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Phytoliths As a Tool for Investigations of Agricultural Origins and Dispersals Around the World

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Abstract

Agricultural origins and dispersals are subjects of fundamental importance to archaeology as well as many other scholarly disciplines. These investigations are world-wide in scope and require significant amounts of paleobotanical data attesting to the exploitation of wild progenitors of crop plants and subsequent domestication and spread. Accordingly, for the past few decades the development of methods for identifying the remains of wild and domesticated plant species has been a focus of paleo-ethnobotany. Phytolith analysis has increasingly taken its place as an important independent contributor of data in all areas of the globe, and the volume of literature on the subject is now both very substantial and disseminated in a range of international journals. In this paper, experts who have carried out the hands-on work review the utility and importance of phytolith analysis in documenting the domestication and dispersals of crop plants around the world. It will serve as an important resource both to paleo-ethnobotanists and other scholars interested in the development and spread of agriculture.

Keywords: Phytoliths, Crop Plants, Diagnostic Criteria

1. Introduction

The domestication of plants and development and spread of agriculture were transformative events in human and ecological history. Present records show that beginning around 11,000 to 10,000 years ago plant cultivation and domestication developed independently in at least seven to eight regions of the world, shortly after spreading into others (Larson et al., 2014).
Understanding agricultural origins through archaeological enquiry is of fundamental importance for a diversity of scholarly disciplines in addition to anthropology, including genetics, environmental history, and agronomy. Accordingly, developing methods for identifying the remains of crop plants and their wild progenitors has been a focus of paleoethnobotany during the past 25 years. Phytoliths have increasingly taken their place in these endeavors alongside macro-remains, pollen, and starch grains in all regions of the world (for reviews see Pearsall, 2000, 2015a; Piperno, 2006, 2009; Hart, 2014; Marsten et al., 2014). Standardization of identification criteria for various crops and wild ancestors is now accomplished, and on-line resources along with monographs and books containing numerous phytolith images for wide dissemination of criteria used to discriminate taxa are already substantial and growing. Among the web resources are: 1) the Pearsall Neotropical phytolith data base--http://phytolith.missouri.edu, 2) the PhytCore International Data base housed by GEPEG, University of Barcelona and co-ordinated by Rosa Albert and colleagues, which will be a single source with phytolith data bases and images from many scholars around the world—access is through www.archeoscience.com, 3) the Institute of Archaeology, London’s web page on Old World phytoliths-- www.homepages.ucl.ac.uk/~tcrndfu/phytoliths.html, and 4) the Department of Archaeology, University of Sheffield (UK) Wiki online tutorial--http://archaeobotany.dept.shef.ac.uk/wiki/index.php/Main_Page. For monographs and books with numerous phytolith images for various world regions also see Piperno and Pearsall, 1998a, Piperno, 1988, 2006, and Kealhofer and Piperno, 1998. The volume of phytolith-related work on prehistoric agriculture along with its appearance in numerous journals published in different countries is such that few archaeologists and other interested scholars may have the time or expertise to keep up with the literature. This paper
addresses this issue by reviewing the state-of-the-art of phytolith analysis for documenting the origin and spread of crop plants around the world. Since the last review of the subject (Piperno, 2006) new crops have been investigated, refinements of identification techniques for others have taken place, and archaeological applications have expanded. Investigations also now routinely incorporate analysis of numerous wild species related to crop plants, including their wild ancestors when known, as well as constructions of large modern reference collections of regional flora. Table 1 contains a summary of findings from crops and wild progenitors that have been examined in detail (it also contains information on little understood crops not discussed in the text). More information on the phytoliths follows.

2. Crops of the Americas

A number of major and now-minor New World crops contribute phytoliths diagnostic at either the genus or species level, while others contribute forms identifiable at higher taxonomic levels such as the family, sub-family, or tribe.

2.1 Zea mays L. (Maize)

Maize is the pre-eminent cereal crop of the Americas and is now known to be native to the Central Balsas River region of tropical southwest Mexico (e.g., van Heerwaarden et al., 2011). The ability to isolate plant remains and identify maize and teosinte (wild Zea) in environments inimical to the preservation of macroremains, which includes maize’s homeland, is fundamental to understanding the domestication and early history and spread of this crop. More than three decades of research has demonstrated that maize leaf and cob phytoliths are diagnostic and distinguishable from those of its wild ancestor, the teosinte Zea mays ssp. parviglumis, and wild non-Zea grasses native to North, Central, and South America. Phytoliths will be of high utility in investigations of wild maize use, early stages of domestication, and subsequent spread. Present
phytolith and starch grain evidence from the Central Balsas region in Mexico indicates maize was domesticated by 8700 cal BP (Piperno et al., 2009; Ranere et al., 2009), and phytolith research has contributed greatly to documenting maize spread and usage throughout the Americas (e.g., Piperno et al., 1985; Pearsall, 2000, et al., 2004; Bozarth, 1993, et al., 2009; Mulholland, 1993; Hart et al., 2003, 2007; Iriarte et al., 2004; Thompson et al., 2004; Piperno, 2006:140-153; Zarillo et al., 2008; Boyd and Surette, 2010; Dickau et al., 2012; Iriarte et al., 2012; Logan et al., 2012; Hart and Lovis 2013; Hart 2014; Biwar and VanDerwarker, 2015; Corteletti et al., 2015).

Identification criteria employ size and morphology, and as with phytoliths from other crop plants (below), deposition of vegetative and inflorescence structures can be distinguished (leaf, stalk, seed chaff), making the phytoliths potential tools also for examining hypotheses related to teosinte and maize usage in different periods and regions (e.g., whether early cultivation was for alcohol from stalk sugar) (Piperno et al., 2009; Logan et al., 2012; Biwar and VanDerwarker, 2015). Size and three-dimensional morphologies of cross-shaped phytoliths from maize distinguish maize from wild grasses other than *Zea* and *Tripsacum* (Pearsall, 1978; Piperno, 1984; Piperno and Pearsall, 1993; Iriarte, 2003; Piperno, 2006:52-60) (Fig. 1). Cross-shaped phytoliths also distinguish maize from *Tripsacum* and wild *Zea* if representation of these taxa in phytolith assemblages is ruled out using other phytolith types found in their fruitcases that are diagnostic to genus (below) (Piperno and Pearsall, 1993; Piperno, 2006:60-65).

With respect to inflorescence phytoliths, a number of phytolith types in teosinte fruitcases (the hard structure composed of a glume and rachid that encloses the teosinte kernel) and maize cobs separate teosinte from maize (e.g., Piperno and Pearsall, 1993; Pearsall, et al., 2003; Piperno, 2006:60-65), and both maize and teosinte from non-*Zea* wild grasses native to the Americas.
The formation of these phytoliths is genetically controlled by the major maize domestication gene *teosinte glume architecture 1* (*tga1*), which also underwrites fruitcase hardness (lignification) and the degree to which the kernel is enveloped by the glume (Dorweiler and Doebley 1997; Piperno, 2006:61, 63). The fruitcase and cob phytolith types were formalized by Pearsall et al. (2003), who compared maize and teosinte phytoliths with those from numerous wild grasses common in the lowland Neotropics. They showed that previously described phytoliths produced in cobs and fruitcases (Bozarth, 1993; Mulholland, 1993; Piperno and Pearsall, 1993), called wavy-topped and ruffle-topped rondels (rondels are often circular to oval or square) are diagnostic of maize and *Zea* (maize/teosinte), respectively, in the Neotropical lowlands (Fig. 2). Blind-testing of their protocol showed that there was little chance of mis-identifying wild grass phytoliths as maize cob bodies, although wavy-top rondels may be under-identified (Pearsall et al, 2003). Logan et al. 2012 subsequently examined phytolith production in leaf and inflorescence material of numerous species from all grass genera native to the Andes above 3000 m. and found considerable overlap occurs between some rondel types produced in maize cobs and those produced in grasses of this high elevation region. Two phytolith morphotypes were found to be unique in maize glumes and cupules in this setting; the ruffle top rondel, and a new diagnostic, the narrow elongate rondel.

A number of other types of fruitcase phytoliths are diagnostic of teosinte (Piperno and Pearsall, 1993; Pearsall et al., 2003, Piperno, 2006:60-65) (Fig. 3). *Tripsacum* species produce their own set of unique fruitcase phytoliths diagnostic to the genus (Fig. 4) (Piperno and Pearsall, 1993; Piperno, 2006:61). A recent study using multiple discriminant analyses of rondel phytoliths also showed that the different species and sub-species of teosinte can be discriminated,
which will potentially enhance understanding of teosinte use before domestication when appropriately-aged sites are found (Hart et al., 2011).

2.2 Squashes and gourds of Cucurbita and other Cucurbitaceae

As with maize, squashes and gourds of the genus *Cucurbita* and other Cucurbitaceae genera were major early cultivars and domesticates of the Americas, were spread considerably outside their areas of origin, and produce phytoliths of high utility in archaeological documentation of their history. Six different species ranging from eastern North America to southern South America were domesticated in prehistory, and phytolith research points to an early Holocene domestication of species native to the lowland Neotropics of Mesoamerica (*C. argyrosperma*) and northern South America (*C. moschata* and *C. ecuadorensis*; the latter was probably semi-domesticated) (Piperno and Stothert, 2003; Piperno et al., 2009, Piperno, 2011). Many parts of the plants make high amounts of phytoliths; those derived from fruit rinds are the most diagnostic and are well-preserved over long periods of time. Intensive studies of different regional floras of the Americas including the Cucurbitaceae show that *Cucurbita* fruit rinds produce genus and, probably in some cases, species-specific phytoliths (see Piperno, 2006:65-66). They are spherical, aspherical, or elliptical forms with deeply and contiguously scalloped surfaces (Fig. 5) (Bozarth, 1987, 1992; Piperno, 2006:65-71, Piperno et al., 2000, 2002; Pearsall, 2015b). As with maize and teosinte, the formation of these fruit phytoliths is genetically controlled by a gene called *hard rind* (*Hr*) that also underwrites fruit lignification (Piperno et al., 2002).

Size and/or morphology are used to discriminate between wild and domesticated *Cucurbita* species. Domesticated fruits often have much larger and thicker phytoliths than their wild ancestors and other wild squashes and there is a significant relationship between fruit size and
phytolith length (Piperno, 2006: 68-69 and Figs. 3.7 a-c therein). Thus, as with macro-remain
analysis phytolith size can be a straightforward discriminator between wild and domesticated
Cucurbita. Studies of modern fruits undertaken to date also suggest that species-specific
identifications will sometimes be possible based on morphological attributes. Examples are C.
maxima, another South American domesticate, and its wild progenitor C. maxima subsp.
andreae, and varieties of C. moschata (Piperno, 2006:67 and Figs. 3.6 d-f therein, Piperno et
al., 2000).

A potentially complicating factor in searching for Cucurbita phytoliths in ancient contexts is
that because prehistoric farmers sometimes selected for softer fruits over time, and the Hr gene
controls both hardness (lignification) and phytolith formation, soft-rinded fruits will have left a
slim or no phytolith record. This particularly appears to be the case for deposits dating to the last
4000 to 5000 years of prehistory or so (Piperno, 2006:143-144). On the other hand, all wild
Cucurbita species, possessing the dominant Hr gene for lignification/silicification, have very
hard rinds with high amounts of scalloped phytoliths, and should be visible if they were
exploited. As with maize, numerous archaeological phytolith records exist for early domesticated
Cucurbita spp. and their spread throughout the Americas (e.g., Piperno and Pearsall, 1998b;
Piperno et al., 2000; Hart et al., 2003, 2007; Iriarte et al., 2004; Pearsall, 2003; Piperno and
Stoithert, 2003; Pohl et al., 2006; Bozarth et al., 2009; Piperno et al., 2009; Dickau et al., 2012;
Corteletti et al., 2015).

Bottle gourd (Lagenaria siceraria) is indigenous to Africa from whence it spread to other
continents by the early Holocene. Its large, scalloped phytoliths from fruit rinds can be identified
through morphological attributes to species in the Americas (Fig. 6) (Piperno, 2006:71; Pearsall
et al. 2015b) and have been recovered from early Holocene-aged and later deposits in Central and South America (e.g., Piperno and Stothert, 2003, Piperno et al., 2009; Piperno, 2011).

2.3 The Tropical Root Crops: Maranta and Calathea (arrowroot and llerén, Marantaceae); Canna (achira, Cannaceae); manioc (Manihot esculenta, Euphorbiaceae)

These crops, grown for their underground roots, rhizomes, tubers, and corms, are, with the exception of manioc, minor root crops today. However, phytolith evidence has shown they had greater importance in prehistory (below). The Zingiberales (Marantaceae and Cannaceae) overall are abundant phytolith producers, and order, family, genus, and species level diagnostics are present (Piperno 1989, 2006; Chen and Smith, 2013; Chandler-Ezell et al. 2006; Pearsall, 2015b). An important class of silicified epidermal cells are complex cylindrical phytoliths produced in seed and root epidermis of the Marantaceae. Calathea allouia seeds produce one type of diagnostic cylinder, other diagnostic forms are produced in Maranta arundinacea seeds and Calathea rhizomes (Figs. 7, 8). While not as abundantly produced as Marantaceae leaf phytoliths, seed and root phytoliths of this family are fairly robust and have been recovered archaeologically. Canna produces the type of sphere characteristic of the Zingiberales as a whole—a robust form with an irregularly angled/folded surface—while large (> 12 µM), well-silicified spheres with smooth to slightly roughened surfaces (not rugose) have only been observed in Canna (Pearsall, 2015b).

Manioc, one of the major root crops of the Americas, has long been known to be a low silica accumulator (Piperno, 1988). By processing large quantities of tissues, Chandler-Ezell et al. (2006) were able to document the presence of silicified secretory bodies (resembling pores or nectaries) in manioc root rind, leaf, stem, and fruit. These occurred rarely in one wild species tested, M. hunzikerii. Manioc secretory phytoliths were subsequently recovered from
pounding/grinding stones from the Real Alto site (ca. 6000 to 5000 cal BP), in association with
silicified transport tissues of roots and fruits, maize starch and phytoliths, and microfossils of
arrowroot, *Calathea*, and *Canna* (Chandler-Ezell et al., 2006). A phytolith matching the
description of a manioc secretory cell was recovered from the raised fields of Campo España,
western Llanos de Moxos, Bolivia (R. Dickau, pers. comm.). Ecuadorian and Panamanian pre-
ceramic deposits dating from ca. 9000 to 7000 BP frequently contain phytoliths from arrowroot
and ilerén, indicating these now-minor root crops were significant components of early
horticultural systems in the Neotropics (Piperno, 2011).

3. Crops of Southwest Asia

3.1 *Triticum* and *Hordeum* spp. (Wheat and Barley)

Wheat and barley species are heavy silica accumulators that produce many phytolith
morphotypes. Morphotypes produced by silicification of epidermal cells such as short cells, long
cells, cork cells, papillae, trichomes, and trichome bases are the most characteristic and
diagnostic for the taxa, as well as the most often observed in archaeological samples (Figs. 9-11).
Both morphotypic and morphometric studies have been conducted to name, describe and
discriminate among the phytoliths produced by wheat and barley taxa. Morphotypic studies
include Kaplan et al. (1992), Mulholland and Rapp (1992), Rosen (1992), Tubb et al. (1993), and
Ball et al. (1993, 1999, 2001, 2009). Morphometric studies include Tubb et al. (1993) and Ball et
and barley species at the genus level, and some success at the species level, primarily based on
the morphotypic and/or morphometric differences observed in the short cell (rondel), dendritic,
and/or papilla phytoliths produced by the taxa (e.g. Ball et al., 1999; Rosen, 1992; Tubb et al.,
1993).
Moreover, some features of the anatomy displayed in the medial section of the glume, lemma, and palea epidermal tissue differ between genera of cereals and small-grained grasses. Thus, there is the potential to identify wheat or barley phytoliths and to distinguish them from wild weed grasses by examining the features of multi-cell phytoliths that are produced in the Triticeae. Distinguishing features include a combination of the wave height, amplitude and frequency of the joined dendritic long-cell walls, the size and configuration of the papillae, and the shape of the cork cells (Figs. 9-11). Confidence in these determinations varies by the numbers of characteristics visible on an individual multi-cell phytolith (Rosen, 1992).

Phytoliths produced by wheat or barley are regularly found in archaeological contexts and have been used to make inferences about plant and site use (e.g. Albert et al., 2008; Cabanes et al., 2009; Ishida et al., 2003; Madella et al. 2014; Portillo et al., 2012; Power et al., 2014; Rosen, 2010; Shillito, 2011a; Zhang et al., 2013), about tool and vessel use (e.g. Anderson et al., 2000; Berlin et al., 2003; Hart, 2011; Ma et al., 2014), about irrigation (e.g. Jenkins et al., 2011; Madella et al., 2009; Rosen and Weiner, 1994) and about taphonomy (e.g. Cabanes et al., 2012; Shillito, 2011b).

4. Crops of East Asia

4.1 Setaria and Panicum Millets (Foxtail and Broomcorn millets)

Phytoliths from the genus Setaria and Panicum are highly useful for identifying Setaria italica (foxtail millet), Setaria viridis (green foxtail) and Panicum miliaceum (common or broomcorn millet) and documenting the earliest history of domesticated millets in Eurasia (García-Granero, et al., 2015; Lu, et al., 2009a, b; Zhang, et al., 2011, 2013). Research carried out by Lu et al. published recently has established five key, efficient diagnostic characteristics for distinguishing phytoliths from S. italica and P. miliaceum (Table 2) (Lu et al., 2009a). They
include: silica body shape, papillae characteristics including presence/absence, epidermal long cell patterns, and glume surface sculpture.

Cross-shaped silica body phytoliths are formed in the lower lemma and glumes of *S. italica*, whereas bilobate shapes are formed in those of *P. miliaceum*. However, bilobates are not diagnostic to *P. miliaceum*. Regularly arranged papillae on the surface of the upper lemma and palea are diagnostic of *S. italica*. However, it should be cautioned that the identification of *P. miliaceum* cannot be confirmed based solely on the absence of papillae, because papillae may sometimes not be visible on the smooth surfaces of upper lemmas and paleas in *S. italica*.

With respect to epidermal long cells, the epidermal long cell walls are $\Omega$-undulated ($\Omega$-I, II, III) in *S. italica*, and $\eta$-undulated ($\eta$-I, II, III) in *P. miliaceum* (Figs. 12 a, b). The different undulated patterns occur at different parts through gradual change from base and top ($\Omega/\eta$-I), to side ($\Omega/\eta$-II), and to center ($\Omega/\eta$-III) of the silicified structure. The ends of epidermal long cells can also be divided into a wavy type in *S. italica* and a finger type in *P. miliaceum* (Fig. 12 c, d). The former is significantly shorter than the latter ($W=4.37 \pm 0.89 \mu M (N=2774)$ vs. $W=8.95 \pm 2.02 \mu M (N=3303)$). Therefore, the R value (ratio of the width of endings to the amplitude of undulations) is lower in *S. italica* ($0.33 \pm 0.11, N=2774$) than in *P. miliaceum* ($0.79 \pm 0.12, N=3303$). With respect to surface sculpture, a ridgy line sculpture type of the upper lemma of the glume is diagnostic of *S. italica*, which is characterized by having an adnate silicon extracellular sheet and outer epidermis, forming a very heavy silicon layer that is a reliable feature in distinguishing them from *P. miliaceum*. In contrast, *P. miliaceum* has a unique smooth, spotted sculpture with an adnate silica extracellular sheet and outer epidermis, or a saw-toothed sculpture with an adnate silicon outer epidermis and hypodermal fibres.
In practical terms, the ideal archaeological sampling contexts for these and other cereal husks are storage and other pits, where phytoliths are more abundant than in other contexts. In order to obtain a clear outline of phytolith patterns, phase-contrast and microscopic interferometer at 400× magnification are highly recommended. For identification, the undulated patterns and epidermal-ending characteristics are the most effective features for identification, because they are clearly present in almost every glume sample examined. Indeed, epidermal endings are easily divided into wavy and finger types and these combined with undulated patterns permit accurate identification without the measurement of the W and R value in most cases.

Differentiating crop phytoliths from their Panicoid weedy wild relatives in archaeological contexts can present challenges due to similarities of identifiable Panicoid husk morphotypes, and large pristine sheets of identifiable multicellular aggregations that identification criteria listed above are, in part, based on are sometimes rare. Having strict identification criteria as described here is essential.

Moving to the discrimination of *S. italica* and its wild ancestor, *S. viridis*, using phytoliths, the focus shifts to the size of phytoliths in the upper lemma and palea. It is established through a study carried out by Zhang *et al.* (2011) that the size of the ΩIII type of *S. italica* is larger than that from *S. viridis*. This means the difference between the two species is predicated on the width/expansion of the lemma and palea, also resulting in a visible difference of phytolith morphology at the center of lemma and palea, where silicified epidermal long cells are most complex, but can be differentiated. The discriminant function analysis accurately classifies a significant majority of the plants, 78.4% of foxtail millets and 76.9% of green foxtails. However, about 25% data are incorrectly classified. More samples should be analyzed to detect the presence of other potentially diagnostic features. Morphological and basic morphometric studies
of glumes of other minor millets also show the potential of phytoliths for differentiating these important crops in the prehistory of Eurasia and Africa (below) (Madella et al., 2014).

4.2 Oryza sativa (Rice)

Phytoliths have played a very important role in the identification of rice remains recovered from archaeological sites. In the past two decades, a number of identification criteria have been used. To date, three distinct phytolith morphotypes have been identified: double-peaked glume cells from the rice husk, bulliform (fan-shaped or motor cell) phytoliths from bulliform cells in leaves, and articulated bilobate phytoliths from stems and leaves (Fujiwara, 1976, 1993; Lu et al., 1997; Pearsall et al., 1995; Piperno, 2006; Wang and Lu, 1993; Zhao et al., 1998; Zheng, et al., 2003; Gu et al., 2013).

Double-peaked glume cell phytoliths (Fig. 13) are unique to the genus Oryza and can separate domesticated rice from the nine wild rice species of South and Southeast Asia based on linear discriminant function analysis of three glume cell measurements (Pearsall, et al., 1995, Zhao and Piperno, 2000, Zhao, 1998, Zhao, et al., 1998). A recent study carried out by Gu et al. showed that three-dimensional measurements of double-peaked glume cells can also successfully distinguish cultivated from wild Oryza species (Gu, et al., 2013).

Bulliform cell phytoliths are produced in high quantity in stems and leaves, and like glume phytoliths may be common in sites (Wang and Lu, 1993). Their morphological features appear to be under genetic control and therefore directly reflect taxonomical significance (Gu, et al., 2013, Zheng, et al., 2003). In the past two decades, morphological features including surface ornamentations have been employed to distinguish domesticated from wild rice using these phytoliths (Fig. 14) (Lu et al., 2002; Ma and Fang, 2007; Huan et al., 2014). Pearsall, et al., (1995) found that bulliform size alone could not distinguish rice from related species. Lu et al.
(2002) studied the number of scale-like ornamentations at the edge of bulliform phytoliths from seven species of wild rice and six species of domesticated rice and found the number of scale-like decorations in wild species is less than 9, while 8 to 14 are present in domesticated rice. This feature as a distinctive characteristic of cultivated rice needs further validation (Qin, 2012; Wang and Lu 2012); however, to date, phytoliths with greater than 9 scale-like decorations are widely used signatures of domestication (Lu et al., 2002; Wu et al., 2014) (Fig. 14). According to this criterion, recent studies indicate that rice domestication began around 10,000 BP in the Lower Yangtze, China (Wu et al., 2014).

Bilobates with scooped ends and a parallel arrangement in leaf tissue are typical of the genera in the Oryzeae tribe, in contrast to the characteristic features of Oryza plants (Pearsall et al., 1995; Lu, et al., 1997; Xiujia et al., 2014). Pearsall et al. (1995) and Gu et al. (2013) showed that this bilobate was produced by all members of the tribe, and cannot be used to distinguish any one genus, including Oryza.

Phytoliths can also be used as a tool for understanding the development and spread of rice (Oryza sp.) arable systems using arable weed ecologies. Different proportions of crop weeds appear in different field systems and the ratios of phytolith morphotypes in soils from these fields reflect this. Modern analogues were created from sediment samples from traditionally farmed fields using correspondence analysis (Canoco) to demonstrate the constituents of the samples, groups of phytolith morphotypes, from different field types reflect their arable system. When applied to archaeological samples the results demonstrate changing farming practices over time (Fuller and Weisskopf, 2011; Weisskopf et al., 2014).

The development of water management in rice farming can be seen using ratios of specific phytoliths from grass weeds in rice fields (Weisskopf et al., in press). Ratios of phytolith
morphotypes that are genetically predisposed to take up silica in grasses (short cells) to those that take up water under circumstances of greater transpiration (long cells and stomata) (Madella et al, 2009, Jenkins et al 2011) were used to develop a wet versus dry index on samples from traditionally farmed modern rice fields. This method was applied to phytoliths assemblages collected from palaeosols and the corresponding archaeological sites in the Lower Yangtze Valley. The results show a change from probable decrue farming on the river’s edge at Tianluoshan (4800-4300BC) to small drier dugout fields at Caoxieshan (3950-3700BC) to large managed irrigated fields at Maoshan (3000-2300BC) (Weisskopf, et al. in press).

5. Crops of Southern and Southeast Asia

5.1 Musa spp. (true bananas)

The domestication and spread of true bananas belonging to the genus Musa is a complicated issue. Domesticated bananas derive from the Eumusa (Musa acuminata [AA] and M. balbisiana [BB]) and Australimusa (M. maclayi) sections of Musaceae. Domestication appears to have involved intra and interspecific hybridization, polyploidyization and somaclonal mutations, ending in seed sterility and parthenocarpy (De Langhe et al., 2009). Accordingly, phytoliths produced by the Musaceae sections Eumusa and Australimusa have great relevance in archaeological research. Humans likely spread domesticated Eumusa throughout the tropics. Archaeological evidence for bananas helps researchers make inferences about crop diffusion and how people in antiquity managed plant resources in tropical rainforests. Outside Asia, any evidences for Musa phytoliths are indicative of cultivation (Vrydaghs and De Langhe, 2003). Phytoliths can be produced in various plant tissues and organs of bananas (e.g., Lentfer, 2009a; Chen and Smith, 2013) with seed and leaf phytoliths being the most studied to date. In archaeological contexts, finding both seed and leaf phytoliths together may indicate an early
phase of domestication, while finding only leaf phytoliths could indicate a latter phase. Lentfer (2009) and Perrier et al. (2011) discuss and illustrate several seed phytolith morphotypes and conclude that they are diagnostic at the genus, section, and sometimes seed levels for Musaceae (Figs. 15, 16). Lentfer (2009a) further discusses other globular and polygonal morphotypes produced in various plant parts and uses morphometric analysis to separate those produced in seeds from those produced in other plant organs and tissues.

In leaves, silicification of cells surrounding the vascular tissue of *Musa* and *Ensete* species produces volcaniform (volcano shaped) phytoliths (Ball et al., 2006) (Fig. 17). Both morphotypic (Ball et al., 2006; Lentfer and Green, 2004; Mbida et al., 2001; Vrydaghs et al., 2009; Wilson, 1985) and morphometric studies (Ball et al., 2006; Lentfer, 2009a; Vrydaghs et al., 2009) have been conducted to distinguish among the volcaniform phytoliths produced by different *Musa* and *Ensete* species. These phytoliths can be discriminated at the genus level allowing bananas to be distinguished from the ensets in archaeological records (Lentfer, 2009a; Mbida et al., 2001), but reliable identification at the species level is still wanting.

Archaeological evidences for *Musa* phytoliths have been recently summarized by Donohue and Denham (2009), with the earliest evidence for banana cultivation at Kuk Swamp in highland New Guinea, dated at 7000-6500 years ago (Denham et al., 2003). This suggests an early and long process of domestication of *M. acuminata* ssp. *banksii* in the area. Archaeological evidence of Musaceae in Melanesia (Horrocks et al., 2009; Lentfer et al., 2010), in Polynesia (Khan et al., 2014), and early evidence (from 5000 BP) in Southeast Asia falls within the natural range of several wild banana species (Kealhofer, 2003) making it difficult to disentangle cultivation versus exploitation of wild plants, but later evidence in east Asia seems to suggest human agency (Zhao and Piperno, 2000). The earliest findings in South Asia are from sites of the greater Indus
Valley at Loteshwar (3681 to 2243 cal BC) in North Gujarat, India (García-Granero et al., 2015) and the Mature Harappan levels (2500-1900 BC) of Kot Diji, Pakistan (Fuller and Madella, 2002). The evidence is scant and may actually highlight contacts (trade) with the Western Ghats to the south more than local cultivation. Cameroon Nkang evidence represents, with all probability, the dispersal of cultivars to West Africa by at least 2500 years ago (Mbida et al., 2001).

6. Crops of Africa

6.1 Ensete ventricosum (Ethiopian banana, Abyssinian banana), Lagenaria siceraria (bottle gourd), Sorghum bicolor (sorghum), Pennisetum glaucum (pearl millet)

Crop plants native to Africa have seen the smallest amount of focused research. *Ensete ventricosum* was domesticated in antiquity in the eastern highlands of Africa for its starchy stem and is an important crop today. The genus has a pantropical distribution. Its phytoliths have been studied largely as parts of analyses to compare and distinguish them from those of *Musa* spp. (see above), and it indeed appears that *Ensete* can be identified to at least the genus (Figs. 15, 17). Work is needed to determine if wild and domesticated species can be distinguished. Another crop of African origin is the bottle gourd. It can be identified to species in American contexts, where wild varieties are not native (see above under New World). Work is needed on wild *Lagenaria* in Africa and Asia to determine if wild and domesticated varieties can be discriminated.

A handful of recent studies has outlined phytolith production in inflorescences of African domesticated grains and their wild progenitors (Logan 2012; Madella et al., 2013; Novello and Barboni 2015; Radomski and Neumann 2011). However, with only one study on phytolith production in the inflorescences of wild grasses (Novello and Barboni 2015), there is still...
considerable work to do vis-à-vis isolating specific morphotypes diagnostic to the genus or species level. Consequently, most Africanist phytolith researchers favor quantitative or semi-quantitative methodologies that take into account multiple phytolith forms for strong positive identifications.

The most promising potential for identification using phytoliths appears to be *Sorghum bicolor*, likely domesticated relatively late (c. 2000 years ago), but probably used in a wild but cultivated form many millennia earlier. Of special diagnostic interest is heavily silicified elongate dendritic cell forms described by several authors (Novello and Barboni 2015; Radomski and Neumann 2011; Logan and D’Andrea 2008 in Logan 2012: 96-100; Madella et al., in press).

These forms appear to be quite distinctive, occur in some quantity in domesticated sorghum inflorescence (36.9% of all phytoliths), but are uncommon in wild sorghum or other grasses studied to date (Radomski and Neumann 2011:157). In addition, one complex short cell form, with a bilobate to rondel base and saddle-like top may be distinctive to *Sorghum bicolor* (Radomski and Neumann 2011). Since very little comparative work on wild African grass inflorescences has been completed, it is difficult to establish at what level these forms are diagnostic, but early results look very promising.

Pearl millet (*Penniseum glaucum*) is the oldest domesticated crop on the continent (~4500 bp; Manning et al., 2011), yet little is known about phytolith production in this important crop (see Radomski and Neumann, 2011 for a discussion).

**7. Discussion**

Phytolith analysis has substantially contributed to study and understanding of agricultural origins and dispersals around the world. Genus- or species-level identifications are routinely achieved for crop plants, and when a crop is found outside of the natural distribution of it and its...
closest wild relatives (as, for example, maize in South America and eastern North America and
tropical Africa), genus-level identification alone serves the purpose of securely identifying it.
Research by numerous investigators over decades summarized here has, therefore, made it
possible to develop consensus identification criteria for archaeobotanists to employ and for other
scholars to bring to bear in formulating broad conceptual and synthetic works. A recent paper, in
fact, that reviews potential starting dates for the onset of the proposed new geologic epoch, the
Anthropocene, defines phytoliths as one of two primary stratigraphic markers and one of a few
potential auxiliary stratotypes for the origin and expansion of farming globally (Lewis and
Maslin, 2015). Phytoliths are also named as a stratotype marker for Lewis and Maslin’s (2015)
suggested choice of the event that would mark the Anthropocene beginning, the “New-Old
World Collision” at the date of 1610.
Phytoliths can and have served a number of different roles in agricultural origin and dispersal
research: 1) as stand-alone markers of cultivation and domestication, 2) complementary avenues
of plant identification in multi-proxy research, 3) identifiers at more refined taxonomic levels
than possible with other fossil markers, or of taxa and plant structures often not visible with other
fossils, 4) markers of crop presence and human environmental modification in paleo-ecological
records, 5) markers of range expansions of crops and other plant taxa. Increasingly, phytolith and
starch grain analyses are being used in tandem in many regions of the world, significantly
increasing the recoverability of a number of New and Old World crop species, including major
root crops, that leave slim or no phytolith records, and allowing finer discrimination of others,
along with identifications of different structures of the same crop (a few examples are Chandler
et al., 2006; Zarillo et al., 2008; Duncan et al., 2009; Lentfer, 2009b; Piperno, 2009, et al., 2009;
Boyd and Surette, 2010; Dickau et al., 2007, 2012; Yang et al., 2012a, b, 2014; Liu et al., 2011;
Iriarte et al., 2012; Madella et al., 2014; Barton and Torrence, 2015; Corteletti et al., 2015; García-Granero et al., 2015) (see Table 1 for crop plants and wild progenitors known to have diagnostic starch grains). As with other fossil indicators of plant exploitation and agriculture such as macro-remains of seeds and their chaffs (e.g., Wilcox, 2007; Fritz and Nesbitt, 2014), the taxonomic levels to which phytolith identification can be made will differ from species to species, and at times the separation of important taxa will not be possible. There are also many crops and wild progenitors for which phytolith analysis may not turn out to be of significant utility, although further work is needed on many.

Issues such as phytolith formation, taphonomy, and preservation, encompassing initial phytolith production in plants and their subsequent depositional and post-depositional histories are not the foci of this paper. These aspects have been well-considered elsewhere and the reader can consult a number of reviews summarizing information accumulated from numerous studies on crop and other plants from around the world (e.g., Pearsall, 2000, 2014, 2015a; Piperno, 1985, 1988, 2006; Madella et al., 2009; Madella and Lancelotti 2012). Briefly, the following points can be made. With regard to phytolith formation, genetic control of phytolith formation is demonstrated in a number of crops and their wild ancestors, including Cucurbita (fruit rinds), Zea (fruitcases and cobs), Oryza (leaves and probably glumes), and also wheat awns (Dorweiler and Doebley, 1997; Piperno et al., 2002; Zheng et al., 2003; Ma et al., 2006, 2007; Peleg et al., 2010; Gu et al., 2013). This means that the visibility of these phytoliths in archaeological sites should not have been biased by environmental variability. In other crop/wild ancestor pairs where production of individual phytoliths has not to this point been linked to specific genetic loci, studies of different populations from different environmental regions demonstrate that phytoliths used in identification are both consistently produced in modern flora and commonly
recovered from archaeological sites. In sum, these and other studies indicate a considerable
degree of genetic and metabolic control over the mechanisms and patterns of silica deposition
(e.g., Hodson et al., 2005; Piperno, 2006; Madella et al., 2009; Tsartsidou et al., 2007; Pearsall,
2014).

Investigations of infraspecific variability in phytolith formation also document which
phytolith types do appear to be significantly affected by environmental factors such as water
availability and bedrock chemistry, such that particular morphotypes are/are not produced in
certain environments, or formed in such low amounts that they would be difficult to recover
(e.g., Piperno, 2006; Madella et al., 2009; Tsartsidou et al., 2007). Phytoliths involved (e.g., from
jigsaw-shaped epidermal phytoliths of woody taxa; long epidermal cells of grass leaves) are not
usually among the corpus of silicified forms used in crop identification and discussed herein. As
discussed above, in wheat, barley, and rice an increased silicification of long epidermal cells in
their husks in well-watered conditions provide a means to investigate ancient irrigation and water
regimes.

Other issues such as depositional and post-depositional histories, including preservation and
downward phytolith movement in soils and sediments, have seen detailed investigation, in part
by crop plant researchers who have taken into account and controlled for these factors (a few
studies and reviews include Harvey and Fuller, 2005; Piperno, 1985, 1988, 2006; Fishkis et al.,
2009, 2010; Madella, et al., 2009, Madella and Lancelotti 2012; Devos et al., 2013; Pearsall
2014, 2015a; Cabanes et al., 2015). It is well-understood, for example, that phytoliths follow the
biogenic silica curve for erosion and dissolution, so that when the pH exceeds a value above
about 9--an unusual circumstance in archaeological contexts that did not influence records
discussed here--some phytolith corrosion and dissolution may at times be expected (see reviews
in Piperno, 1988:46-47 and Piperno, 2006:22, 108, and recent experimental work by Cabanes et al., 2015). Other recent efforts combining phytolith analysis with micromorphology also serve to address the various issues outlined (Vrydaghs et al., this issue).

The utility of phytoliths for investigating agricultural origins and dispersals around the world is clear and despite the considerable range of crop examples and geographic regions heretofore investigated, possibilities for future expansions of research are many. Moreover, micro-fossil assemblage composition and distribution can provide information about currently under-investigated domestication processes related to crop improvement in prehistory, such as the development of parthenocarpy (seedless fruits) and of new crop varieties in general. Phytolith (and starch) studies are complementary to all aspects of archaeological investigation aimed at understanding agricultural origins, and given well-proven and potential outcomes we should now be at a stage where such studies are incorporated into broader archaeological framework as a matter of routine research.

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28


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Zhao, Z.J., 1998. The Middle Yangtze region in China is one place where rice was domesticated: phytolith evidence from the Diaotonghuan Cave, Northern Jiangxi. Antiquity 72, 885–897.


Figure Captions

Fig. 1. Typical cross-shaped phytolith three-dimensional structures from maize, teosinte, and non-Zea grasses. Maize produces high proportions of Variant 1 (mirror-image) cross-shapes while many wild grasses produce high proportions of other types unlike maize. Balsas teosinte, maize’s wild progenitor, produces many Variant 2 cross-shapes in its leaves unlike maize. From Piperno, 2006.

Fig. 2. Wavy-top (top, bottom left) and ruffle-top rondels (bottom, right) from maize. Ruffle-top rondels occur much more frequently in teosinte than maize. From Piperno, 2006.

Fig. 3. The various kinds of non-rondel phytoliths found in teosinte fruitcases. Those diagnostic of teosinte are in the center (a, oblong, one-half decorated; b, elongated spiney; c, elongated with one wavy and one serrated edge). Phytoliths a-f occur in some non-Zea grasses, but they like the others are always produced in teosinte and can be used to rule out its presence if absent from samples. The phytoliths range in size from about 10 (phytolith f) to 35 µM in diameter (phytolith b). From Piperno, 2006.

Fig. 4. Tripsacum fruitcase phytoliths. Unlike those of teosinte or maize, they have serrated edges and ridges across the top. From Piperno, 2006.

Fig. 5. Scalloped phytoliths from the domesticated species Cucurbita moschata. Wild squash phytoliths have the same morphology but are often much smaller than in domesticates. From Piperno, 2006.

Fig. 6. Scalloped phytoliths from bottle gourd. Unlike in Cucurbita, scallops are irregularly-shaped and one hemisphere of the phytolith is flat and undecorated. Size ranges from 64 to 112 µM. From Piperno, 2006.

Fig. 7. Seed phytoliths from arrowroot. From Piperno, 2006.
Fig. 8. Seed phytolith from llerén. It is 40 µM long. From Piperno, 2006.

Fig. 9. An articulated aggregation of inflorescence bract phytoliths from Triticum aestivum showing the long cell wave patterns and papillae characteristic of Triticum sp. Photo by Arlene M. Rosen from modern plant phytolith reference collection at ICREA, University of Barcelona, courtesy of Rosa M. Albert.

Fig. 10. An articulated aggregation of inflorescence bract phytoliths from Hordeum vulgare showing the long cell wave patterns and papillae characteristic of Hordeum sp. Photo by Arlene M. Rosen from modern plant phytolith reference collection at ICREA, University of Barcelona, courtesy of Rosa M. Albert.

Fig. 11. Drawing of a papilla. Domesticated grasses have a consistent papilla diameter found throughout the multi-cell, as measured by the outer ring of the papillae, while wild ‘weed’ grass will exhibit a range of papillae diameters. From Piperno, 2006; originally reprinted from Tubb et al. (1993).

Fig. 12. Undulated patterns and ending structures of epidermal long cells in the upper lemma and palea for the two millet species. Ω-undulated pattern (A) and wavy type (C) of ending structure in S. italic; η-undulated pattern (B) and finger type (D) of ending structure in P. miliaceum.

Fig. 13. Double-peaked glume cell phytoliths from Oryza. From Piperno, 2006. Originally re-printed from Zhao et al., 1998.

Fig. 14. Comparison of the scale-like decorations on bulliform phytoliths in domesticated and wild rice. Modified from Fujiwara (1976).

Fig. 15. Seed phytoliths from Musa acuminata subsp. banksii (left) and Ensete, right. From Piperno, 2006; originally courtesy of Carol Lentfer.
Fig. 16. Seed phytoliths from *Musa ingens*. From Piperno, 2006; originally courtesy of Carol Lentfer.

Fig. 17. A comparison of leaf phytoliths from *Ensete* and *Musa*. From Piperno, 2006. The schematic drawings were originally from Mbida Mindzie et al., 2001 and the photographs were courtesy of Carol Lentfer.
**Table 1. Crop Plant Phytolith Production and Levels of Taxonomic Specificity**

<table>
<thead>
<tr>
<th>Plant Part</th>
<th>Plant Phytolith Production</th>
<th>Taxonomic Specificity</th>
<th>Plant Part</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>The Americas</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Zea mays (maize)</strong></td>
<td>Very high</td>
<td>Species</td>
<td>Cob (glume/cupule)</td>
</tr>
<tr>
<td><strong>Zea mays (maize)</strong></td>
<td>High</td>
<td>Species</td>
<td>Leaf</td>
</tr>
<tr>
<td><strong>Zea mays (maize)</strong></td>
<td>Low to moderate</td>
<td>Species</td>
<td>Husk</td>
</tr>
<tr>
<td><strong>Cucurbita spp.</strong>, <em>(squashes and gourds)</em></td>
<td>Very high</td>
<td>Genus and Species Family (Genus?)</td>
<td>Fruit rind</td>
</tr>
<tr>
<td><strong>Lagenaria siceraria</strong>, <em>(bottle gourd)</em></td>
<td>High</td>
<td>Species Family</td>
<td>Leaf</td>
</tr>
<tr>
<td><strong>Siciana odorifera</strong>, <em>(cassabanana)</em></td>
<td>High</td>
<td>Genus</td>
<td>Fruit rind</td>
</tr>
<tr>
<td><strong>Manihot esculenta</strong> <em>(manioc or yuca)</em></td>
<td>Very low</td>
<td>Genus</td>
<td>Most plant parts</td>
</tr>
<tr>
<td><strong>Maranta arundinacea</strong> <em>(arrowroot)</em></td>
<td>Very high</td>
<td>Species</td>
<td>Seed</td>
</tr>
<tr>
<td><strong>Calathea allouia</strong> <em>(llerén)</em></td>
<td>Very high</td>
<td>Species</td>
<td>Seed</td>
</tr>
<tr>
<td><strong>Ananas comosus</strong> <em>(pineapple)</em></td>
<td>Very high</td>
<td>Species</td>
<td>Family</td>
</tr>
<tr>
<td><strong>Canna edulis</strong> <em>(achira)</em></td>
<td>Very high</td>
<td>Genus (?)</td>
<td>Leaf and seed</td>
</tr>
<tr>
<td><strong>Phaseolus vulgaris</strong> <em>(common bean)</em></td>
<td>Moderate</td>
<td>Genus</td>
<td>Pod</td>
</tr>
<tr>
<td><strong>Phaseolus lunatus</strong> <em>(lima bean)</em></td>
<td>Moderate</td>
<td>Genus</td>
<td>Pod</td>
</tr>
<tr>
<td><strong>Helianthus annuus</strong></td>
<td>High</td>
<td>Family (Genus?)</td>
<td>Achene</td>
</tr>
<tr>
<td><strong>Arecaceae (palms)</strong></td>
<td>Very high</td>
<td>Family or subfamily</td>
<td>All parts</td>
</tr>
<tr>
<td><strong>Southwest Asia</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Triticum spp.</strong>(Einkorn, other wheats)</td>
<td>Very high</td>
<td>Genus*</td>
<td>Inflorescence bracts (glumes, lemmas, and paleae)</td>
</tr>
<tr>
<td><strong>Triticum spp.</strong>(Emmer, other wheats)</td>
<td>Very high</td>
<td>Genus*</td>
<td>Inflorescence bracts (glumes, etc.)</td>
</tr>
<tr>
<td><strong>Hordeum spp.</strong>(Barley, other wheats)</td>
<td>Very high</td>
<td>Genus*</td>
<td>Inflorescence bracts (glumes, etc.)</td>
</tr>
<tr>
<td><strong>East Asia</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Oryza sativa</strong> <em>(rice)</em></td>
<td>Very high</td>
<td>Species</td>
<td>Glume</td>
</tr>
<tr>
<td><strong>Setaria spp.</strong>(Foxtail millets)</td>
<td>Very high</td>
<td>Genus**</td>
<td>Glume</td>
</tr>
<tr>
<td><strong>Panicum spp.</strong>(Broomcorn millets)</td>
<td>Very high</td>
<td>Genus**</td>
<td>Glume</td>
</tr>
</tbody>
</table>
Southern and Southeast Asia

| **Musa spp.**<sup>SG-G</sup> (bananas) | High | Genus, Section, Species | Leaf, Seed |
| Benincasa hispida (wax gourd) | Very high | Genus (?) | Fruit rind |
| Cocus nucifera (coconut) | Very high | Family or sub-family | All plant parts |

Africa

| Lagenaria siceraria (bottle gourd) | Moderate | Genus?**** | Fruit rind |
| Ensete ventricosum (Abyssinian or Ethiopian bananas) | High | Genus | Leaf and seed |
| Sorghum bicolor (sorghum) | High | ?see text | Glume |

WA= phytoliths are diagnostic in the wild ancestor. WA? = wild ancestor is unknown, or known but not yet studied for phytoliths. SG = starch grains diagnostic of genus (SG-G), species (SG-S), or tribe (SG-T) occur in the same or other parts of the plants as listed for phytoliths (e.g., Maize kernels; Cucurbita fruit flesh; Phaseolus seeds; arrowroot roots; ilerén roots; wheat, barley, and millet grains; banana fruit flesh). SG? = potentially diagnostic starch but further study is needed. *Hordeum* starch grains have been identified to genus in SW Asia and China. *Setaria* and *Panicum* domesticated millet starch grains may be identifiable to species in some cases. Starch grains from other Old World crops may have considerable promise (e.g., various legumes and root crops). For starch grain references, see Chandler et al., 2006; Zarillo et al., 2008; Duncan et al., 2009; Piperno, 2009, Piperno and Dillehay, 2008, Piperno et al., 2009; Boyd and Surette, 2010; Dickau et al., 2007, 2012; Lentfer, 2009b; Yang et al., 2012a, b, 2014; Liu et al., 2011; Iriarte et al., 2012; Madella et al., 2014; Barton and Torrence, 2015; Corteletti et al., 2015; García-Granero et al., 2015.

*Wild/domesticated wheat and barley phytoliths can be distinguished from each other at the genus level and from common weed genera expected in archaeological contexts in certain regions of southwestern Asia. More work is needed with other wild taxa outside of *Triticum* and *Hordeum* to more broadly apply phytolith identification schemes when congeneric non-cultigens may be present. Certain kinds of domesticated wheats can currently be distinguished from others and from barley using specific types of phytoliths (e.g., papillae) or combinations of them.

**Foxtail and broomcorn millet phytoliths can be distinguished from each other. Further work is needed to develop distinguishing criteria for them and their weedy wild Panicoideae relatives. ***There is a new revision for *Musa* proposed by Häkkinen (2013) on the basis of new molecular data, which has not been used in this review so that the taxonomic names used here are consistent with the published phytolith work cited. In the new revision, the *Rhodochlamys* section was merged into the *Eumusa* section and renamed *Musa*. The *Australimusa* and *Ingentimusa* sections were merged into the *Callimusa* section The new section kept the name *Callimusa* (Häkkinen, 2013).****Bottle gourd has been studied with relation to regional flora in the New World only. African and other Old World research is needed to establish its diagnostic potential there.

See Bozarth, 1990, Piperno, 2006 and Pearsall, 2015b for information on *Phaseolus* pod phytoliths, and Piperno, 2006 for discussions of various palm phytoliths. Cassabanana (*Sicana odorifera*) is a little understood Neotropical domesticate of possible Amazonian origin. Its genus-diagnostic scalloped phytoliths (Piperno, 2006:71 and Fig. 3.7e therein) have not as yet been isolated from archaeological deposits, but further work may elucidate its origins and history. *Benincasa hispida* (the wax gourd) phytoliths appear promising compared to New World Cucurbitaceae but Asian study is needed.
Table 2. Discrimination of *S. italic*a and *P. miliaceum*

<table>
<thead>
<tr>
<th>No</th>
<th>Parts of Spikelet</th>
<th>Diagnostic Criteria</th>
<th><em>Setaria italic</em>a (Foxtail millet)</th>
<th><em>Panicum miliaceum</em> (Common millet)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Lower lemma and glume</td>
<td>Shape of silica bodies</td>
<td>Cross-shaped type</td>
<td>Bilobate-shaped type</td>
</tr>
<tr>
<td>2</td>
<td>Upper lemma and palea</td>
<td>Presence or absence of papillae</td>
<td>Regularly arranged papillae</td>
<td>Smooth surface without papillae</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>The undulated patterns of epidermal long cells</td>
<td>Ω-undulated (Ω-I, II, III)</td>
<td>η-undulated (η-I, II, III)</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>The ending structures of epidermal long cells</td>
<td>Cross wavy type</td>
<td>Cross finger type</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>W</em> = 4.37±0.89 µm</td>
<td><em>W</em> = 8.95±2.02 µm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>R</em> = 0.33±0.11</td>
<td><em>R</em> = 0.79±0.12</td>
</tr>
<tr>
<td>5</td>
<td>Surface sculpture</td>
<td>Surface ridgy line sculpture</td>
<td>Smooth, spotted sculpture or saw-toothed sculpture</td>
<td></td>
</tr>
</tbody>
</table>
Leaf Cross-shaped bodies 3-D Variants

<table>
<thead>
<tr>
<th>Var. 1</th>
<th>Var. 2</th>
<th>Var. 3/8/10</th>
<th>Var. 5 and 6</th>
<th>Other Variants</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image" /></td>
<td><img src="image2.png" alt="Image" /></td>
<td><img src="image3.png" alt="Image" /></td>
<td><img src="image4.png" alt="Image" /></td>
<td><img src="image5.png" alt="Image" /></td>
</tr>
<tr>
<td>Mirror-image Maize</td>
<td>Tent-like arch Balsas Teosinte Many non-Zea grasses</td>
<td>Nodules/Blocky Bambusoideae</td>
<td>Sloping Trapezoids/Rectangular Many non-Zea grasses</td>
<td>Scooped/Concave/Other Bambusoideae/Brachypodioideae/Pooideae</td>
</tr>
</tbody>
</table>


Domesticated rice

Wild rice

scale-like decorations

40 μm
Experts from around the world who have carried the hands-on work reviewed the utility and importance of phytolith analysis in investigating agricultural origins and dispersals.

Phytoliths have been and will continue to be of significant, often unique, importance for this fundamental topic.