



# Relevance of Banana Seeds in Archaeology

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## Research

### Abstract

In this contribution, the importance of banana seeds collected during archaeological investigations is indicated. Because fully-formed seeds are not ordinarily produced in bananas cultivated for food, the archaeological relevance of banana seeds may initially appear to be limited. However, there are a number of contexts in which the recovery and identification of seeds can be important for understanding the initial domestication and dispersal of bananas by people. In this respect, the possible existence of naturalized species and/or subspecies is hereby reported. Several innovative hypotheses are advanced based on botanical considerations, which may have profound consequences for the reconstruction of the prehistory of banana domestication and the involved regions, and which archaeology can assist in confirming, modulating or refuting.

### The “Center of primary *Musa* diversity” is not a rigid concept

The center of primary diversity in the genus *Musa* is large and very complex (Figure 1). It was the grand achievement of Cheesman to classify and to describe most of the numerous taxa in a series of articles that appeared in Kew Bulletin (Cheesman 1947, 1948, 1949, 1950). He was obliged to coin the botanically uncommon term of “Section” for the highest order of differentiation in the genus. This classification has since been widely adopted with satisfaction and extended mainly by Simmonds through the addition of newly found species (De Langhe *et al.* 2009).

Any banana plant with fully-developed seeds that is found under natural conditions in the center of primary diversity is usually considered to belong to a wild *Musa* species. However, such an assumption ignores the possibility that seedy banana plants may have been ‘naturalized’ (see De Langhe *et al.* 2009 for an explanation of the terminology)

in some places after they were introduced there through human intervention. The present contribution reports such cases and suggests that naturalized occurrences of *Musa* species are more common within the center of primary diversity than previously thought.

In this paper, it is demonstrated that research focused on the presence of naturalized banana plants would not only prove their existence at a particular locale in the past, which would be most helpful for botanists and geneticists, but at the same time such a finding opens up new prospects for understanding the prehistory of human populations.

### Seeds in bananas

An extensive histochemical and macromolecular study has recently shed much light on the composition and possible roles of the banana seed coat (Graven *et al.*, 1996). The extremely hard coat of banana seeds consists of an exotesta and a massive, sclerotised mesotesta. Seed phytoliths form a tight and continuous silicious upper layer of the exotesta which appears to be a first barrier against environmental forces, such as low pH in soil,

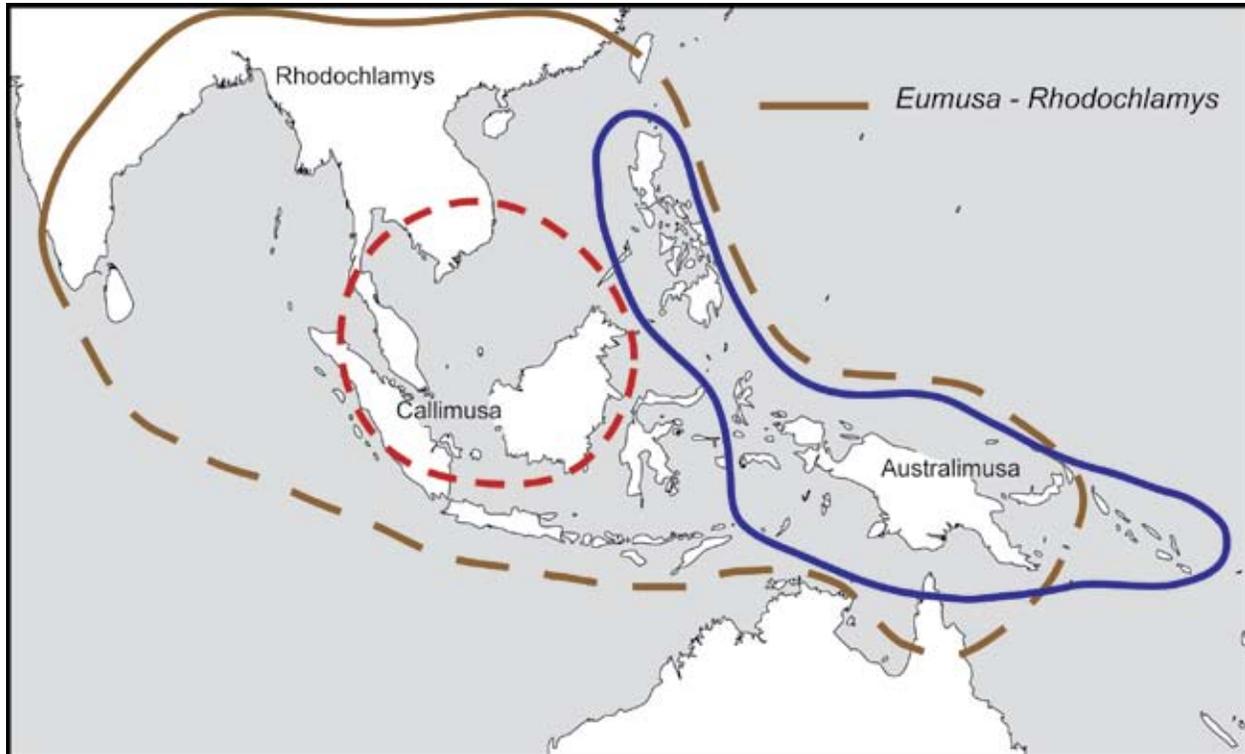
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**Figure 1.** Sections of the genus *Musa* (based on Simmonds, 1962). The boundaries are uncertain, especially for Section *Callimusa* and for the western limits of Section *Australimusa*.

pathogens, chewing insects and other predators. Various polyphenols in the mesotesta would protect against fungi. An opening in the coat, through which the radicle and hypocotyle of the embryo will emerge at germination, is protected by a hard plug (operculum).

It has been shown that the seeds remain unharmed – although with decreased germination capacity – after digestion by animals that consumed the ripe seedy fruits (Simmonds 1959b). Depending upon the species, banana seeds in the soil will normally undergo a relatively long period of dormancy, of which the mechanism is still not well understood. However, it has been estimated that most seeds lose germination capacity after one year (Simmonds 1959b).

As a consequence of the above, seeds that remain in various burial environments should persist for an indeterminate time due to the highly resistant coat. It is therefore remarkable that seeds are not readily found in the deeper soil profiles that interest archaeologists. In part, the paucity of archaeobotanical records of banana seeds reflects the lack of systematic archaeobotanical investigation in parts of Island Southeast Asia and especially Melanesia, and the inadequacies of suitable modern reference collections against which archaeological specimens are compared (Tim Denham pers. comm. 2008).

Due to more or less advanced stages of female and male infertility, most edible bananas will never produce viable

seeds under cultivation or when naturalized. However, when the female flowers are abundantly pollinated by artificial means, some varieties can produce a few mature seeds per bunch, which is how genetic improvement became possible. Therefore, some of these seedy fruits may plausibly contain one or more mature seeds in natural conditions when the plants are in the proximity of wild banana plants. Such cases have indeed been noticed and are even rather common for the '**Pisang Awak**' subgroup, belonging to the hybrid ABB genome-group (Simmonds 1959a).

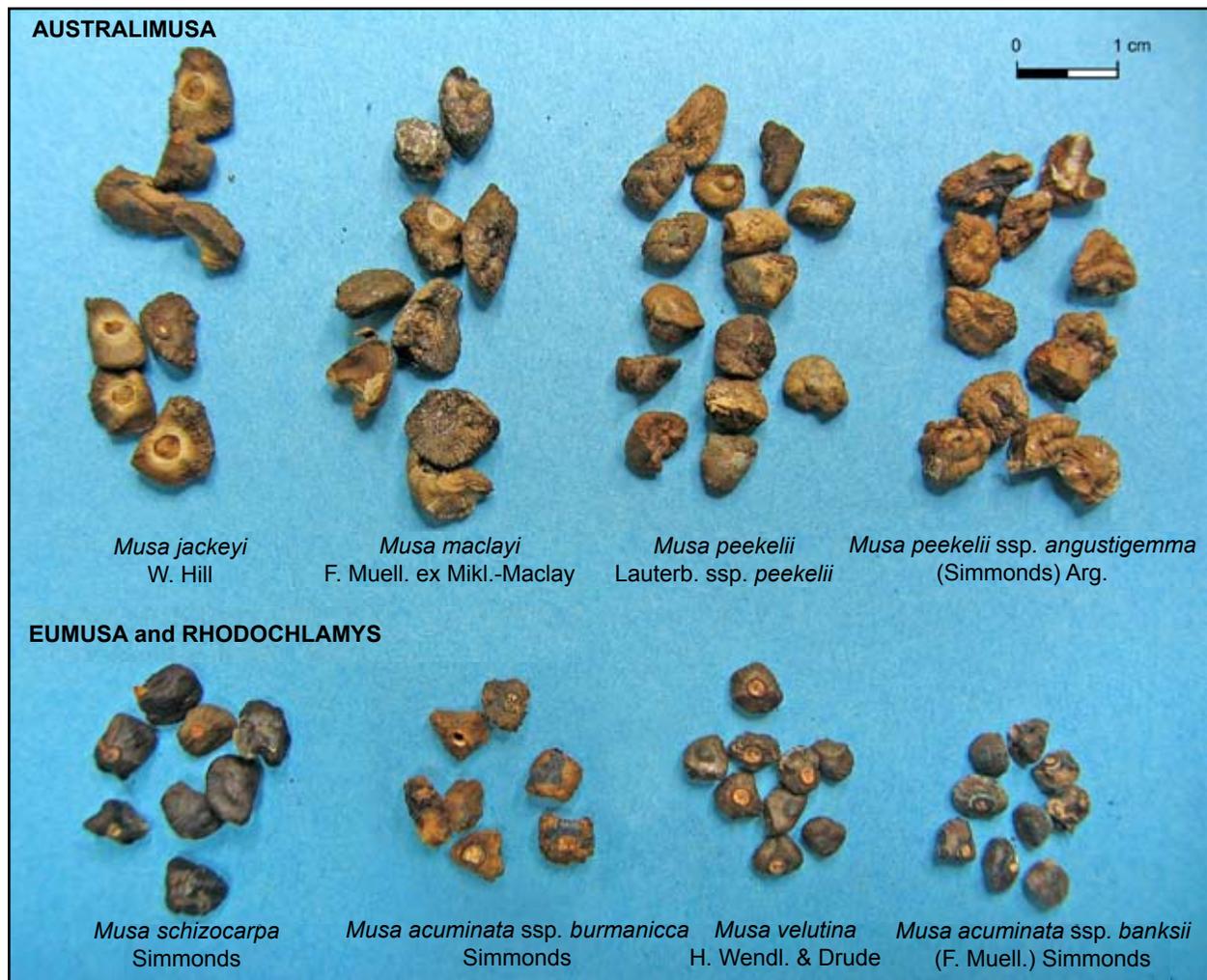
In conclusion, although the occurrence of seeds from edible bananas in archaeological contexts should be rare, their presence should be considered for older portions of the stratigraphy that correspond to the periods when the first semi-seeded edible diploids developed. Consequently, archaeological research should theoretically observe a decrease in banana seeds upwards through the stratigraphy at sites within the primary *Musa* diversity center; namely in places where wild and cultiwild plants have progressively been replaced by semi-seedy diploids and later by sterile, seed-suppressed diploid and triploid cultivars.

### Seed identification

Seeds of wild species have been macroscopically observed on collected specimens (Cheesman 1947, 1948, 1949, 1950, Simmonds 1956) and examined in the field (mostly for the sections *Australimusa* and *Callimusa*; Ar-

**Table 1.** Taxonomic determination key for banana seeds.

|  |   |
|--|---|
| 1.1. Globular; surface very smooth; large (8 to >11 mm) .....                  | Genus <i>Ensete</i>   |
| 1.2. Globular; surface warty; small (5 to 6 mm) .....                          | <i>Musa balbisiana</i> Colla<br>(Section Eumusa)  |
| 2. Rounded-angular; surface smooth; small (5 to 6 mm) .....                    | <i>Musa schizocarpa</i> Simmonds<br>(Section Eumusa)  |
| 3. (ob)Pyriform .....  | Section Callimusa   |
| 4.1. Dorsiventrally flattened; sunken hilum with contrasting ring; large ..... | Section Australimusa  |
| 4.2. Dorsiventrally flattened; without sunken hilum .....                      | Section Eumusa: <i>Musa acuminata</i> Colla,<br><i>Musa basjoo</i> von Siebold ex Y. Inuma,<br><i>Musa itinerans</i> Cheesman<br>and Section Rhodochlamys |

**Figure 2.** Photographs of seeds from sections Australimusa, Eumusa and Rhodochlamys (courtesy of Jeff Daniells). Note the sunken hilum with contrasting ring on the ventral side of the Australimusa seeds, and the remarkable smooth surface of the *Musa schizocarpa* Simmonds seeds.

gent 1976, 2000, Häkkinen 2003, 2004a,b, 2005, 2006a,b, Häkkinen & Meekiong 2005a,b). On the basis of the resultant publications, there is considerable variation between the seeds of different banana species and sections, but no intraspecific variation. Table 1 provides a simplified seed determination key for banana species and sections (also see Figure 2). Seed size in irregular forms corresponds with the longest dimension.

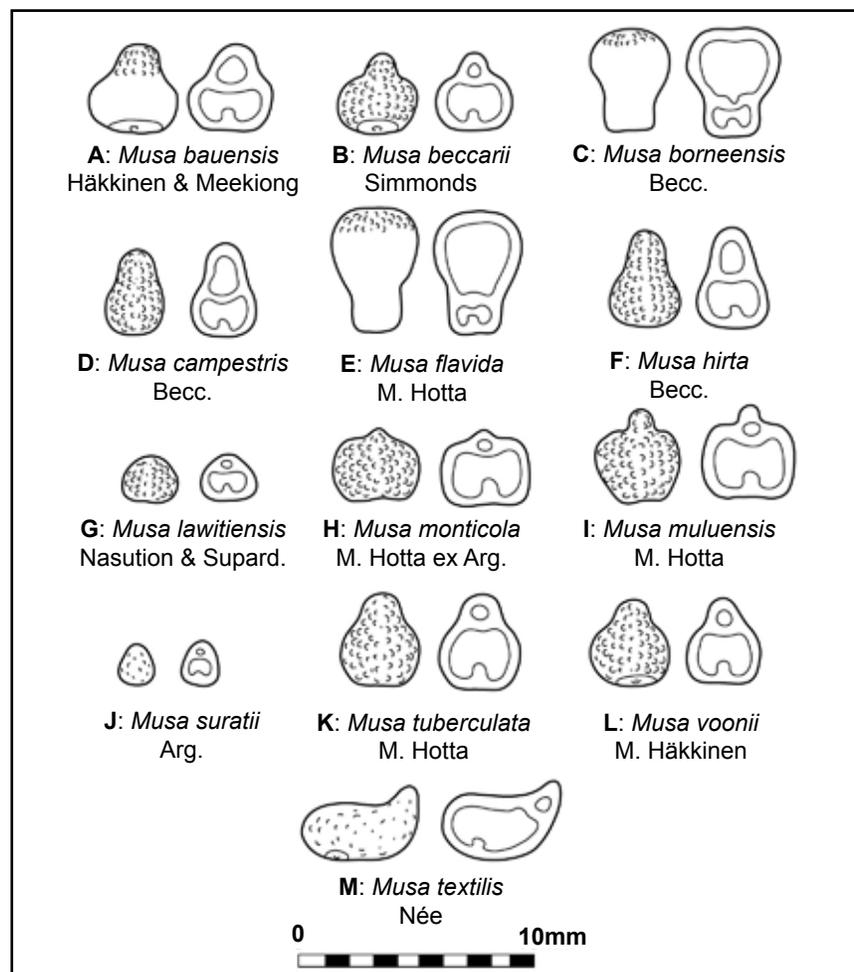
Confusion with the genera *Strelitzia* and *Ravenala* is excluded because both have seeds with an aril. The large globular *Ensete* seeds with their smooth surface are strikingly different from any of the *Musa* seeds. The nearly globular seeds of *M. balbisiana* with the warty surface are unique in the genus *Musa* (Figure 3). The seeds in the Section Callimusa have a distinct (ob) pyriform form with a ring around the perisperm in some species such as *M. coccinea*. Slight variations in this form for this species have recently been described in detail (Häkkinen, 2004) and are shown on Figure 4.

For the Section Eumusa, Table 1 includes only five species, *M. balbisiana*, *M. schizocarpa*, *M. acuminata*, *M. basjoo* and *M. itinerans*. The habitats of the other Eumusa species are strictly confined to the mountainous region in mainland South-and-Southeast Asia, from Nepal to Yunnan. These other species have not dispersed widely and are not important for understanding the history of domestication of bananas for food.

*Musa schizocarpa* seeds are rounded-angular and could at first sight be mistaken for *M. balbisiana* seeds. However, they can be distinguished by the smooth seed surface. They are clearly smaller than *Ensete glaucum* (Roxb.) Cheesman seeds (see Table 1). Moreover, they tend to have an umbo on the opposite side of the hilum. The habitat of *M. schizocarpa* is confined to New Guinea and extreme



**Figure 3.** Photograph of seeds of *Musa balbisiana* Colla. Each seed is approximately 5-6 mm in diameter.



**Figure 4.** Drawings of seeds of banana species from Borneo: (A-L) species of Callimusa, and (M) of Australimusa (Häkkinen 2004:84).

eastern Indonesian islands, but the exact boundaries remain poorly defined.

The seed type 4.2 in Table 1 is shared by several species and even sections, consequently the precise identification of the corresponding plants within archaeobotanical assemblages looks at first sight to be problematic. The risk of confusion can be minimized by a consideration of the geographical occurrence of each species or section occurring within this seed type grouping. The cold-hardy *M. basjoo*, probably originally from the mountainous Yunnan region, is present on Taiwan and the southernmost islands of Japan, where the only other *Musa* species present is *M. balbisiana*; the latter species produces the rather unique seed type 1.2 enabling clear differentiation. The seeds of the *Rhodochlamys* species cannot be readily distinguished from others with seed type 4.2 using morphological or morphometric criteria. However, *Rhodochlamys* is confined to a limited area of the Asian mainland (Figure 1). *Musa itinerans* presents a problem because the scattered occurrences in lowland Southeast Asia of this originally mountainous species suggest it was moved to low altitudes by human activity. Certainly it is culturally important; its chopped pseudostem is a regular food for pigs and its male bud is a popular vegetable. On the other hand, if this very vigorous species was much more common in the lowlands in the past, it certainly would have been sympatric with *M. acuminata*.

*Musa acuminata* is the only species of seed type 4.2 found in insular Southeast Asia and Melanesia. The morphology of *M. acuminata* seeds is clearly distinguishable from those of other bananas also found in these regions, namely *M. balbisiana*, *Australimusa* and *Callimusa*.

## Archaeobotany of banana seeds

Reports of banana seeds found in the course of archaeological research are sparse. This is perhaps not surprising since edible bananas produce few or no seeds. As already stated, however, the possibility has been largely overlooked that seedy banana plants have been 'naturalized' in some places after they were introduced there through human intervention, thus pointing to the use of wild bananas in areas where edible bananas were not yet introduced or at least not abundant. Such findings would open new prospects for tracking the early stages of banana domestication.

A striking example is Kajale's demonstration that wild banana fruits were roasted and their pulp consumed by Terminal Pleistocene/early Holocene times in Sri Lanka (Kajale 1989). The seeds found were from the species *M. balbisiana* and *Musa* cf. *acuminata*. While this certainly is not proof that the plants were cultivated, the evidence shows that seedy bananas were a part of human diets in this remote period. An indirect example is the detection of seed

phytoliths in early Holocene sediments from archaeological contexts at Kuk Swamp in the highlands of Papua New Guinea (Lentfer 2009). These have been instrumental in the reconstruction of the timing of early banana domestication at the Kuk site, New Guinea (Denham *et al.* 2003, 2004).

Although the work to date has been limited, the use of banana seeds and seed phytoliths does open up possibilities for understanding the domestication of the banana, the dispersal of early cultivars, and hence the histories of the people involved.

## 'Wild bananas' as outliers of the *Musa* center of diversity

Wild-growing, seedy bananas are present on islands that are very distant from the *Musa* center of diversity (Figure 1), including Pemba and the Samoan Islands. Banana fruits "are poorly adapted to long-range transoceanic transport" so that it is "hard to believe that this is an example of 'natural' spread" (Simmonds 1962:22-23, 27). If bananas had dispersed naturally to these islands, it might be expected that they would also be present on many other remote islands outside the area of primary *Musa* diversity.

A more rigorous test of the natural state of these bananas on Pemba and the Samoan Islands would be to find remains of seeds, or seed phytoliths, in sediment horizons that correspond with the periods of human occupation during the Holocene, but not from deeper and earlier contexts. Even a single seed found *in situ* from Pleistocene horizons would exclude an anthropogenic origin.

### The Pemba case

The island of Pemba is about 50 km offshore of the east coast of Africa (at about 5°S) and about 50 km north of Zanzibar. According to conventional history (Oliver & Fage 1988), the island was first populated by Bantu-speaking people around the beginning of the CE, who soon thereafter would have participated in trade over the western Indian Ocean. Persian and even Indian traders settled there later and by the end of the 10th century an important settlement by Omani Arabs was established that brought the island under Islamic influence.

Seedy *M. acuminata* plants grow on Pemba and, since discovery, have formed an active part in genetic studies (Shepherd 1999). The traditional bananas in Africa are triploids. However, a few edible diploid bananas are grown in the coastal zone of tropical East Africa and on islands nearby (Simmonds 1959a).

The unusual location of the seedy plants, so far from the center of infrageneric diversity, led Simmonds to conclude

that “human transport seems a much more likely agency and it may be that the apparent Indonesian affinity of the plants is significant” (Simmonds 1962: Section I.9). Such an inference has far-reaching implications regarding the role of Austronesian-speaking voyagers, or perhaps other populations, in the introductions of other Asian or Melanesian crops to Africa, such as taro (*Colocasia esculenta* (L.) Schott) and greater yam (*Dioscorea alata* L.). If correct, people may have introduced the seedy plants together with initial edible diploids that would still have been partly seed-fertile, in a very remote period when triploids had seemingly not yet been generated.

### **The Samoa case**

The islands of Samoa form, together with Fiji, Tonga and Tuvalu, a key region in the prehistory of Polynesia. A branch of the Austronesian-speaking population, typified by the Eastern Lapita culture, arrived in the region by 1000 BC from ‘the west’ and apparently settled there for a millennium before their descendants colonized the archipelagos further east (Kirch 2000). The agricultural baggage of the original Lapita people was impressive and included the banana, judging from reflexes of the inferred Proto-Malayo-Polynesian term \***punti** for this crop (see more on this prototerm in Donohue & Denham 2009a,b).

The question is: which bananas did these Lapita colonists bring, apart from the very distinct **Fe`i** bananas which have no genetic relation with the *Eumusa* species (see De Langhe *et al.* 2009)? Could they have been the triploid AAB Pacific Plantains, now cultivated all over the Pacific, which Simmonds (1962) argues had been generated in the New Guinea-Melanesia region? Alternatively, were they the diploid ancestors of these triploids? Were the triploids, or at least a major part of them, generated in the Samoa region during the millennium-long settlement there? For, although Pacific Plantains have been traditionally grown in Melanesia (Arnaud & Horry 1997), it is unlikely that they were generated there because, in that case, they would have long ago almost certainly replaced the countless edible *M. acuminata* diploids which are less vigorous/productive and yet still widely grown in New Guinea. The possibility of a Polynesian origin of the Pacific Plantains is also reinforced by what the linguists have coined ‘the Samoic outliers’, namely (Western-)Polynesian languages spoken in Melanesia due to a back-migration of peoples from Samoa and neighboring islands (Gordon 2005, [www.ethnologue.com/show\\_family.asp?subid=90448](http://www.ethnologue.com/show_family.asp?subid=90448)).

Plants of *M. acuminata* ssp. *banksii* were found growing ‘in the wild’ in Samoa. As Simmonds stated, “The marked discontinuity in distribution and apparent failure to occur in suitable sites in the intervening islands...” (i.e., between New Guinea and Samoa) “...strongly suggests that human movements were responsible for the outlier” (Simmonds 1962: Sections I.9 & VIII.3f).

Finding evidence for seeds restricted to sediment profiles and/or archaeological sections reflecting the first 1000 years of human settlement would enable a test of the hypothesis that the first bananas reaching the Samoa region were not the triploid Pacific Plantains, but rather a mixture of edible and seedy *Eumusa* diploids besides the Australimusa cultivars (**Fe`i** bananas). Such confirmation would have deep implications for the reconstructions of the peopling of Pacific Islands, and the use of plants in the past.

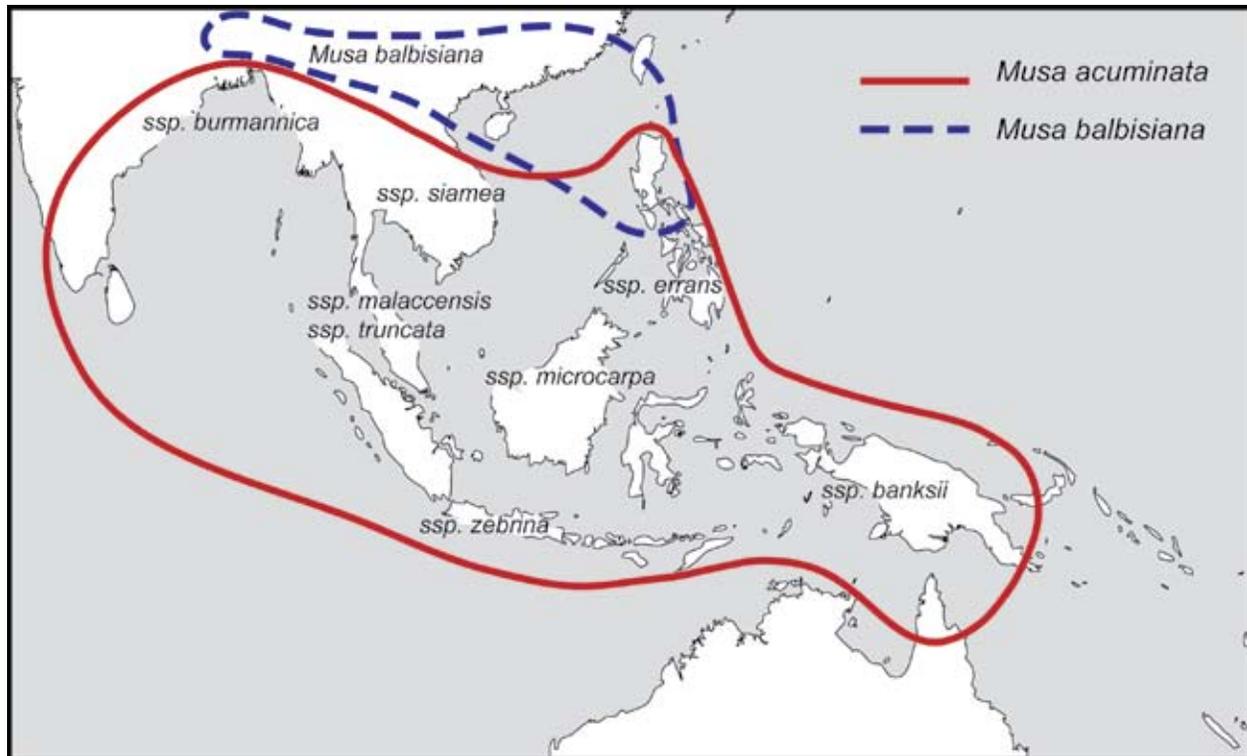
### **Naturalized *Musa balbisiana* within the center of *Musa* diversity?**

There is enough evidence to conclude that people originally used wild banana plants for purposes quite different from fruit consumption, such as for textile making and medicines, as can still be observed in some places (Kennedy 2009). If at later stages some populations moved to areas where these plants did not grow naturally, people may have carried with them seedy fruits that founded stands of these plants near new settlements and that were eventually naturalized as ‘cultiwilds’ outside of the natural distribution of the individual species. If such plant movements occurred within the centre of primary *Musa* diversity, it would be difficult to detect from naturalized occurrences alone.

For example, the existence of naturalized *M. balbisiana* populations has been suspected or even demonstrated (e.g., Simmonds 1956, for island and lowland Southeast Asia as explained below). Confirmation of naturalized populations in seemingly ‘anomalous’ places could be achieved using archaeobotany if seeds were found only in the upper parts of sediment profiles, whereas they would be expected in deeper horizons if present naturally. The same technique could be applied for other species such as *M. acuminata*. In contrast with the ‘outlier’ cases, a major challenge here is to reliably differentiate the seeds of all involved species.

### **The uncertain status of *Musa balbisiana* (BB) in Southeast Asia**

As is shown on Figure 5, one of the two parent species of edible bananas, *M. balbisiana*, is seemingly not native within the lowland regions of Southeast Asia, nor to Island Southeast Asia and New Guinea (Argent 1976, Simmonds 1956). In the Ryukyu Islands of Japan, where *M. balbisiana* was formerly called *Musa liukiensis* (Matsumura) Makino ex Kuroiwa and even confused with *M. basjoo*, it is considered to be introduced (Constantine 2008, Jarret & Gaweil 1995) and perhaps relatively recently (Hendrickx 2007). The situation in Taiwan and the Philippines is complex due to human influences. The present author does not exclude the possibility that introduced *M. balbisiana* plants may have crossed with a natural population of *M. balbisiana*, and that ensuing back crosses may have gen-



**Figure 5.** Inferred natural distributions of ancestors of common edible bananas. The commonly accepted natural status of *M. balbisiana* in India is questioned in the present contribution.

erated the current extraordinary diversity, which has as yet not been satisfactorily classified.

The AAB Pacific Plantains in Oceania and the AAB Plantains in Africa display an exceptionally high tertiary diversity via many somatic mutations. In what area would a contact between *M. balbisiana* and edible AAs have led to hybridization and the formation of these particular AABs?

The following facts are significant when noticed in traditional cultivation context: (1) the apparent absence of AAB Pacific Plantains to the west of New Guinea; (2) the maximal expression of AAB Pacific Plantain diversity on the islands of the Pacific; (3) the absence of any African Plantain diversity in the Pacific, in mainland Southeast Asia and in most of South Asia, as well as on the major islands of Indonesia – the only African Plantain cultivar (rather rarely) observed in this whole area being one single type of Horn Plantain (**Pisang Tandoc**); (4) a weak diversity of African Plantains in extreme southern India; (5) the non-existence of AAB African Plantain diversity in New Guinea (Jeff Daniells pers. comm.); (6) the uncertain diversity status of African Plantains in Maluku and the Lesser Sunda islands; (7) a surprising diversity of African Plantains among tribal people in the Philippines (De Langhe & Valmayor 1979); and, (8) the greatest diversity of African Plantains in Africa. These geographical configurations indicate that the basic cultivars of these two sub-

groups were generated, selected and initially cultivated in two distinct areas and that the people involved were never in contact at the time.

Hence the original areas of contact between *M. balbisiana* and edible AAs would have been: (a) for the African Plantains, a probably quite narrow zone embracing the Philippines and perhaps Maluku and Lesser Sunda; and, (b) for the Pacific Plantain, an area slightly more to the east, including New Guinea and Bismarck archipelago, but perhaps extending to the Solomon islands and even Samoa. Bearing in mind that *M. balbisiana* is not natural in these areas, people must have been instrumental in transporting the plant and thereby ensured contacts with edible *M. acuminata* bananas.

Two hypotheses are hereby offered for the generation of the AAB Plantains. First, early diffusion of *M. balbisiana* was associated with the dispersal of Austronesian-speaking voyagers who had become familiar with the plant in its wild status in the hilly parts of mainland Southeast Asia and/or the Philippines. Such people would have brought the plant with them as they migrated via Taiwan and Philippines further south, with an early branch bringing it in contact with the edible AA bananas and then moving further to the west carrying with them the initial African Plantains, and a later branch starting the odyssey into Near Oceania and the Pacific, thus causing a second contact

between *M. balbisiana* and edible AA (De Langhe & de Maret 1999).

Alternatively, *M. balbisiana*, like many other plants and material cultural items, became incorporated into exchange networks in Island Southeast Asia including the Philippines, and perhaps even up to Taiwan, as well as Near Oceania, before any Austronesian influence from Taiwan (Donohue & Denham, 2009a,b). This would imply that cultiwild BB were dispersed from the Philippines into these networks during the earlier periods of the Holocene preceding the dispersal of Austronesian languages from Taiwan. This second option leaves open the question of how the two subgroups were generated in two separate areas.

In evaluating these historical hypotheses, 'likely' is not 'certainly'; hard facts or at least much stronger indications for the human involvement in the dispersal of *M. balbisiana* are necessary. In this case, if *M. balbisiana* was native to parts of Island Southeast Asia, its seeds should be found among seeds of other *Musa* species across all investigated horizons. If BB seeds are not found among the other seeds in lower horizons, one could conclude that cultiwild *M. balbisiana* in Island Southeast Asia was introduced by people and eventually estimate the critical time period of introduction.

#### ***Is Musa balbisiana (BB) truly native to South Asia?***

If the presence of *M. balbisiana* plants in insular, and potentially peninsular, Southeast Asia is anthropogenic, then there is reason to revisit the status of the apparently wild BB plants in peninsular India and Sri Lanka.

The mountainous region stretching from Nepal, over Assam and northern Myanmar/Thailand to southern China and northern Vietnam, including perhaps the Philippines, form the most likely habitat of natural *M. balbisiana* populations (Simmonds 1956). While it has been commonly accepted following Simmonds that *M. balbisiana* is also natural in India and Sri Lanka, the evidence is much less clear. Cheesman found, for example, that a collected *M. balbisiana* specimen from Sri Lanka, when cloned, displayed a large range in bunch size similar to that of cloned specimens from Assam, with both clones having the same fruit form (Cheesman 1947: sub 'a. *Musa balbisiana*', text with Plate 2). The weak morphological variation among the *M. balbisiana* plants, compared to that within *M. acuminata*, is mostly restricted to the infrutescence, with variable fruit shape, bract persistence and male bud form; variations in plant stature and bunch size have repeatedly been recognized as due to local growth conditions.

Consequently, and in sharp contrast to *M. acuminata*, no geographically distinct subspecies of *M. balbisiana* have yet been identified. In such circumstances, there is no reason to discount the possibility that people may have

been responsible in the remote past for an artificial expansion of the species over the entire Indian peninsula down to Sri Lanka.

On the other hand, the hypothesis of a natural existence of *M. balbisiana* in lowland Southeast Asia can be defended as well. In an exhaustive examination of the literature about wild and edible bananas in India, Fuller and Madella (2009) conclude that the natural distribution of *M. balbisiana* is confined to mountainous northeastern India and the hilly landscapes of Orissa, as well as to the island of Sri Lanka. They suppose that wild bananas were more common under wetter conditions during the Terminal Pleistocene/early Holocene and suggest that "the disjunct distributions of *M. balbisiana* and *M. acuminata* in southern India and Sri Lanka presumably attest to migration and separation of populations from the northeast, and ultimately Southeast Asia through the processes of interglacial wetting and glacial drying" (Fuller & Madella 2009:336).

Today, the cultivation of *M. balbisiana* for various purposes is common in the northeastern Indian states of Assam and Manipur (Fuller & Madella 2009, Simmonds 1956), despite the presence of edible (ABB) banana varieties. Such tenacious tradition points to a deep past. The cultivation of *M. balbisiana* must have been relatively intense and of long duration because semi-parthenocarpic, although still partly seedy, varieties exist, such as the **Bimkhol**, which was originally from northeastern India and is now widespread across the country.

*Musa* leaf phytoliths have been identified during excavations in southern Pakistan (Sindh) and dated to the second half of the third millennium BC (Madella 2003). It was suggested that these phytoliths were produced by domesticated hybrid (AxB) banana plants. However, such an early arrival of edible bananas at a place quite distant from the major areas of AxB diversity looks problematic. The possibility that cultivated *M. balbisiana* plants were producing these phytoliths seems a plausible alternative. However, firm confirmation of such a possibility requires *M. balbisiana* seeds or phytoliths to be found and identified to the species level in the same area.

In Figure 5, the natural distribution of *M. balbisiana* does not include peninsular India or Sri Lanka. The provocative hypothesis developed here is that *M. balbisiana* was spread by people across peninsular India down to Sri Lanka, as opposed to having naturally dispersed there.

An archaeological method for differentiating natural from anthropogenic introductions of *M. balbisiana* to peninsular India and Sri Lanka is relatively simple since no other wild-growing *Musa* species have been recorded on the island, with the possible exception of *M. acuminata* (see below). In case of human intervention, the typical *M. balbisiana* seeds would only be found in the corresponding

strata. If the species is truly natural there, its seeds would also be present in lower (and older) horizons.

### *Is Musa acuminata native to South Asia?*

In Figure 5, the natural range of *M. acuminata* (AA) is shown extending over peninsular India, conforming to the classical viewpoint. The extension can be questioned, as with *M. balbisiana* though on weaker climatic grounds, since it is true that wild AA plants thrive by preference in non-mountainous, warm-humid regions and their natural presence in the peninsula is therefore plausible.

An apparent anomaly arises in the lack of variation among *M. acuminata* similar to that exhibited by *M. balbisiana*. While *M. acuminata* shows great diversity in mainland and Island Southeast Asia, a diversity that called for its classification into no less than six subspecies, only one subspecies, *M. acuminata* ssp. *burmannica*, is observed over a large area stretching from Myanmar in the north to Sri Lanka in the south, namely, over the entire Indian subcontinent. If *M. acuminata* has diversified in the eastern part of its range into a clade of several subspecies, why did a comparable diversification not take place in the western part?

The lack of variation could be due to a recent expansion of *M. acuminata* during the Holocene, like that suggested for *M. balbisiana*. As with that species, the subspecies *burmannica* may have been important for people. The leaves of this particular subspecies are quite robust and are used in western Thailand for fibres and the construction of thatched roofs (personal observation).

As noted above, *Musa* cf. *acuminata* seeds, along with those of *M. balbisiana*, were found in Terminal Pleistocene/early Holocene archaeological contexts in Sri Lanka (Kajale 1989). Since truly natural *M. acuminata* ssp. *burmannica* populations are common in Myanmar and western Thailand, their artificial expansion in the south would imply an analogous diffusion to that of *M. balbisiana* during the Terminal Pleistocene/early Holocene. As for *M. balbisiana*, the possibility that *M. acuminata* ssp. *burmannica* was introduced could be tested by searching for pre-Holocene seeds.

Seeds of *M. acuminata* are distinguishable from those of *M. balbisiana* or *Ensete*. Confusion with seeds of other *Eumusa* species can be discounted because no other wild species have ever been observed on the Indian peninsula. The only possible exception would be the enigmatic *Musa ochracea* K.Sheph., described by Shepherd (1963), of which the origin was not clear (potentially in Pakistan) and of which the existence has never been subsequently reported.

## Conclusion

The evolution from seedy wild bananas to seedless edible varieties has been a very complex one. The results of recent genetic research are showing how the process comprised a long period of hybridizations among taxa from different areas (Perrier *et al.* 2009). Humans have been instrumental in bringing these taxa into areas where the hybridizations took place. This implies that people were initially interested in seedy bananas for various purposes and carried the propagules with them during their movements. Finding the traces of such movements and of the involved taxa is now a challenge for disciplines such as archaeology, archaeobotany and linguistics.

This contribution draws attention to some configurations where ancient traces of human aided dispersal could be detected in the form of precisely identified seeds and seed phytoliths preserved in sediment or at archaeological sites. Because such tangible traces have not been widely documented, with few exceptions, it is acknowledged that this contribution has a rather speculative character. It is hoped, however, that the botanical arguments for the likelihood of finding seeds and seed phytoliths in specific places may help in the construction of focussed research hypotheses, lead to the adoption of the necessary methodologies, and eventually shed more light on the early stages of banana domestication.

## Acknowledgements

Tim Denham and an anonymous reviewer are thanked for their many stimulating comments. They prompted me among others to dig somewhat deeper in the documentation for the offered arguments throughout the contribution. The presence of seedy bananas in Hawai'i has been a matter of speculation on their possible role in prehistoric times. I am indebted to Angela Kepler for having convinced me that these specimens are relatively recent introductions.

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