buka** | Kuanua | Eaten ripe. Leaves used for **mumu**. |
| ENB12 | BB? | Takabua Mission Station | Lowlands | 4°22′29.8″ | 152°13′3.1″ | **Okaoko** | Kuanua | Eaten ripe. Leaves used for **mumu**. |
| ENB13 | **Fe`i** | Raolo | Lowlands | 4°5′40.5″ | 152°4′31.2″ | **Auro=Vuro** | Kuanua | Eaten ripe and cooked. |
| ENB14 | **Fe`i** | Malmaluan Training College | Lowlands | 4°17′49.6″ | 152°1′41.0″ | **Vuro** | Kuanua | Eaten ripe and cooked. Leaves used for **mumu**. |
| ENB15 | AA | L.A.E.S. Kerevat | Lowlands | 4°20′7.0″ | 152°1′41.0″ | **Gulum** | Kuanua | Cooking banana. Leaves easily torn and unsuitable for cooking and wrapping. |
| ENB16 | **Fe`i** | L.A.E.S. Kerevat | Lowlands | 4°20′7.5″ | 152°1′48.2″ | **Vuro/Pitu** | Kuanua | Eaten ripe. Leaves used for **mumu**. |
| ENB17 | AB? | L.A.E.S. Kerevat | Lowlands | 4°20′7.5″ | 152°1′48.2″ | **Taupen** | Kuanua | Cooking banana. |
| ENB18 | AAA | L.A.E.S. Kerevat | Lowlands | 4°20′7.5″ | 152°1′48.2″ | **Malam** red | Kuanua | Eaten ripe and cooked. |
| ENB19 | AS? | L.A.E.S. Kerevat | Lowlands | 4°20′7.5″ | 152°1′48.2″ | | | |
| ENB20 | *M. textilis* | L.A.E.S. Kerevat | Lowlands | 4°20′9.2″ | 152°1′52.1″ | | | Pseudostem and sheath used for making rope. Suckers sold by L.A.E.S. to agricultural supply stores. |
| NI1 | ABB? cf. **Tukuru** (**Kokopo**) | Kulangit Village, Kavieng | Lowlands | 2°33′43.1″ | 150°47′54.6″ | **Sukuru** | Tigak | Cooking banana but also eaten ripe. Leaves strong and used for **mumu**, and wrapping. Male bud also eaten. |
| NI2 | AA? | Kulangit Village, Kavieng | Lowlands | 2°33′43.1″ | 150°47′54.6″ | **Papat** (cf. **Garamut** in Kuanua) | Tigak | Cooking banana - fruits boiled and roasted. Leaves weak - used for covering **mumu** only. |
| NI3 | AA | Kulangit Village, Kavieng | Lowlands | 2°33′43.1″ | 150°47′54.6″ | **Kikiyou** | Tigak | Cooking banana - fruits boiled, fried and roasted. Leaves weak - used for covering **mumu** only. |
| NI4 | ABB? | Kulangit Village, Kavieng | Lowlands | 2°33′45.5″ | 150°47′54.1″ | **Wan kina**, **Wan pound** | Pisin | Cooked in **mumu** and eaten raw. |
| NI5 | ? | Kulangit Village, Kavieng | Lowlands | 2°33′45.5″ | 150°47′54.1″ | **Boa** | Tigak | Cooked in **mumu** and eaten raw and boiled. Sweet. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| NI6 | **Fe`i**? | Kulangit Village, Kavieng | Lowlands | 2°33'45.5" | 150°47'54.1" | **Suluklamuk** | Tigak | Eaten ripe and cooked. Yellow flesh with poorly formed seeds eaten by ants. Turns urine yellow. Bunch drooping. Possibly intermediate form. Leaves strong and used in **mumu**. |
| NI7 | ? | Kulangit Village, Kavieng | Lowlands | 2°33'45.5" | 150°47'54.1" | **Darip** | Tigak | Eaten ripe and cooked. Yellow flesh. Leaves not used. |
| NI8 | AAA | Kulangit Village, Kavieng | Lowlands | 2°33'41.7" | 150°47'52.1" | **Palang** | Tigak | Eaten ripe and cooked. Yellow flesh. Leaves not used. |
| NI9 | AA | Kulangit Village, Kavieng | Lowlands | 2°33'41.7" | 150°47'52.1" | **Ngitingsakai** | Tigak | Cooking banana - boiled and roasted. Leaves not used. Fruit occurs in continuous spiral around rachis. |
| NI10 | AA | Kulangit Village, Kavieng | Lowlands | 2°33'42.5" | 150°47'56.4" | **Ulungan** | Tigak | Fruit roasted or boiled. Leaves not used. |
| NI11 | AAB | Kulangit Village, Kavieng | Lowlands | 2°33'48.4" | 150°47'56.1" | **Bavaya** | Tigak | Fruit cooked or eaten raw. Leaves used for wrapping. |
| NI12 | AA | Miom/Caranas, Kavieng | Lowlands | 2°35'25.6" | 150°49'41.4" | **Papat Wung** | Tigak | Fruit roasted or boiled. Leaves used for **mumu** and wrapping. |
| N13 | AAB | Miom/Caranas, Kavieng | Lowlands | 2°35'25.6" | 150°49'41.4" | **White bavaya** | English/Tigak | Mostly roasted. |
| NI14 | **Fe`i** | Namasalang | Lowlands | 3°2'45.4" | 151°24'57.1" | **Utafan** | Malik | Cooked and eaten raw - sweet. Sap used as a dye for **malangan** masks. |
| NI15 | ? | Lelet | <1000m | 3°16'20.7" | 151°55'39.0" | **Siaman**/ German | Mandak | Eaten ripe. |
| NI16 | **Fe`i** | Kaluan, Lelet | <1000m | 3°19'28.8" | 151°54'22.9" | **Manui/ Namnam** | Manui (Manus Island)/ Mandak | Eaten ripe or cooked. Leaves used for **mumu** and wrapping. Bunch drooping but at an angle and almost horizontal. |
| NI17 | **Fe`i** | Kaluan, Lelet | <1000m | 3°17'58.3" | 151°54'48.7" | **Loskauk** | Mandak | Eaten ripe or cooked. Leaves used for **mumu** and wrapping. Bunch drooping but at an angle and almost horizontal. |
| NI18 | **Fe`i** | Kabagong, Lelet | <1000m | 3°16'55.4" | 151°55'30.2" | **Loskauk** | Mandak | Cooking banana. Flesh sulfur-yellow. |
| NI19 | *Musa maclayi* F. Muell. ex Mikl.-Maclay ssp. *maclayi* Arg. var. *namatani* Arg. | Karu | <1000m | 3°29'52.7" | 152°11'46.9" | **Agigilai** | Barok | Wild. Said not to be eaten but sweet bright yellow flesh surrounds seeds. Leaves used for wrapping and **mumu**. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| NI20 | *M. maclayi*?<br>**Fe`i**? | Karu | <1000m | 3°30'20.3" | 152°12'21.2" |  | Barok | Wild. Tall, robust banana with shiny pseudostem. Not fruiting at time of collection. |
| NI21 | *M. maclayi* ssp. *maclayi* var. *namatani* | Karu | <1000m | 5°27'0.4" | 150°5'3.6" | **Agigilai** | Barok | Wild. Said not to be eaten but sweet bright yellow flesh surrounds seeds. Leaves used for wrapping and **mumu**. |
| NI22 | *Musa peekelii* Lauterb. ssp. *peekelii* Arg. | Rosirik | <1000m | 5°27'0.4" | 150°5'3.6" | **Wawa** | Sokiri | Wild robust banana. Bunch erect at first then drooping. Fruit cooked or roasted. Leaves used to cover **mumu**. |
| NI23 | *M. peekelii* ssp. *peekelii* | Rosirik | <1000m | 5°27'0.4" | 150°5'3.6" | **Wawa** | Sokiri | Wild robust banana. Bunch erect at first then drooping. Fruit cooked or roasted. Leaves used to cover **mumu**. |
| WH1 | *Musa ingens* Simmonds | Tubang, Kauil | 2000m | 5°27'0.4" | 150o5'3.6" | **Wuluk donu** | Jiwaka | Wild tall banana growing to 16m to 18m height at 2000m in creek gully. Fruit with yellow flesh and large seeds, green turning yellow when ripe. Cuscus, parrots and flying fox eat fruit. Leaves used for making temporary shelters and for covering **mumu**. |
| WH2 | *M. ingens* | Tubang, Kauil | 2000m | 5°27'0.4" | 150°5'3.6" | **Wuluk donu** | Jiwaka | Wild tall banana growing to 16m to 18m height at 2000m altitude in creek gully. Fruit with yellow flesh and large seeds. Leaves used for making temporary shelters and for covering **mumu**. |
| WH3 | *M. ingens* | Tubang, Kauil | 2000m | 5°27'0.4" | 150°5'3.6" | **Wuluk donu** | Jiwaka | As above. |
| WH4 | **Fe`i** | Balga, Kuk | 1630m | 5°27'0.4" | 150°5'3.6" | **Rua mema** (**rua** = banana, **mema** = red) |  | Cooking banana, roasted and boiled - preferably roasted. |
| WH5 | *Musa schizocarpa* Simmonds | Baiyer Zoo | 1177m | 5°27'0.4" | 150°5'3.6" | ? | ? | Wild banana growing in rainforest with gingers, ferns, Rubiaceae shrubs, tree ferns and wild taro in rainforest in shade under canopy. |
| ES1 | AAT? | Ranimbo, Hawain | Lowlands | 5°27'0.4" | 150°5'3.6" | **Yesing** (=wild banana) | Mino | Tall robust banana with edible fruit. Feral rather than wild. Fruit eaten when raw or cooked. Leaves used for **mumu** and wrapping. Fruit also fed to pigs. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| ES2 | AA? | CCRI station, Hawain | Lowlands | 5°31'12.9'' | 149°58'29.4'' | **Yesing** (=wild banana) | Mino | Fruit green turning yellow when ripe. Leaves used as decoration in **singsing** celebrations after heating on fire to make pliable. |
| ES3 | *M. schizocarpa* | CCRI station, Hawain | Lowlands | 5°28'25.2'' | 150°27'27.2'' | **Yesing** (=wild banana) | Mino | Wild seeded banana with yellowish sap. |
| ES4 | *M. schizocarpa* | Ranimbo, Hawain | Lowlands | 4°08'47.0'' | 152°10'02.4'' | **Yesing** (=wild banana) | Mino | Wild seeded banana with clear sap. Leaves used for **mumu**, wrapping food and for **singsing** decoration as well as roofs for bush houses. |
| ES5 | **Fe`i** | Koikin Village, Wewak | Lowlands | 4°08'47.0'' | 152°10'02.4'' | **Taweyawa** | Mino | Cultivated banana with red sap. Fruit large 4-5cm diameter, 10-23cm long with bottle-necked apex and pronounced ridging. Mostly cooked. |
| ES6 | *M. acuminata* ssp. *banksii* | Koikin Village, Wewak | Lowlands | 4°08'58.9'' | 152°10'27.1'' | **Yesing** (=wild banana) | Mino | Wild seeded banana with clear sap. Fruit turns yellowish when ripe. Not eaten. Said to often colonize landslides with gingers and grasses. Species common along Sepik Highway towards Maprik. Often grows in association with *M. schizocarpa*. This specimen growing on well-drained loam along roadside next to gardens and close to regrowth forest. One plant only. |
| ES7 | ABBT? | Japaraga 1, Maprik Road | <1000m | 4°13'26.3'' | 152°10'27.1'' | **Giant kalapua** | Pisin | Cooking banana. Leaves used for wrapping and **mumu**. |
| ES8 | AA | Japaraga 1, Maprik Road | <1000m | 4°08'58.9'' | 152°08'59.0'' | **Salamua**, **pisang jari buaya** (crocodile fingers) | ?, Mino | Fruit eaten ripe or cooked. Leaves used for **mumu** and dried leaves dried and used for making cigarettes. Clear sap. |
| ES9 | AA | Japaraga 1, Maprik Road | <1000m | 4°24'38.0'' | 152°14'48.6'' | **Heifeli' To`o** | Mino, Madang language? | Fruit eaten ripe or cooked. Leaves used for **mumu**. |
| ES10 | *M. acuminata* x *schizocarpa* | Japaraga 1, Nagam River | <1000m | 4°24'36.7'' | 152°14'51.6'' | **Yesing** (=wild banana) | Mino | Wild banana growing on sandy river bank. Sap clear. Fruit not eaten. |
| ES11 | *M. acuminata* ssp. *banksii* | Japaraga 1, Nagam River | <1000m | 4°24'36.1'' | 152°14'49.1'' | **Yesing** (=wild banana) | Mino | Wild banana growing in shady regrowth forest with moss understory. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| M1 | **Fe`i** | Motonau/Midiba, Madang | cl | 4°24'36.1" | 152°14'49.1" | **Wahin** | Ari | Cultivated banana with red sap growing on well-drained red/brown loam. Fruit large with pronounced ridging and sulfur-yellow flesh. Mostly cooked. **Fe`i** bananas once common in the district but said to be gradually dying out, often surviving in abandoned garden settings. Notable **Fe`i** bananas are referred to as "**yelo pispis**" in Pisin because urine turns yellow after the fruit is eaten. Fruit cooked and used for coloring other food stuffs and enhancing flavours. Red sap used by children for making stencils on clothing. |
| M2 | AA | Stewart Research Station, Madang | Lowlands | 4°22'29.8" | 152°13'3.1" | **Manameg** (red) | Amele | Small cultivated banana. Cooking banana referred to as plantain although strictly speaking it isn't. Leaves used for **mumu**. |
| M3 | AA? | Stewart Research Station, Madang | Lowlands | 4°23'6.0" | 152°12'18.3" | **Kekiau** | Kuanua | Cooking banana, boiled or roasted. Leaves used for **mumu** and wrapping food. |
| M4 | *M. schizocarpa* | Baitata Road, Madang | Lowlands | 4°22'29.8" | 152°13'3.1" | **Maror** | Em | Wild banana growing on poorly drained limestone soil in regrowth forest along roadside. Growing near *Musa peekelii* ssp. *angustigemma*. (NB. Site used for making the film "Robinson Crusoe"). Fruit self-peels to give a star-like appearance to the apex. Skin green when ripe. Flesh white. Leaves used to make temporary bush shelters. |
| M5 | *M. peekelii* ssp. *angustigemma* | Baitata Road, Madang | Lowlands | 4°5'40.5" | 152°4'31.2" | **Dor** | Em | Tall robust wild banana growing near *M. schizocarpa*. Common in well-drained locations on coral/limestone soils in regrowth forest. Bunch drooping, falling straight. Flowers eaten - mixed with salt. Young pseudostem also eaten opportunistically. Flowers and pseudostem used to garnish taro. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| M6 | *M. acuminata* ssp. *banksii* | Baitata Village, Madang | Lowlands | 4°17'49.6" | 152°1'41.0" | **Tilja** | Em | Wild banana growing in association with *M. peekelii* ssp. *angustigemma* on coral/limestone soils at edges of regrowth forest. |
| M7 | *M. acuminata* ssp. *banksii* | Barum junction, Madang | Lowlands | 4°20'7.0" | 152°1'41.0" | **Mabul kulal** (**mabul**=wild: **kulal**=inedible, left to dry) | Kein | Wild banana in moderately dense stand growing on well-drained soil in regrowth forest along roadside. In close association with *M. schizocarpa* and AS hybrids. |
| M8 | AS | Barum junction, Madang | Lowlands | 4°20'7.5" | 152°1'48.2" | **Mabul jus** (**jus**= water snail because the snail has a pointed shell and the banana has a long pointed apex). | Kein | Wild banana growing on well-drained soil in regrowth forest along roadside. Growing amongst mixed stand of *M. acuminata*, *M. schizocarpa* and hybrids. |
| M9 | *M. schizocarpa* | Barum junction, Madang | Lowlands | 4°20'7.5" | 152°1'48.2" | **Hirunag** (**hiru**=ginger; **nag**=son) | Kein | Wild banana growing on well-drained soil in regrowth forest along roadside. Growing amongst mixed stand of *M. acuminata* and *M. schizocarpa* and AS hybrids. |
| M10 | AA | Jobtou, Madang | Lowlands | 5°27'0.4" | 150°5'3.6" | **Bagui** | Kein | Cultivated species very much like the wild *M. acuminata* ssp. *banksii* in appearance. Male bud green. |
| MB1 | *E. glaucum* | Naura Village | Lowlands | 5°27'0.4" | 150°5'3.6" | **Gudu gudu** | Haigwai | Growing in neglected coconut plantation. Seeds used to make necklaces. |
| MB2 | *M. schizocarpa* | Naura Village | Lowlands | 5°27'0.4" | 150°5'3.6" | **Lau moi moi** (**lau**=inedible; **moi**=banana) | Haigwai | Wild banana growing in overgrown gardens. Leaves sometimes used for covering food. Species also found at Gomila Village. |
| MB3 | *M. maclayi* ssp. *maclayi*? | Gomila Village, Ahioma | Lowlands | 5°27'0.4" | 150°5'3.6" | **Bihibihiya** (**bihibihi**= wild banana; **bihi** = cultivated banana) | Tawala | Wild banana with dark, milky purple-red sap and erect bunch. Fruit with sulfur-yellow flesh. Growing in cool, sheltered gully in regrowth forest. Another small stand found growing nearby on rocky talis slope beside creek in old garden bordering regrowth forest. |

| Code | Type | Location | Altitude (m) | Latitude S | Longitude E | Vernacular Name | Language | Notes |
|---|---|---|---|---|---|---|---|---|
| MB4 | *M. maclayi* ssp. *maclayi*? | Gomila Village, Ahioma | Lowlands | 5°27'0.4" | 150°5'3.6" | **Bihibihiya** (**bihibihi**= wild banana; **bihi** = cultivated banana) | Tawala | One of stand of wild bananas with dark, milky purple-red sap growing on talis slope in old garden alongside creek. Small stands of species found in dense regrowth forest on steep banks bordering creek. |
| MB5 | *M. maclayi* ssp. *maclayi*? | Gomila Village, Ahioma | Lowlands | 5°27'0.4" | 150°5'3.6" | **Bihibihiya** (**bihibihi**= wild banana; **bihi** = cultivated banana) | Tawala | Wild banana with pink sap and erect bunch, tight but lax at proximal end. Fruit with sulfur-yellow flesh. Growing in gardens on raised sandy gravel deposits bordered by creek channels. |
| MB6 | *M. maclayi* ssp. *maclayi*? | Daduwe area, Northeast Coast Road | Lowlands | 5°27'0.4" | 150°5'3.6" | **Bihibihiya** (**bihibihi**= wild banana; **bihi** = cultivated banana) | Tawala | Wild banana in small stand of bananas growing on well-drained soil along roadside in tall grassland. |
| MB7 | *M. maclayi* ssp. *maclayi*? | Daduwe area, Northeast Coast Road | Lowlands | 5°27'0.4" | 150°5'3.6" | **Bihibihiya** (**bihibihi**= wild banana; **bihi** = cultivated banana) | Tawala | Wild banana growing in small scattered stand on well-drained soil along roadside in tall grassland. Some specimens feature retention of bracts on the rachis while others shed bracts. Notably bract retention is a characteristic of *M. maclayi* ssp. *ailului* Arg. but in other respects the specimens fit more closely with *M. maclayi* ssp. *maclayi* according to Argent's key. |
| MB0 | *M. maclayi* ssp. *maclayi*? | Kuiaro Village, China Strait | Lowlands | 5°27'0.4" | 150°5'3.6" | | | Specimen found on hillside in regrowth forest recently cleared for gardening. Also noted to be growing in forest areas inland from the coast. |
| MB0 | *M. maclayi* ssp. *maclayi*? | Tue Village | Lowlands | 5°31'12.9" | 149°58'29.4" | **Lau moi moi** (**lau**=false; **moi**=banana) | Daiamoni | Said to be growing in bush in creek catchment. Not collected. |
| MB8 | AA | Tue Village | Lowlands | 5°28'25.2" | 150°27'27.2" | **Kokoluyu** | Daiamoni | Cultivated banana. Fruit eaten cooked or ripe. |
| MB9 | AA? AS? | Tue Village | Lowlands | 4°08'47.0" | 152°10'02.4" | **Masi masi** | Daiamoni | Cultivated banana. Fruit eaten cooked or ripe. |

**Table 4**. Accessions selected for the 'New Guinea Banana Project' analyses.

| Section | | Number analyzed | Accession code |
|---|---|---|---|
| | **Wild species** | | |
| Eumusa | *Musa acuminata* ssp. *banksii* | 5 | ES11, ES6, M7, M6, ENB10 |
| | *Musa schizocarpa* | 5 | ES3, WH5, MB2, M9, ES4 |
| | *Musa acuminata* ssp. *banksii* x *schizocarpa* | 2 | M8, ES10 |
| Australimusa | *Musa peekelii* | 2 | M5, NI22 |
| | *Musa maclayi* | 5 | NI21, MB7, MB4, MB3, MB5 |
| | *Musa textilis* | 2 | ENB20, WNB6 |
| Ingentimusa | *Musa ingens* | 3 | WH1, WH2, WH3 |
| N/A | *Ensete glaucum* | 4 | WNB1, WNB11, MB1, MB1/2 |
| | **Cultivars*** | | |
| Eumusa | AA | 5 | NI12, ENB13, Nari064, Nari164, MB8 |
| | AAA | 5 | NI8, NariOBB5, NariNB420, NariOBN14, ENB18 |
| | BB? | 1 | ENB12 |
| | AAB | 5 | NI13, Nari206, Nari146, NI11, NB1 |
| | ABB | 5 | Nari1047, NariNBG11, NariNBI10, Nari171, NariNBL20 |
| | AB | 1 | ENB17 |
| Australimusa | TT(**Fe`i**) | 5 | WH4, ES5, ENB13, M1, ENB14 |
| Eumusa x Australimusa | AAT | 2 | Nari186, ES1? |
| | ABBT? | 1 | ES7 |

*Genome labels for diploid, triploid and polyploid cultivars: A = acuminata, B = balbisiana, T = Australimusa.

**Table 5**. Expanded list of categories and attributes used in analysis of volcaniform leaf phytoliths for the 'New Guinea Banana Project'.

| Category | Attribute |
|---|---|
| Base, 3D shape | tabular, blocky, spherical( globose), platy (planar) |
| Base, 2D shape | round, oval, square, rectangle, quadrilateral, boat (oblong), irregular |
| Body length | - |
| Body width | - |
| Body height | short (h<1/3 length), medium (h=1/3 to ½ length), tall (h≥1/2 length) |
| Crater length | - |
| Crater width | - |
| Crater shape (dorsal view) | round (orbicular), oval, quadrilateral, irregular |
| Rim | present, absent |
| Rim shape | regular, irregular, skirt (crenate) |
| Sides | straight, convex, concave, straight/concave, concave/convex, straight/convex |
| Body texture | psilate, granulate, verrucate, nodulose, tuberculate, psilate/verrucate, psilate/granulate, granulate/verrucate |
| Base ornamentation | absent, short (<1.25μm), medium (1.25-2.5μm), long (>2.5μm), long/tuberculate/dendritic, short/medium, medium/long |

ferentiated from phytoliths generated by other plant parts, and the absence of seed phytoliths in an archaeobotanical assemblage can signal presence of seedless/domesticated bananas. However, parthenocarpy and sterility, processes inherent in banana domestication, evolved over several generations, and populations of seeded cultivated diploid bananas are still common in Papua New Guinea. Therefore, it can be difficult to determine the status of bananas (wild or cultivated) in the archaeobotanical record unless there is unequivocal evidence for bananas either being outside their natural range, associated with archaeological and pedogenic features indicative of cultivation, and/or associated with other known cultigens. In the absence of diagnostic seed phytoliths identification is reliant on volcaniform leaf phytoliths. Studies show that some species and cultivars can be discriminated according to crater size and body length and by the presence of certain rare morphotypes. Nevertheless, there is large morphotype variation within and between species; consequently, identification is currently reliant on large sample sizes rarely encountered in fossil assemblages. Therefore, more work is needed to clarify the extent of variability across the geographic range and within different habitats. The 'New Guinea Banana Project' commenced in 2002 with the field collection of samples and resultant analysis of 58 additional accessions. The outcome of these analyses should help to resolve many of the outstanding issues regarding the differentiation of volcaniform leaf phytoliths in the archaeobotanical record, particularly in the Pacific/Papua New Guinea region.

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