Accepted Manuscript

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

Terry Ball, Professor, Karol Chandler-Ezell, Neil Duncan, Ruth Dickau, Thomas C. Hart, Jose Iriarte, Professor of Archaeology, Carol Lentfer, Amanda Logan, Houyuan Lu, Marco Madella, Deborah M. Pearsall, Professor Emerita, Dolores Piperno, Senior Scientist Emerita, Arlene M. Rosen, Professor, Luc Vrydaghs, Alison Weisskopf, Jianping Zhang

Please cite this article as: Ball, T., Chandler-Ezell, K., Duncan, N., Dickau, R., Hart, T.C., Iriarte, J., Lentfer, C., Logan, A., Lu, H., Madella, M., Pearsall, D.M., Piperno, D., Rosen, A.M., Vrydaghs, L., Weisskopf, A., Zhang, J., Phytoliths As a Tool for Investigations of Agricultural Origins and Dispersals Around the World, *Journal of Archaeological Science* (2015), doi: 10.1016/j.jas.2015.08.010.

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

2   World*

3   Terry Ball[1], Karol Chandler-Ezell[2], Neil Duncan[3], Ruth Dickau[4], Thomas C. Hart[5], Jose Iriarte[6],

4   Carol Lentfer[7], Amanda Logan[8], Houyuan Lu[9], Marco Madella[10], Deborah M. Pearsall[11],

5   Dolores Piperno[12], Arlene M. Rosen[13], Luc Vrydaghs[14], Alison Weisskopf[15], Jianping Zhang[9]

6

7   [1.] Professor, Brigham Young University; [2.] Dept. Social & Cultural Analysis, Stephen F. Austin

8   State University, LAN 351, P. O. Box 13047, SFA Station, Nacogdoches, TX 75962-3047;

9   [3.] Stanford Archaeology Center & Dept. of East Asian Languages & Cultures; [4.] HD Analytical

10   Solutions, 952 Oxford St. West, London, ON, Canada, N6H 1V3; [5.] Environmental Archaeology

11   Laboratory, Anthropology Department, University of Texas at Austin; [6.] Professor of

12   Archaeology, Department of Archaeology, Exeter University, England; [7.] School of Social

13   Science, University of Queensland, Brisbane St Lucia, QLD 4072, Australia and Service de

14   Préhistoire, Department des Sciences Historiques, University de Liège, 4000 Liège, Belgium; [8.]

15   Department of Anthropology, Northwestern University, Evanston, IL, 60208 USA, [9.] Key

16   Laboratory of Cenozoic Geology and Environment, Institute of Geology and Geophysics,

17   Chinese Academy of Sciences, Beijing 100029, China; [10.] ICREA Research Professor in

18   Environmental Archaeology, CaSEs Research Group (Complexity and Socio-Ecological

19   Dynamics), Universitat Pompeu Fabra and IMF-CSIC, Spain; [11.] Professor Emerita, University

20   of Missouri, Columbia; [12.] Senior Scientist Emerita, Smithsonian Tropical Research Institute,

21   Panama and Department of Anthropology, Smithsonian National Museum of Natural History,

22   Washington DC; [13.] Professor, Department of Anthropology, University of Texas at Austin;

23   [14.]Centre de Recherches en Archéologie et Patrimoine, Université Libre de Bruxelles, Brussels,

24   Belgium and Research Team in Archaeo and Paleoenvironmental Sciences, Brussels; Belgium;

25   15. Institute of Archaeology, University College London

26   Corresponding author: Dolores R. Piperno, email pipernod@si.edu

27   *Author listing is alphabetical; all co-authors contributed equally to the manuscript.

28   **Abstract**

29   Agricultural origins and dispersals are subjects of fundamental importance to archaeology as

30   well as many other scholarly disciplines. These investigations are world-wide in scope and

31   require significant amounts of paleobotanical data attesting to the exploitation of wild

32   progenitors of crop plants and subsequent domestication and spread. Accordingly, for the past

33   few decades the development of methods for identifying the remains of wild and domesticated

34   plant species has been a focus of paleo-ethnobotany. Phytolith analysis has increasingly taken its

35   place as an important independent contributor of data in all areas of the globe, and the volume of

36   literature on the subject is now both very substantial and disseminated in a range of international

37   journals. In this paper, experts who have carried out the hands-on work review the utility and

38   importance of phytolith analysis in documenting the domestication and dispersals of crop plants

39   around the world. It will serve as an important resource both to paleo-ethnobotanists and other

40   scholars interested in the development and spread of agriculture.

41   Keywords: Phytoliths, Crop Plants, Diagnostic Criteria

42   **1. Introduction**

43   The domestication of plants and development and spread of agriculture were transformative

44   events in human and ecological history. Present records show that beginning around 11,000 to

45   10,000 years ago plant cultivation and domestication developed independently in at least seven

46   to eight regions of the world, shortly after spreading into others (Larson et al., 2014).

47   Understanding agricultural origins through archaeological enquiry is of fundamental importance

48   for a diversity of scholarly disciplines in addition to anthropology, including genetics,

49   environmental history, and agronomy. Accordingly, developing methods for identifying the

50   remains of crop plants and their wild progenitors has been a focus of paleoethnobotany during

51   the past 25 years. Phytoliths have increasingly taken their place in these endeavors alongside

52   macro-remains, pollen, and starch grains in all regions of the world (for reviews see Pearsall,

53   2000, 2015a; Piperno, 2006, 2009; Hart, 2014; Marsten et al., 2014). Standardization of

54   identification criteria for various crops and wild ancestors is now accomplished, and on-line

55   resources along with monographs and books containing numerous phytolith images for wide

56   dissemination of criteria used to discriminate taxa are already substantial and growing. Among

57   the web resources are: 1) the Pearsall Neotropical phytolith data base--

58   http://phytolith.missouri.edu, 2) the PhytCore International Data base housed by GEPEG,

59   University of Barcelona and co-ordinated by Rosa Albert and colleagues, which will be a single

60   source with phytolith data bases and images from many scholars around the world—access is

61   through www.archeoscience.com, 3) the Institute of Archaeology, London's web page on Old

62   World phytoliths-- www.homepages.ucl.ac.uk/~tcrndfu/phytoliths.html, and 4) the Department

63   of Archaeology, University of Sheffield (UK) Wiki online tutorial--

64   http://archaeobotany.dept.shef.ac.uk/wiki/index.php/Main_Page. For monographs and books

65   with numerous phytolith images for various world regions also see Piperno and Pearsall, 1998a,

66   Piperno, 1988, 2006, and Kealhofer and Piperno, 1998.

67   The volume of phytolith-related work on prehistoric agriculture along with its appearance in

68   numerous journals published in different countries is such that few archaeologists and other

69   interested scholars may have the time or expertise to keep up with the literature. This paper

70   addresses this issue by reviewing the state-of-the-art of phytolith analysis for documenting the

71   origin and spread of crop plants around the world. Since the last review of the subject (Piperno,

72   2006) new crops have been investigated, refinements of identification techniques for others have

73   taken place, and archaeological applications have expanded. Investigations also now routinely

74   incorporate analysis of numerous wild species related to crop plants, including their wild

75   ancestors when known, as well as constructions of large modern reference collections of regional

76   flora. Table 1 contains a summary of findings from crops and wild progenitors that have been

77   examined in detail (it also contains information on little understood crops not discussed in the

78   text). More information on the phytoliths follows.

79   **2. Crops of the Americas**

80   A number of major and now-minor New World crops contribute phytoliths diagnostic at either

81   the genus or species level, while others contribute forms identifiable at higher taxonomic levels

82   such as the family, sub-family, or tribe.

83   *2.1 Zea mays L. (Maize)*

84   Maize is the pre-eminent cereal crop of the Americas and is now known to be native to the

85   Central Balsas River region of tropical southwest Mexico (e.g., van Heerwaarden et al., 2011).

86   The ability to isolate plant remains and identify maize and teosinte (wild *Zea*) in environments

87   inimical to the preservation of macroremains, which includes maize's homeland, is fundamental

88   to understanding the domestication and early history and spread of this crop. More than three

89   decades of research has demonstrated that maize leaf and cob phytoliths are diagnostic and

90   distinguishable from those of its wild ancestor, the teosinte *Zea mays* ssp. *parviglumis*, and wild

91   non-*Zea* grasses native to North, Central, and South America. Phytoliths will be of high utility in

92   investigations of wild maize use, early stages of domestication, and subsequent spread. Present

4

93   phytolith and starch grain evidence from the Central Balsas region in Mexico indicates maize

94   was domesticated by 8700 cal BP (Piperno et al., 2009; Ranere et al., 2009), and phytolith

95   research has contributed greatly to documenting maize spread and usage throughout the

96   Americas (e.g., Piperno et al., 1985; Pearsall, 2000, et al., 2004; Bozarth, 1993, et al., 2009;

97   Mulholland, 1993; Hart et al., 2003, 2007; Iriarte et al., 2004; Thompson et al., 2004; Piperno,

98   2006:140-153; Zarillo et al., 2008; Boyd and Surette, 2010; Dickau et al., 2012; Iriarte et al.,

99   2012; Logan et al., 2012; Hart and Lovis 2013; Hart 2014; Biwar and VanDerwarker, 2015;

100 Corteletti et al., 2015).

101   Identification criteria employ size and morphology, and as with phytoliths from other crop

102 plants (below), deposition of vegetative and inflorescence structures can be distinguished (leaf,

103 stalk, seed chaff), making the phytoliths potential tools also for examining hypotheses related to

104 teosinte and maize usage in different periods and regions (e.g., whether early cultivation was for

105 alcohol from stalk sugar) (Piperno et al., 2009; Logan et al., 2012; Biwar and VanDerwarker,

106 2015). Size and three-dimensional morphologies of cross-shaped phytoliths from maize

107 distinguish maize from wild grasses other than *Zea* and *Tripsacum* (Pearsall, 1978; Piperno,

108 1984; Piperno and Pearsall, 1993; Iriarte, 2003; Piperno, 2006:52-60) (Fig. 1). Cross-shaped

109 phytoliths also distinguish maize from *Tripsacum* and wild *Zea* if representation of these taxa in

110 phytolith assemblages is ruled out using other phytolith types found in their fruitcases that are

111 diagnostic to genus (below) (Piperno and Pearsall, 1993; Piperno, 2006:60-65).

112   With respect to inflorescence phytoliths, a number of phytolith types in teosinte fruitcases (the

113 hard structure composed of a glume and rachid that encloses the teosinte kernel) and maize cobs

114 separate teosinte from maize (e.g., Piperno and Pearsall, 1993; Pearsall, et al., 2003; Piperno,

115 2006:60-65), and both maize and teosinte from non-*Zea* wild grasses native to the Americas

5

116 (e.g., Bozarth, 1993; Mulholland, 1993; Pearsall et al., 2003; Hart et al., 2003, 2007, 2011;

117 Thompson, 2006; Logan et al., 2012). The formation of these phytoliths is genetically controlled

118 by the major maize domestication gene *teosinte glume architecture 1* (*tga1*), which also

119 underwrites fruitcase hardness (lignification) and the degree to which the kernel is enveloped by

120 the glume (Dorweiler and Doebley 1997; Piperno, 2006:61, 63). The fruitcase and cob phytolith

121 types were formalized by Pearsall et al. (2003), who compared maize and teosinte phytoliths

122 with those from numerous wild grasses common in the lowland Neotropics. They showed that

123 previously described phytoliths produced in cobs and fruitcases (Bozarth, 1993; Mulholland,

124 1993; Piperno and Pearsall, 1993), called wavy-topped and ruffle-topped rondels (rondels are

125 often circular to oval or square) are diagnostic of maize and *Zea* (maize/teosinte), respectively, in

126 the Neotropical lowlands (Fig. 2). Blind-testing of their protocol showed that there was little

127 chance of mis-identifying wild grass phytoliths as maize cob bodies, although wavy-top rondels

128 may be under-identified (Pearsall et al, 2003). Logan et al. 2012 subsequently examined

129 phytolith production in leaf and inflorescence material of numerous species from all grass genera

130 native to the Andes above 3000 m. and found considerable overlap occurs between some rondel

131 types produced in maize cobs and those produced in grasses of this high elevation region. Two

132 phytolith morphotypes were found to be unique in maize glumes and cupules in this setting; the

133 ruffle top rondel, and a new diagnostic, the narrow elongate rondel.

134   A number of other types of fruitcase phytoliths are diagnostic of teosinte (Piperno and

135 Pearsall, 1993; Pearsall et al., 2003, Piperno, 2006:60-65) (Fig. 3). *Tripsacum* species produce

136 their own set of unique fruitcase phytoliths diagnostic to the genus (Fig. 4) (Piperno and Pearsall,

137 1993; Piperno, 2006:61). A recent study using multiple discriminant analyses of rondel

138 phytoliths also showed that the different species and sub-species of teosinte can be discriminated,

139   which will potentially enhance understanding of teosinte use before domestication when

140   appropriately-aged sites are found (Hart et al., 2011).

141   *2.2 Squashes and gourds of Cucurbita and other Cucurbitaceae*

142   As with maize, squashes and gourds of the genus *Cucurbita* and other

143   Cucurbitaceae genera were major early cultivars and domesticates of the Americas, were spread

144   considerably outside their areas of origin, and produce phytoliths of high utility in archaeological

145   documentation of their history. Six different species ranging from eastern North America to

146   southern South America were domesticated in prehistory, and phytolith research points to an

147   early Holocene domestication of species native to the lowland Neotropics of Mesoamerica (*C.*

148   *argyrosperma*) and northern South America (*C. moschata* and *C. ecuadorensis*; the latter was

149   probably semi-domesticated) (Piperno and Stothert, 2003; Piperno et al., 2009, Piperno, 2011).

150   Many parts of the plants make high amounts of phytoliths; those derived from fruit rinds are the

151   most diagnostic and are well-preserved over long periods of time. Intensive studies of different

152   regional floras of the Americas including the Cucurbitaceae show that *Cucurbita* fruit rinds

153   produce genus and, probably in some cases, species-specific phytoliths (see Piperno, 2006:65-

154   66). They are spherical, aspherical, or elliptical forms with deeply and contiguously scalloped

155   surfaces (Fig. 5) (Bozarth, 1987, 1992; Piperno, 2006:65-71, Piperno et al., 2000, 2002; Pearsall,

156   2015b). As with maize and teosinte, the formation of these fruit phytoliths is genetically

157   controlled by a gene called *hard rind* (*Hr*) that also underwrites fruit lignification (Piperno et al.,

158   2002).

159   Size and/or morphology are used to discriminate between wild and domesticated *Cucurbita*

160   species. Domesticated fruits often have much larger and thicker phytoliths than their wild

161   ancestors and other wild squashes and there is a significant relationship between fruit size and

7

162   phytolith length (Piperno, 2006: 68-69 and Figs. 3.7 a-c therein). Thus, as with macro-remain

163   analysis phytolith size can be a straightforward discriminator between wild and domesticated

164   *Cucurbita*. Studies of modern fruits undertaken to date also suggest that species-specific

165   identifications will sometimes be possible based on morphological attributes. Examples are *C.*

166   *maxima*, another South American domesticate, and its wild progenitor *C. maxima* subsp.

167   *andreana*, and varieties of *C. moschata* (Piperno, 2006:67 and Figs. 3.6 d-f therein, Piperno et

168   al., 2000).

169   A potentially complicating factor in searching for *Cucurbita* phytoliths in ancient contexts is

170   that because prehistoric farmers sometimes selected for softer fruits over time, and the *Hr* gene

171   controls both hardness (lignification) and phytolith formation, soft-rinded fruits will have left a

172   slim or no phytolith record. This particularly appears to be the case for deposits dating to the last

173   4000 to 5000 years of prehistory or so (Piperno, 2006:143-144). On the other hand, all wild

174   *Cucurbita* species, possessing the dominant *Hr* gene for lignification/silicification, have very

175   hard rinds with high amounts of scalloped phytoliths, and should be visible if they were

176   exploited. As with maize, numerous archaeological phytolith records exist for early domesticated

177   *Cucurbita* spp. and their spread throughout the Americas (e.g., Piperno and Pearsall, 1998b;

178   Piperno et al., 2000; Hart et al., 2003, 2007; Iriarte et al., 2004; Pearsall, 2003; Piperno and

179   Stothert, 2003; Pohl et al., 2006; Bozarth et al., 2009; Piperno et al., 2009; Dickau et al., 2012;

180   Corteletti et al., 2015).

181   Bottle gourd (*Lagenaria siceraria*) is indigenous to Africa from whence it spread to other

182   continents by the early Holocene. Its large, scalloped phytoliths from fruit rinds can be identified

183   through morphological attributes to species in the Americas (Fig. 6) (Piperno, 2006:71; Pearsall

8

184 et al. 2015b) and have been recovered from early Holocene-aged and later deposits in Central

185 and South America (e.g., Piperno and Stothert, 2003, Piperno et al., 2009; Piperno, 2011).

186 *2.3 The Tropical Root Crops: Maranta and Calathea (arrowroot and llerén, Marantaceae);*

187 *Canna (achira, Cannaceae); manioc (Manihot esculenta, Euphorbiaceae)*

188 These crops, grown for their underground roots, rhizomes, tubers, and corms, are, with the

189 exception of manioc, minor root crops today. However, phytolith evidence has shown they had

190 greater importance in prehistory (below). The Zingiberales (Marantaceae and Cannaceae) overall

191 are abundant phytolith producers, and order, family, genus, and species level diagnostics are

192 present (Piperno 1989, 2006; Chen and Smith, 2013; Chandler-Ezell et al. 2006; Pearsall,

193 2015b). An important class of silicified epidermal cells are complex cylindrical phytoliths

194 produced in seed and root epidermis of the Marantaceae. *Calathea allouia* seeds produce one

195 type of diagnostic cylinder, other diagnostic forms are produced in *Maranta arundinacea* seeds

196 and *Calathea* rhizomes (Figs. 7, 8). While not as abundantly produced as Marantaceae leaf

197 phytoliths, seed and root phytoliths of this family are fairly robust and have been recovered

198 archaeologically. *Canna* produces the type of sphere characteristic of the Zingiberales as a

199 whole--a robust form with an irregularly angled/folded surface--while large (> 12 µM), well-

200 silicified spheres with smooth to slightly roughened surfaces (not rugose) have only been

201 observed in *Canna* (Pearsall, 2015b).

202 Manioc, one of the major root crops of the Americas, has long been known to be a low silica

203 accumulator (Piperno, 1988). By processing large quantities of tissues, Chandler-Ezell et al.

204 (2006) were able to document the presence of silicified secretory bodies (resembling pores or

205 nectaries) in manioc root rind, leaf, stem, and fruit. These occurred rarely in one wild species

206 tested, *M. hunzikerii*. Manioc secretory phytoliths were subsequently recovered from

9

207 pounding/grinding stones from the Real Alto site (ca. 6000 to 5000 cal BP), in association with

208 silicified transport tissues of roots and fruits, maize starch and phytoliths, and microfossils of

209 arrowroot, *Calathea*, and *Canna* (Chandler-Ezell et al., 2006). A phytolith matching the

210 description of a manioc secretory cell was recovered from the raised fields of Campo España,

211 western Llanos de Moxos, Bolivia (R. Dickau, pers. comm.). Ecuadorean and Panamanian pre-

212 ceramic deposits dating from ca. 9000 to 7000 BP frequently contain phytoliths from arrowroot

213 and llerén, indicating these now-minor root crops were significant components of early

214 horticultural systems in the Neotropics (Piperno, 2011).

215 **3. Crops of Southwest Asia**

216 *3.1 Triticum* and *Hordeum* spp. (Wheat and Barley)

217   Wheat and barley species are heavy silica accumulators that produce many phytolith

218 morphotypes. Morphotypes produced by silicification of epidermal cells such as short cells, long

219 cells, cork cells, papillae, trichomes, and trichome bases are the most characteristic and

220 diagnostic for the taxa, as well as the most often observed in archaeological samples (Figs. 9-11).

221 Both morphotypic and morphometric studies have been conducted to name, describe and

222 discriminate among the phytoliths produced by wheat and barley taxa. Morphotypic studies

223 include Kaplan et al. (1992), Mulholland and Rapp (1992), Rosen (1992), Tubb et al. (1993), and

224 Ball et al. (1993, 1999, 2001, 2009). Morphometric studies include Tubb et al. (1993) and Ball et

225 al. (1993, 1999, 2001, 2009). Some studies report good success at discriminating among wheat

226 and barley species at the genus level, and some success at the species level, primarily based on

227 the morphotypic and/or morphometric differences observed in the short cell (rondel), dendritic,

228 and/or papilla phytoliths produced by the taxa (e.g. Ball et al., 1999; Rosen, 1992; Tubb et al.,

229 1993).

230   Moreover, some features of the anatomy displayed in the medial section of the glume,

231   lemma, and palea epidermal tissue differ between genera of cereals and small-grained grasses.

232   Thus, there is the potential to identify wheat or barley phytoliths and to distinguish them from

233   wild weed grasses by examining the features of multi-cell phytoliths that are produced in the

234   Triticeae. Distinguishing features include a combination of the wave height, amplitude and

235   frequency of the joined dendritic long-cell walls, the size and configuration of the papillae, and

236   the shape of the cork cells (Figs. 9-11). Confidence in these determinations varies by the

237   numbers of characteristics visible on an individual multi-cell phytolith (Rosen, 1992).

238   Phytoliths produced by wheat or barley are regularly found in archaeological contexts and

239   have been used to make inferences about plant and site use (e.g. Albert et al., 2008; Cabanes et

240   al., 2009; Ishida et.al., 2003; Madella et al. 2014; Portillo et al., 2012; Power et al., 2014; Rosen,

241   2010; ; Shillito, 2011a; Zhang et al., 2013), about tool and vessel use (e.g. Anderson et al., 2000;

242   Berlin et al., 2003; Hart, 2011; Ma et al., 2014), about irrigation (e.g. Jenkins et al., 2011;

243   Madella et al., 2009; Rosen and Weiner, 1994) and about taphonomy (e.g. Cabanes et al., 2012;

244   Shillito, 2011b).

245   **4. Crops of East Asia**

246   *4.1 Setaria and Panicum Millets (Foxtail and Broomcorn millets)*

247   Phytoliths from the genus *Setaria* and *Panicum* are highly useful for identifying *Setaria*

248   *italica* (foxtail millet), *Setaria viridis* (green foxtail) and *Panicum miliaceum* (common or

249   broomcorn millet) and documenting the earliest history of domesticated millets in Eurasia

250   (García-Granero, et al., 2015; Lu, et al., 2009a, b; Zhang, et al., 2011, 2013). Research carried

251   out by Lu *et al*. published recently has established five key, efficient diagnostic characteristics

252   for distinguishing phytoliths from *S. italica* and *P. miliaceum* (Table 2) (Lu et al., 2009a). They

253 include: silica body shape, papillae characteristics including presence/absence, epidermal long

254 cell patterns, and glume surface sculpture.

255   Cross-shaped silica body phytoliths are formed in the lower lemma and glumes of *S. italica*,

256 whereas bilobate shapes are formed in those of *P. miliac*eum. However, bilobates are not

257 diagnostic to *P. miliaceum*. Regularly arranged papillae on the surface of the upper lemma and

258 palea are diagnostic of *S. italica*. However, it should be cautioned that the identification of *P.*

259 *miliaceum* cannot be confirmed based solely on the absence of papillae, because papillae may

260 sometimes not be visible on the smooth surfaces of upper lemmas and paleas in *S. italica*.

261 With respect to epidermal long cells, the epidermal long cell walls are Ω-undulated (Ω-I, II, III)

262 in *S. italica*, and η - undulated (η -I, II, III) in *P. miliaceum* (Figs. 12 a, b). The different

263 undulated patterns occur at different parts through gradual change from base and top (Ω/ η -I), to

264 side (Ω/ η -II), and to center (Ω/ η -III) of the silicified structure. The ends of epidermal long

265 cells can also be divided into a wavy type in *S. italica* and a finger type in *P. miliaceum* (Fig. 12

266 c, d). The former is significantly shorter than the latter (W=4.37$\pm$0.89 μM (N= 2774) vs.

267 W=8.95$\pm$2.02 μM (N=3303)). Therefore, the R value (ratio of the width of endings to the

268 amplitude of undulations) is lower in *S. italica* (0.33$\pm$0.11, N = 2774) than in *P. miliaceum*

269 (0.79$\pm$0.12, N = 3303). With respect to surface sculpture, a ridgy line sculpture type of the

270 upper lemma of the glume is diagnostic of *S. italica*, which is characterized by having an adnate

271 silicon extracellular sheet and outer epidermis, forming a very heavy silicon layer that is a

272 reliable feature in distinguishing them from *P. miliaceum*. In contrast, *P. miliaceum* has a unique

273 smooth, spotted sculpture with an adnate silica extracellular sheet and outer epidermis, or a saw-

274 toothed sculpture with an adnate silicon outer epidermis and hypodermal fibres.

12

275   In practical terms, the ideal archaeological sampling contexts for these and other cereal husks

276   are storage and other pits, where phytoliths are more abundant than in other contexts. In order to

277   obtain a clear outline of phytolith patterns, phase-contrast and microscopic interferometer at

278   400× magnification are highly recommended. For identification, the undulated patterns and

279   epidermal-ending characteristics are the most effective features for identification, because they

280   are clearly present in almost every glume sample examined. Indeed, epidermal endings are easily

281   divided into wavy and finger types and these combined with undulated patterns permit accurate

282   identification without the measurement of the W and R value in most cases.

283   Differentiating crop phytoliths from their Panicoid weedy wild relatives in archaeological

284   contexts can present challenges due to similarities of identifiable Panicoid husk morphotypes,

285   and large pristine sheets of identifiable multicellular aggregations that identification criteria

286   listed above are, in part, based on are sometimes rare. Having strict identification criteria as

287   described here is essential.

288   Moving to the discrimination of *S. italica* and its wild ancestor, *S. viridis*, using phytoliths,

289   the focus shifts to the size of phytoliths in the upper lemma and palea. It is established through a

290   study carried out by Zhang *et al*. (2011) that the size of the ΩIII type of *S. italica* is larger than

291   that from *S. viridis*. This means the difference between the two species is predicated on the

292   width/expansion of the lemma and palea, also resulting in a visible difference of phytolith

293   morphology at the center of lemma and palea, where silicified epidermal long cells are most

294   complex, but can be differentiated. The discriminant function analysis accurately classifies a

295   significant majority of the plants, 78.4% of foxtail millets and 76.9% of green foxtails. However,

296   about 25% data are incorrectly classified. More samples should be analyzed to detect the

297   presence of other potentially diagnostic features. Morphological and basic morphometric studies

298   of glumes of other minor millets also show the potential of phytoliths for differentiating these

299   important crops in the prehistory of Eurasia and Africa (below) (Madella et al., 2014).

300   *4.2 Oryza sativa (Rice)*

301   Phytoliths have played a very important role in the identification of rice remains recovered

302   from archaeological sites. In the past two decades, a number of identification criteria have been

303   used. To date, three distinct phytolith morphotypes have been identified: double-peaked glume

304   cells from the rice husk, bulliform (fan-shaped or motor cell) phytoliths from bulliform cells in

305   leaves, and articulated bilobate phytoliths from stems and leaves (Fujiwara, 1976, 1993; Lu et

306   al., 1997; Pearsall et al., 1995; Piperno, 2006; Wang and Lu, 1993; Zhao et al., 1998; Zheng, et

307   al., 2003; Gu et al., 2013).

308   Double-peaked glume cell phytoliths (Fig. 13) are unique to the genus *Oryza* and can

309   separate domesticated rice from the nine wild rice species of South and Southeast Asia based on

310   linear discriminant function analysis of three glume cell measurements (Pearsall, et al., 1995,

311   Zhao and Piperno, 2000, Zhao, 1998, Zhao, et al., 1998). A recent study carried out by Gu *et al*.

312   showed that three-dimensional measurements of double-peaked glume cells can also successfully

313   distinguish cultivated from wild *Oryza* species (Gu, et al., 2013).

314   Bulliform cell phytoliths are produced in high quantity in stems and leaves, and like glume

315   phytoliths may be common in sites (Wang and Lu, 1993). Their morphological features appear to

316   be under genetic control and therefore directly reflect taxonomical significance (Gu, et al., 2013,

317   Zheng, et al., 2003). In the past two decades, morphological features including surface

318   ornamentations have been employed to distinguish domesticated from wild rice using these

319   phytoliths (Fig. 14) (Lu et al., 2002; Ma and Fang, 2007; Huan et al., 2014). Pearsall, et al.,

320   (1995) found that bulliform size alone could not distinguish rice from related species. Lu et al.

14

321 (2002) studied the number of scale-like ornamentations at the edge of bulliform phytoliths from

322 seven species of wild rice and six species of domesticated rice and found the number of scale-

323 like decorations in wild species is less than 9, while 8 to 14 are present in domesticated rice. This

324 feature as a distinctive characteristic of cultivated rice needs further validation (Qin, 2012; Wang

325 and Lu 2012); however, to date, phytoliths with greater than 9 scale-like decorations are widely

326 used signatures of domestication (Lu et al., 2002; Wu et al., 2014) (Fig. 14). According to this

327 criterion, recent studies indicate that rice domestication began around 10,000 BP in the Lower

328 Yangtze, China (Wu et al., 2014).

329 Bilobates with scooped ends and a parallel arrangement in leaf tissue are typical of the

330 genera in the Oryzeae tribe, in contrast to the characteristic features of *Oryza* plants (Pearsall et

331 al., 1995; Lu, et al., 1997; Xiujia et al., 2014). Pearsall et al. (1995) and Gu et al. (2013) showed

332 that this bilobate was produced by all members of the tribe, and cannot be used to distinguish any

333 one genus, including *Oryza*.

334 Phytoliths can also be used as a tool for understanding the development and spread of rice

335 (*Oryza* sp.) arable systems using arable weed ecologies. Different proportions of crop weeds

336 appear in different field systems and the ratios of phytolith morphotypes in soils from these

337 fields reflect this. Modern analogues were created from sediment samples from traditionally

338 farmed fields using correspondence analysis (Canoco) to demonstrate the constituents of the

339 samples, groups of phytolith morphotypes, from different field types reflect their arable system.

340 When applied to archaeological samples the results demonstrate changing farming practices over

341 time (Fuller and Weisskopf, 2011; Weisskopf et al., 2014).

342 The development of water management in rice farming can be seen using ratios of specific

343 phytoliths from grass weeds in rice fields (Weisskopf et al., in press). Ratios of phytolith

15

344 morphotypes that are genetically predisposed to take up silica in grasses (short cells) to those that

345 take up water under circumstances of greater transvaporation (long cells and stomata) (Madella

346 et al, 2009, Jenkins et al 2011) were used to develop a wet versus dry index on samples from

347 traditionally farmed modern rice fields. This method was applied to phytoliths assemblages

348 collected from palaeosols and the corresponding archaeological sites in the Lower Yangtze

349 Valley. The results show a change from probable decrue farming on the river's edge at

350 Tianluoshan (4800-4300BC) to small drier dugout fields at Caoxieshan (3950-3700BC) to large

351 managed irrigated fields at Maoshan (3000-2300BC) (Weisskopf, et al. in press).

352 **5. Crops of Southern and Southeast Asia**

353 *5.1 Musa spp. (true bananas)*

354   The domestication and spread of true bananas belonging to the genus *Musa* is a complicated

355 issue. Domesticated bananas derive from the Eumusa (*Musa acuminata* [AA] and *M. balbisiana*

356 [BB]) and Australimusa (*M. maclayi*) sections of Musaceae. Domestication appears to have

357 involved intra and interspecific hybridization, polyploidization and somaclonal mutations,

358 ending in seed sterility and parthenocarpy (De Langhe et al., 2009). Accordingly, phytoliths

359 produced by the Musaceae sections Eumusa and Australimusa have great relevance in

360 archaeological research. Humans likely spread domesticated Eumusa throughout the tropics.

361 Archaeological evidence for bananas helps researchers make inferences about crop diffusion and

362 how people in antiquity managed plant resources in tropical rainforests. Outside Asia, any

363 evidences for *Musa* phytoliths are indicative of cultivation (Vrydaghs and De Langhe, 2003).

364 Phytoliths can be produced in various plant tissues and organs of bananas (e.g., Lentfer, 2009a;

365 Chen and Smith, 2013) with seed and leaf phytoliths being the most studied to date. In

366 archaeological contexts, finding both seed and leaf phytoliths together may indicate an early

367 phase of domestication, while finding only leaf phytoliths could indicate a latter phase. Lentfer

368 (2009) and Perrier et al. (2011) discuss and illustrate several seed phytolith morphotypes and

369 conclude that they are diagnostic at the genus, section, and sometimes seed levels for Musaceae

370 (Figs. 15, 16). Lentfer (2009a) further discusses other globular and polygonal morphotypes

371 produced in various plant parts and uses morphometric analysis to separate those produced in

372 seeds from those produced in other plant organs and tissues.

373   In leaves, silicification of cells surrounding the vascular tissue of *Musa* and *Ensete* species

374 produces volcaniform (volcano shaped) phytoliths (Ball et al., 2006) (Fig. 17). Both morphotypic

375 (Ball et al., 2006; Lentfer and Green, 2004; Mbida et al., 2001; Vrydaghs et. al., 2009; Wilson,

376 1985) and morphometric studies (Ball et al., 2006; Lentfer, 2009a; Vrydaghs et. al., 2009) have

377 been conducted to distinguish among the volcaniform phytoliths produced by different *Musa* and

378 *Ensete* species. These phytoliths can be discriminated at the genus level allowing bananas to be

379 distinguished from the ensets in archaeological records (Lentfer, 2009a; Mbida et al., 2001), but

380 reliable identification at the species level is still wanting.

381   Archaeological evidences for *Musa* phytoliths have been recently summarized by Donohue

382 and Denham (2009), with the earliest evidence for banana cultivation at Kuk Swamp in highland

383 New Guinea, dated at 7000-6500 years ago (Denham et al., 2003). This suggests an early and

384 long process of domestication of *M. acuminata* ssp. *banksii* in the area. Archaeological evidence

385 of Musaceae in Melanesia (Horrocks et al., 2009; Lentfer et al., 2010), in Polynesia (Khan et al.,

386 2014), and early evidence (from 5000 BP) in Southeast Asia falls within the natural range of

387 several wild banana species (Kealhofer, 2003) making it difficult to disentangle cultivation

388 versus exploitation of wild plants, but later evidence in east Asia seems to suggest human agency

389 (Zhao and Piperno, 2000). The earliest findings in South Asia are from sites of the greater Indus

17

390   Valley at Loteshwar (3681 to 2243 cal BC) in North Gujarat, India (García-Granero et al., 2015)

391   and the Mature Harappan levels (2500-1900 BC) of Kot Diji, Pakistan (Fuller and Madella,

392   2002). The evidence is scant and may actually highlight contacts (trade) with the Western Ghats

393   to the south more than local cultivation. Cameroon Nkang evidence represents, with all

394   probability, the dispersal of cultivars to West Africa by at least 2500 years ago (Mbida et al.,

395   2001).

396   **6. Crops of Africa**

397   *6.1 Ensete ventricosum (Ethiopian banana, Abyssinian banana), Lagenaria siceraria (bottle*

398   *gourd), Sorghum bicolor (sorghum), Penniseum glaucum (pearl millet)*

399   Crop plants native to Africa have seen the smallest amount of focused research. *Ensete*

400   *ventricosum* was domesticated in antiquity in the eastern highlands of Africa for its starchy stem

401   and is an important crop today. The genus has a pantropical distribution. Its phytoliths have been

402   studied largely as parts of analyses to compare and distinguish them from those of *Musa* spp.

403   (see above), and it indeed appears that *Ensete* can be identified to at least the genus (Figs. 15,

404   17). Work is needed to determine if wild and domesticated species can be distinguished. Another

405   crop of African origin is the bottle gourd. It can be identified to species in American contexts,

406   where wild varieties are not native (see above under New World). Work is needed on wild

407   *Lagenaria* in Africa and Asia to determine if wild and domesticated varieties can be

408   discriminated.

409   A handful of recent studies has outlined phytolith production in inflorescences of African

410   domesticated grains and their wild progenitors (Logan 2012; Madella et al., 2013; Novello and

411   Barboni 2015; Radomski and Neumann 2011). However, with only one study on phytolith

412   production in the inflorescences of wild grasses (Novello and Barboni 2015), there is still

18

413   considerable work to do vis-à-vis isolating specific morphotypes diagnostic to the genus or

414   species level. Consequently, most Africanist phytolith researchers favor quantitative or semi-

415   quantitative methodologies that take into account multiple phytolith forms for strong positive

416   identifications.

417   The most promising potential for identification using phytoliths appears to be *Sorghum*

418   *bicolor*, likely domesticated relatively late (c. 2000 years ago), but probably used in a wild but

419   cultivated form many millennia earlier. Of special diagnostic interest is heavily silicified

420   elongate dendritic cell forms described by several authors (Novello and Barboni 2015; Radomski

421   and Neumann 2011; Logan and D'Andrea 2008 in Logan 2012: 96-100; Madella et al., in press).

422   These forms appear to be quite distinctive, occur in some quantity in domesticated sorghum

423   inflorescence (36.9% of all phytoliths), but are uncommon in wild sorghum or other grasses

424   studied to date (Radomski and Neumann 2011:157). In addition, one complex short cell form,

425   with a bilobate to rondel base and saddle-like top may be distinctive to *Sorghum bicolor*

426   (Radomski and Neumann 2011). Since very little comparative work on wild African grass

427   inflorescences has been completed, it is difficult to establish at what level these forms are

428   diagnostic, but early results look very promising.

429   Pearl millet (*Penniseum glaucum*) is the oldest domesticated crop on the continent (~4500

430   bp; Manning et al., 2011), yet little is known about phytolith production in this important crop

431   (see Radomski and Neumann, 2011 for a discussion).

432   **7. Discussion**

433   Phytolith analysis has substantially contributed to study and understanding of agricultural

434   origins and dispersals around the world. Genus- or species-level identifications are routinely

435   achieved for crop plants, and when a crop is found outside of the natural distribution of it and its

436 closest wild relatives (as, for example, maize in South America and eastern North America and

437 bananas in Africa), genus-level identification alone serves the purpose of securely identifying it.

438 Research by numerous investigators over decades summarized here has, therefore, made it

439 possible to develop consensus identification criteria for archaeobotanists to employ and for other

440 scholars to bring to bear in formulating broad conceptual and synthetic works. A recent paper, in

441 fact, that reviews potential starting dates for the onset of the proposed new geologic epoch, the

442 Anthropocene, defines phytoliths as one of two primary stratigraphic markers and one of a few

443 potential auxiliary stratotypes for the origin and expansion of farming globally (Lewis and

444 Maslin, 2015). Phytoliths are also named as a stratotype marker for Lewis and Maslin's (2015)

445 suggested choice of the event that would mark the Anthropocene beginning, the "New-Old

446 World Collision" at the date of 1610.

447 Phytoliths can and have served a number of different roles in agricultural origin and dispersal

448 research: 1) as stand-alone markers of cultivation and domestication, 2) complementary avenues

449 of plant identification in multi-proxy research, 3) identifiers at more refined taxonomic levels

450 than possible with other fossil markers, or of taxa and plant structures often not visible with other

451 fossils, 4) markers of crop presence and human environmental modification in paleo-ecological

452 records, 5) markers of range expansions of crops and other plant taxa. Increasingly, phytolith and

453 starch grain analyses are being used in tandem in many regions of the world, significantly

454 increasing the recoverability of a number of New and Old World crop species, including major

455 root crops, that leave slim or no phytolith records, and allowing finer discrimination of others,

456 along with identifications of different structures of the same crop (a few examples are Chandler

457 et al., 2006; Zarillo et al., 2008; Duncan et al., 2009; Lentfer, 2009b; Piperno, 2009, et al., 2009;

458 Boyd and Surette, 2010; Dickau et al., 2007, 2012; Yang et al., 2012a, b, 2014; Liu et al., 2011;

459 Iriarte et al., 2012; Madella et al., 2014; Barton and Torrence, 2015; Corteletti et al., 2015;

460 García-Granero et al., 2015) (see Table 1 for crop plants and wild progenitors known to have

461 diagnostic starch grains). As with other fossil indicators of plant exploitation and agriculture

462 such as macro-remains of seeds and their chaffs (e.g., Wilcox, 2007; Fritz and Nesbitt, 2014), the

463 taxonomic levels to which phytolith identification can be made will differ from species to

464 species, and at times the separation of important taxa will not be possible. There are also many

465 crops and wild progenitors for which phytolith analysis may not turn out to be of significant

466 utility, although further work is needed on many.

467   Issues such as phytolith formation, taphonomy, and preservation, encompassing initial

468 phytolith production in plants and their subsequent depositional and post-depositional histories

469 are not the foci of this paper. These aspects have been well-considered elsewhere and the reader

470 can consult a number of reviews summarizing information accumulated from numerous studies

471 on crop and other plants from around the world (e.g., Pearsall, 2000, 2014, 2015a; Piperno, 1985,

472 1988, 2006; Madella, et al., 2009; Madella and Lancelotti 2012). Briefly, the following points

473 can be made. With regard to phytolith formation, genetic control of phytolith formation is

474 demonstrated in a number of crops and their wild ancestors, including *Cucurbita* (fruit rinds),

475 *Zea* (fruitcases and cobs), *Oryza* (leaves and probably glumes), and also wheat awns (Dorweiler

476 and Doebley, 1997; Piperno et al., 2002; Zheng et al., 2003; Ma et al., 2006, 2007; Peleg et al.,

477 2010; Gu et al., 2013). This means that the visibility of these phytoliths in archaeological sites

478 should not have been biased by environmental variability. In other crop/wild ancestor pairs

479 where production of individual phytoliths has not to this point been linked to specific genetic

480 loci, studies of different populations from different environmental regions demonstrate that

481 phytoliths used in identification are both consistently produced in modern flora and commonly

21

482 recovered from archaeological sites. In sum, these and other studies indicate a considerable

483 degree of genetic and metabolic control over the mechanisms and patterns of silica deposition

484 (e.g., Hodson et al., 2005; Piperno, 2006; Madella et al., 2009; Tsartsidou et al., 2007; Pearsall,

485 2014).

486   Investigations of infraspecific variability in phytolith formation also document which

487 phytolith types do appear to be significantly affected by environmental factors such as water

488 availability and bedrock chemistry, such that particular morphotypes are/are not produced in

489 certain environments, or formed in such low amounts that they would be difficult to recover

490 (e.g., Piperno, 2006; Madella et al., 2009; Tsartsidou et al., 2007). Phytoliths involved (e.g., from

491 jigsaw-shaped epidermal phytoliths of woody taxa; long epidermal cells of grass leaves) are not

492 usually among the corpus of silicified forms used in crop identification and discussed herein. As

493 discussed above, in wheat, barley, and rice an increased silicification of long epidermal cells in

494 their husks in well-watered conditions provide a means to investigate ancient irrigation and water

495 regimes.

496   Other issues such as depositional and post-depositional histories, including preservation and

497 downward phytolith movement in soils and sediments, have seen detailed investigation, in part

498 by crop plant researchers who have taken into account and controlled for these factors (a few

499 studies and reviews include Harvey and Fuller, 2005; Piperno, 1985, 1988, 2006; Fishkis et al.,

500 2009, 2010; Madella, et al., 2009, Madella and Lancelotti 2012; Devos et al., 2013; Pearsall

501 2014, 2015a; Cabanes et al., 2015). It is well-understood, for example, that phytoliths follow the

502 biogenic silica curve for erosion and dissolution, so that when the pH exceeds a value above

503 about 9--an unusual circumstance in archaeological contexts that did not influence records

504 discussed here--some phytolith corrosion and dissolution may at times be expected (see reviews

505   in Piperno, 1988:46-47 and Piperno, 2006:22, 108, and recent experimental work by Cabanes et

506   al., 2015). Other recent efforts combining phytolith analysis with micromorphology also serve to

507   address the various issues outlined (Vrydaghs et al., this issue).

508   The utility of phytoliths for investigating agricultural origins and dispersals around the world

509   is clear and despite the considerable range of crop examples and geographic regions heretofore

510   investigated, possibilities for future expansions of research are many. Moreover, micro-fossil

511   assemblage composition and distribution can provide information about currently under-

512   investigated domestication processes related to crop improvement in prehistory, such as the

513   development of parthenocarpy (seedless fruits) and of new crop varieties in general. Phytolith

514   (and starch) studies are complementary to all aspects of archaeological investigation aimed at

515   understanding agricultural origins, and given well-proven and potential outcomes we should now

516   be at a stage where such studies are incorporated into broader archaeological framework as a

517   matter of routine research.

518   **Acknowledgements**

521

522

523

524

525

526

527

528   **References Cited**

529   Albert, R.M., Shahack-Gross, R., Cabanes, D., Gilboa, A., Lev-Yadun, S., Portillo, M.,

530   Sharon, I., Boaretto, E., Weiner, S., 2008. Phytolith-rich layers from the Late Bronze and Iron

531   Ages at Tel Dor (Israel): Mode of formation and archaeological significance. J. Archaeol.Sci. 35,

532   57–75.

533   Anderson, N., Ball, T.B., Thompson, R.G., Gardner, J.S., 2000. A study of phytoliths

534   extracted from food residues taken from a Bronze Age jar. Abstr. 3rd Int. Meet Phytolith Res. p.2.

535   Ball, T. B., Brotherson, J.D., Gardner, J.S., 1993. A typologic and morphometric study of

536   variation in phytoliths from einkhorn wheat (*Triticum monococcum* L.). Can. J. Bot. 71, 1182–

537   1192.

538   Ball, T.B., Gardner, J.S., Anderson, N., 1999. Identifying inflorescence phytoliths from

539   selected species of wheat (*Triticum monoccum, T. dicoccon, T. dicoccoides*, and *T. aestivum*) and

540   barley (*Hordeum vulgare* and *H. spontaneum*). Am. J. Bot. 86, 1615–1623.

541   Ball, T.B., Gardner, J.S., Anderson, N., 2001. An approach to identifying inflorescence

542   phytoliths from selected species of wheat and barley, in: Meunier, J.D., Colin, F. (Eds.),

543   Phytoliths: Applications in Earth Sciences and Human History. A.A. Balkema Publishers,

544   Exton, PA., pp. 289–302.

545   Ball, T.B., Ehlers, R., Standing, M.D., 2009. Review of typologic and morphometric analysis

546   of phytoliths produced by wheat and barley. Breed. Sci. 59, 505–512.

547   Ball, T.B., Vrydaghs, L., Van den Hauwe, I., Manwaring, J., De langhe, E., 2006.

548   Differentiating banana phytoliths: Wild and edible Musa acuminata and Musa balbisiana. J.

549   Archaeol. Sci. 33, 1228–1236.

24

550   Berlin, A.M., Ball, T.B., Thompson, R., Kittleson, D., Herbert, S.C., 2003. Ptolemaic

551   agriculture, "Syrian wheat", and *Triticum aestivum*. J. .Archaeol. Sci. 30, 115–121.

552   Biwer, M.E., VanDerwarker, A.M., 2015. Paleoethnobotany and ancient alcohol production:

553   A mini-review. Ethnobio. Let. 6, 28–31.

554   Bozarth, S.R., 1987. Diagnostic opal phytoliths from rinds of selected *Cucurbita* species.

555   Amer. Anti. 52, 607–615.

556   Bozarth, S.R., 1990. Diagnostic opal phytoliths from pods of selected varieties of common

557   beans (*Phaseolus vulgaris*). Amer. Anti. 55, 98–104.

558   Bozarth, S.R., 1992. Classification of opal phytoliths formed in selected dicotyledons native

559   to the Great Plains, in: Rapp, G., Jr., Mulholland, S.C. (Eds.), Phytolith Systematics: Emerging

560   Issues. Plenum Press, New York, pp. 193–214.

561   Bozarth, S., 1993. Maize (*Zea mays*) cob phytoliths from Central Kansas Great Bend Aspect

562   archaeological site. Plains. Anthro. 38:279–286.

563   Bozarth, S.R., Price, K., Woods, W.I., Neves, E.G., Rebellato, R., 2009. Phytoliths and Terra

564   Preta: The Hatahara Site Example, in: Woods, W.I., Teixeira, W.G., Lehmann, J., Steiner, C.,

565   WinklerPrins, A.M.G.A., Rebellato, L. (Eds.), Amazonian Dark Earths: Wim Sombroek's

566   Vision. Springer, New York, pp. 85–98.

567   Boyd, M., and Surette, C. 2010. Northernmost precontact maize in North America. Amer.

568   Anti. 75, 117–133.

569   Cabanes, D., Burjachs, F., Exposito, I., Rodriguez, A., Allue, E., Euba, I., Verges, J., 2009.

570   Formation processes through archaeobotanical remains: The case of the Bronze Age levels in El

571   Mirador cave, Sierra de Atapuerca, Spain. Quat. Int. 193, 160–173.

572   Cabanes, Dan., Gadot, Y., Cabanes, M., Finkelstein, I., Weiner, S., Shahack-Gross, R., 2012.

573   Human impact around settlement sites: a phytolith and mineralogical study for assessing site

574   boundaries, phytolith preservation, and implications for spatial reconstructions using plant

575   remains. J. Archaeol. Sci. 39, 2697–2705.

576   Cabanes, D., Shahack-Gross, R. 2015. Understanding Fossil Phytolith Preservation: The Role

577   of Partial Dissolution in Paleoecology and Archaeology. PLoS ONE 10(5): e0125532.

578   doi:10.1371/journal.pone.0125532

579   Chandler-Ezell, K., Pearsall, D.M., Zeidler, J.A., 2006. Root and tuber phytoliths and starch

580   grains document manioc (*Manihot esculenta*), arrowroot (*Maranta arundinacea*), and llerén

581   (*Calathea* sp.) at the Real Alto site, Ecuador. Econ. Bot. 60, 213–220.

582   Chen, S.T., Smith, S.Y., 2013. Phytolith variability in Zingiberales: A tool for the

583   reconstruction of past tropical vegetation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 370, 1–12.

584   Corteletti, R., Dickau, R., DeBlasis, P., Iriarte, J., 2015. Revisiting the economy and mobility

585   of southern proto-Jê (Taquara-Itararé) groups in the southern Brazilian highlands: starch grain

586   and phytolith analyses from the Bonin site, Urubici, Brazil. Jour. Archaeol. Sci. 58, 46–61.

587   De Langhe, E., Vrydaghs, L., de Maret, P., Perrier, X., Denham, T., 2009. Why bananas

588   matter: An introduction to the history of banana domestication, in: Denham, T., De Langhe, E.,

589   Vrydaghs, L. (Eds.), Ethnobot. Res. Appl. Special Issue: History of Banana Domestication, 7,

590   165–177.

591   Denham, T.P., Haberle, S.G., Lentfer C., Fullagar, R., Field, J., Therin, M., Porch N.,

592   Winsborough, B., 2003. Origins of agriculture at Kuk Swamp in the Highlands of New. Guinea.

593   Science 301, 189–193.

594   Dickau, R., Ranere, A.J., Cooke, R.G., 2007. Starch grain evidence for the preceramic

595 dispersals of maize and root crops into tropical dry and humid forests of Panama. Proc. Natl.

596 Acad. Sci. U.S.A. 104, 3651–3656.

597 Dickau, R., Bruno, M., Iriarte, J., Prumers, H., Betancourt, C.J., Holst, I., Mayle, F.E., 2012.

598 Diversity of cultivars and other plant resources used at habitation sites in the Llanos de Mojos,

599 Beni, Bolivia: evidence from macrobotanical remains, starch grains, and phytoliths. Jour.

600 Archaeol. Sci. 39, 357–370.

601 Donohue, M., Denham, T., 2009. Banana (Musa spp.) domestication in the Asia- Pacific

602 region: Linguistic and archaeobotanical perspectives, in: Denham, T., De Langhe, E., Vrydaghs,

603 L. (Eds.), Ethnobot. Res. Appl. Special Issue: History of Banana Domestication, 7, 293–332.

604 Dorweiler, J.E., Doebley, J., 1997. Developmental analysis of teosinte glume architecture1: a

605 key locus in the evolution of maize (Poaceae). Amer. Jour. Bot. 84, 1313–1322.

606 Duncan, N., Pearsall, D.M., Benfer, R.A. Jr. 2009. Gourd and squash artifacts yield starch

607 grains of feasting foods from preceramic Peru. Proc. Natl. Acad. Sci. USA 106, 13202–13206.

608 Fritz, G., Nesbitt, M., 2014. Laboratory analysis and identification of plant macroremains, in:

609 Marston, J.M., d'Alpoim Guedes, J., Warinner, C. (Eds.), *Method and Theory in*

610 *Paleoethnobotany*. University of Colorado Press, Boulder, pp.

611 Fuller, D. Weisskopf, A.R. 2011 The early rice project: from domestication to global

612 warming. Archaeol. Int. 13/14, 44–51

613 Fujiwara, H., 1976. Fundamental studies in plant opal analysis. 1. On the silica bodies of

614 motor cell of rice plants and their near relatives, and the method of quantitative analysis,

615 Archaeol. Nat. Sci. 9, 15–29.

616 Fujiwara, H., 1993. Research into the history of rice cultivation using plant opal analysis, in:

617 Pearsall, D.M., Piperno, D.R. (Eds.), Current Research in Phytolith analysis: Applications in

618   Archaeology and Paleoecology, MASCA., University of Pennsylvania Museum, Phiadelphia,

619   vol. 10, pp. 147–158.

620   Fuller, D.Q., Madella, M., 2002. Issues in Harappan archaeobotany: Retrospect and prospect,

621   in: Settar, S., Korisettar, R. (Eds.), Indian Archaeology in Retrospect, Volume II: Protohistory—

622   Archaeology of the Harappan Civilization. Manohar Publishers, New Delhi, pp. 317–90.

623   García-Granero J.J., Lancelotti C., Madella M., Ajithprasad P., 2015. Plant processing

624   activities at Loteshwar (North Gujarat, India): a micro-botanical approach, in: Lefèvre V., Didier

625   A., Mutin B. (Eds.), South Asian Archaeology and Art 2012. Vol. 1: Man and Environment in

626   Prehistoric and Protohistoric South Asia: New Perspectives. Brepols Publishers, Turnhout,

627   Belgium, pp. 99–116.

628   García-Granero, J., Lancelotti, C., Madella, M., 2015. A tale of multi-proxies: integrating

629   macro- and microbotanical remains to understand subsistence strategies. Veg. Hist. Archaeobot.

630   24, 121–133.

631   Gu, Y., Zhao, Z., Pearsall, D.M., 2013. Phytolith morphology research on wild and

632   domesticated rice species in East Asia, Quat. Intl. 287, 141–148.

633   Häkkinen, M., 2013. Reappraisal of sectional taxonomy in Musa (Musaceae). Taxon 62, 809-

634   813.

635   Hart, J.P., Lovis, W.A., 2013. Reevaluating what we nnow about the histories of maize in

636   Northeastern North America: A review of current evidence. Jour. Archaeolog. Res. 21, 175–216.

637   Hart, J., 2014. A critical assessment of current approaches to investigations of the timing,

638   rate, and adoption trajectories of domesticates in the Midwest and Great Lakes, in: Raviele,

639   M.E., Lovis, W.A. (Eds.), Reassessing the Timing, Rate, and Adoption Trajectories of

640   Domesticate Use in the Midwest and Great Lakes. Occasional Papers No. 1, Midwest

641   Archeological Conference, Inc., pp. 136–161.

642   Hart, J.P., Thompson, R.G., Brumbach, H.J., 2003. Phytolith evidence for early maize (*Zea*

643   *mays*) in the Northern Finger Lakes Region of New York. Amer. Anti. 68, 619–640.

644   Hart, J.P., Brumbach, H.J., Lusteck, R., 2007. Extending the phytolith evidence for early

645   maize (Zea mays ssp. mays) and squash (Cucurbita sp.) in central New York. Amer. Anti. 72,

646   563–583.

647   Hart, J.P., R. G. Matson, R.G., Thompson, R.G., Blake, M. 2011. Teosinte inflorescence

648   phytolith assemblages mirror Zea taxonomy. PLoS ONE 6, e18349.

649   Hart, T.C., 2011. Evaluating the usefulness of phytoliths and starch grains found on survey

650   artifacts. J. Archaeol. Sci. 38, 3244–3253.

651   Hodson, M. J., White, P. J., Mead, A., and Broadley, M. R., 2005. Phylogenetic variation in

652   the silicon composition of plants. Ann. Bot. 96, 1027–1046.

653   Horrocks, M., Bedford, S., Spriggs, M., 2009. A short note on banana (*Musa*) phytoliths in

654   Lapita, immediately post-Lapita and modern period archaeological deposits from Vanuatu. J.

655   Archaeol. Sci. 36, 2048–2054.

656   Huan, X., Li, Q., Ma, Z., Jiang, L., Yang, X., 2014. Fan-shaped phytoliths reveal the process

657   of rice domestication at Shangshan site, Zhejiang Province. Quat. Sci. 34, 106–113 (in Chinese).

658   Iriarte, J., 2003. Assessing the feasibility of identifying maize through the analysis of

659   cross-shaped size and three-dimensional morphology of phytoliths in the grasslands of

660   southeastern South America. J. Archaeol. Sci. 30, 1085–1094.

661   Iriarte, J., Holst, I., Marozzi, O., Listopad, C., Alonso, E., Rinderknecht, A., Montaña, J.

662   2004. Evidence for cultivar adoption and emerging complexity during the mid-Holocene in the

663   La Plata Basin, Uruguay. Nature 432, 614–617.

664   Iriarte, J., Power, M.J., Rostain, S., Mayle, F.E., Jones, H., Watling, J., Whitney, B.S.,

665   McKey, D., 2012. Fire-free land use in pre-1492 Amazonian savannas. Proc. Natl. Acad. Sci. U.

666   S. A. 109, 6473–6478.

667   Ishida, S., Parker, A.G., Kennet, D., Hodson, M. J., 2003. Phytolith analysis from the

668   archaeological site of Kush, Ras al-Khaimah, United Arab Emirates. Quat. Res. 59, 310–321.

669   Jenkins, E., Jamjoum, K., Al Nuimat, S., 2011. Irrigation and phytolith formation: an

670   experimental study, in: Mithen, S., Black, E. (Eds.), Water, Life and Civilisation: Climate,

671   Environment and Society in the Jordan Valley. Cambridge University Press, Cambridge, pp.

672   347–372.

673   Khan, J.G., Horrock, M., Nieuwoudt, M.K., 2014. Agriculture, domestic production, and site

674   function: Microfossil analyses and Late Prehistoric landscapes of the Society Islands. Econ. Bot.

675   68, 246–263.

676   Kaplan, L., Smith, M.B., Sneddon L.A., 1992. Cereal grain phytoliths of Southwest Asia and

677   Europe, in: Rapp, G.R., Mulholland, S.C. (Eds.), Phytolith Systematics. Plenum Press, New

678   York, pp. 149–174.

679   Kealhofer, L., 2003. Looking into the gap: Land use and the tropical forests of southern

680   Thailand. Asian Perspect. 42, 72–95.

681   Kealhofer, L., Piperno, D.R., 1998. Opal Phytoliths in Southeast Asian Flora. Smithsonian

682   Contrib. Bot. No. 88, pp. 1-39.

683

684 Larson, G., Piperno, D., Allaby, R.G., Purugganan, M.D., Andersson, L., Arroyo-Kalin, M.,

685 Barton, L., Climer Vigueira, C., Denham, T., Dobney, K., Doust, A.N., Gepts, P., Gilbert,

686 M.T.P., Gremillion, K.J., Lucas, L., Lukens, L., Marshall, F.B., Olsen, K.M., Piress, J.C.,

687 Richersont, P.J., Rubio de Casas, R., Sanjur, O.I., Thomas, M.G., Fuller, D.Q., 2014. Current

688 perspectives and the future of domestication studies. Proc. Natl. Acad. Sci. U.S.A. 111, 6139–

689 6146.

690 Lentfer, C.J., 2009a. Tracing Domestication and Cultivation of Bananas from Phytoliths: An

691 update from Papua New Guinea, in: Denham, T., De Langhe, E., Vrydaghs, L. (Eds.), Ethnobot.

692 Res. Appl. Special Issue: History of Banana Domestication, 7, 247–270.

693 Lentfer C.J., 2009b. Going bananas in Papua New Guinea: a preliminary study of starch

694 granule morphotypes in Musaceae fruit. Ethnobot. Res. App. 7, 217-238.

695 Lentfer, C.J., Green, R. C., 2004. Phytoliths and the evidence for banana cultivation at the

696 Lapita reber-Rakival site on Watom Island, Papua New Guinea, in: Attenbrow, V., Fullagar, R.

697 (Eds.), A Pacific Odyssey: Archaeology and Anthropology in the Western Pacific. Papers in

698 Honour of Jim Specht, Records of the Australian Museum, 29, 75–88.

699 Lentfer, C., Pavlides, C., and Specht, J., 2010. Natural and human impacts in a 35 000-yr

700 vegetation history in central New Britain, Papua New Guinea. Quat. Sci. Rev. 29, 3750-3767.

701 Lewis, S.L., Maslin, M.A. 2015. Defining the Anthropocene. Nature 519, 171–180.

702 Liu, L., Ge, W., Bestel, S., Jones, D., Shi, J., Song, Y., Chen, X., 2011 Plant exploitation of

703 the last foragers at Shizitan in the Middle Yellow River Valley China: evidence from grinding

704 stones. Jour. Archaeol. Sci. 12, 3524–3532.

705 Liu, L., Ma, S., Cui, J., 2014. Identification of starch granules using a two-step identification

706 method, J. Archaeol. Sci. 52, 421–427.

707   Logan, A.L., 2012. A History of Food Without History: Food, Trade, and Environment in

708   West-Central Ghana in the Second Millennium AD (PhD Dissertation). University of Michigan,

709   Ann Arbor.

710   Logan, A.L., Hastorf, C.A., Pearsall, D.M., 2012. "Let's drink together": Early ceremonial

711   use of maize in the Titicaca Basin. Lat. Amer. Anti. 23, 235–258.

712   Lu, H., Wu, N., Liu, B., 1997. Recognition of Rice Phytoliths, in: Pinilla, A., Juan-

713   Tresserras, J., Machado, M.J. (Eds.), The State of the art Phytoliths in Soils and Plants, Centro de

714   Ciencas Medioambientales, Madrid.

715   Lu, H., Liu, Z., Wu, N., Berne, S., Saito, Y., Liu, B., Wang, L., 2002. Rice domestication and

716   climatic change: phytolith evidence from East China. Boreas 31, 378–385.

717   Lu, H., Zhang, J., Wu, N., Liu, K-b, Xu, D. and Li, Q. 2009a. Phytolith Analysis for the

718   Discrimination of Foxtail Millet (*Setaria italica*) and Common Millet (*Panicum miliaceum*).

719   PLoS ONE 4, e4448.

720   Lu. H., et al., 2009b. Earliest domestication of common millet (*Panicum miliaceum*) in

721   East Asia extended to 10,000 years ago. Proc. Natl. Acad. Sci. USA 106, 7367–7372.

722   Ma, X., Fang, J., 2007. Silicas in leaves of eight wild rice species, Acta Bot. Boreali-

723   Occidentalia Sinica, 27, 1531–1536.

724   Ma, J. F., Tamai, K., Yamaji, N., Mitani, N., Konishi, S., Katsuhara, M., Ishiguro, M.,

725   Murata, Y., and Yano, M., 2006. A silicon transporter in rice. Nature 440, 688–691.

726   Ma, J. F., Yamaji, N., Mitani, N., Tamai, K., Konishi, Fujiwara, T., Katsuhara, M., and Yano,

727   M. 2007. An efflux transporter of silicon in rice. Nature 448, 209–212.

728   Ma, Z., Li, Q., Huan, X., Yang, X., Zheng, J., Ye, M., 2014. Plant microremains provide

729   direct evidence for the functions of stone knives from the Lajia site, northwestern China. Chin.

730   Sci. Bull. 59, 1151–1158.

731   Madella, M., Jones, M., Echlin, P., Powers-Jones, A., Moore, M., 2009. Plant water

732   availability and analytical microscopy of phytoliths: Implications for ancient irrigation in arid

733   zones. Quat. Int. 193, 32–40.

734   Madella, M., Lancelotti, C. 2012. Taphonomy and phytoliths: A user manual. Quat. Int. 275,

735   76–83.

736   Madella, M., Jones, M.K., Ecklin, P., Powers-Jones, A., Moore, M., 2009. Plant water

737   availability and analytical microscopy of phytoliths: Implications for ancient irrigation in arid

738   zones. Quat. Int. 193, 32–40.

739   Madella, M., Lancelotti, C., García-Granero, J.J., 2013. Millet microremains—an alternative

740   approach to understand cultivation and use of critical crops in Prehistory. Archaeol. Anthropol.

741   Sci. on-line first DOI 10.1007/s12520-013-0130-y.

742   Madella, M., Garcia-Granero, J., Out, W., Ryan, P., Usai, D., 2014. Microbotanical evidence

743   of domestic cereals in Africa 7000 Years Ago. PLoS ONE, 9 (10).

744   Manning, K., Pelling, R., Higham, T., Schwenniger, J-L., Fuller, D., 2011. 4500-Year old

745   domesticated pearl millet (*Pennisetum glaucum*) from the Tilemsi Valley, Mali: new insights

746   into an alternative cereal domestication pathway. J. Archaeol. Sci. 38(2), 312–322.

747   Marston, J.M., d'Alpoim Guedes, J., and Warinner, C., Eds., 2014. Method and Theory in

748   Paleoethnobotany. University of Colorado Press, Boulder.

749   Mbida, C., Doutrelepont, H., Vrydaghs, L., Swennen, R., Swennen, R., Beeckman, H., De

750   Langhe, E., de Maret, P., 2001. First archaeological evidence of banana cultivation in central

751   Africa during the third millennium before present. Veg. Hist. Archaeobot. 10, 1–6.

752   Mulholland, S.C., 1993. A test of phytolith analysis at Big Hidatsa, North Dakota, in:

753   Pearsall, D.M., Piperno, D.R. (Eds.) Current Research in Phytolith Analysis: Applications in

754   Archaeology and Paleoecology. MASCA Research Papers in Science and Archaeology,

755   University of Pennsylvania, Philadelphia, vol. 10, pp. 131–145.

756   Mulholland, S.C., Rapp, G.R., 1992. A morphological classification of grass silica-bodies,

757   in: Rapp, G.R., Mulholland, S.C. (Eds.), Phytolith Systematic. Plenum Press, New York, pp. 65–

758   89.

759   Novello, A., Barboni, D., 2015. Grass inflorescence phytoliths of useful species and wild

760   cereals from sub-Saharan Africa. J. Archaeol. Sci. 59, 10–22.

761   Pearsall, D.M., 1978. Phytolith analysis of archeological soils: Evidence for maize

762   cultivation in formative Ecuador. Science 199, 177–178.

763   Pearsall, D.M., 2000. Paleoethnobotany: a Handbook of Procedures. 2nd edition. Academic

764   Press, San Diego.

765   Pearsall, D.M., 2003. Plant food resources of the Ecuadorean Formative: An overview and

766   comparison to the Central Andes, in: Archaeology of Formative Ecuador. Raymond, J.S.,

767   Burger, R.L. (Eds.). Dumbarton Oaks, Washington, D.C., pp. 213–257.

768   Pearsall, D.M. 2014. Formation processes of pollen and phytoliths, in: Marston, J.M., J.

769   d'Alpoim Guedes, J., Warinner, C. (Eds), Method and Theory in Paleoethnobotany. University

770   of Colorado Press, Boulder, pp.

771   Pearsall, D.M., 2015a. Paleoethnobotany. A Handbook of Procedures, Third edition. Left

772   Coast Press, Walnut Creek, CA.

773   Pearsall, D.M., 2015b. "The Phytoliths in the Flora of Ecuador Project: Order Tables."

774   [http://phytolith.missouri.edu].

775   Pearsall, D.M., Piperno, D.R., Dinan, E.H., Umlauf, R., Zhao, Z.J., Benfer, R.A., 1995.

776   Distinguishing rice (*Oryza Sativa* Poaceae) from wild *Oryza* Species through phytolith analysis -

777   results of preliminary research, Econ. Bot. 49, 183–196.

778   Pearsall, D.M., Chandler-Ezell, K., Chandler-Ezell, A., 2003. Identifying maize in

779   neotropical sediments using cob phytoliths. J. Archaeol. Sci. 30, 611–627.

780   Pearsall, D.M., Chandler-Ezell, K., Zeidler, J.A., 2004. Maize in ancient Ecuador: results of

781   residue analysis of stone tools from the Real Alto site. Journal of Archaeological Science

782   31:423–442.

783   Peleg, Z., Saranga, Y., Fahima, T., Aharoni, A., Elbaum, R,. 2010. Genetic control over silica

784   deposition in wheat awns. Physiol. Plantarum, 140, 10–20.

785   Perrier, X., De Langhe, E., Donohue, M., Lentfer, C., Vrydaghs, L., Bakrya, F., Carreel, F.,

786   Hippolytea, I., Horrya, J-P., Jenny, C., Leboth, V., Risteruccia, A-M., Tomekpea, K.,

787   Doutreleponte, H., Balli, T., Manwaringi, J., de Maretj, P., Denhamk, T., 2011. Multidisciplinary

788   perspectives on banana (*Musa* spp.) domestication. Proc. Natl. Acad. Sci. U.S.A. 108, 11311–

789   11318.

790   Piperno, D.R., 1984. A comparison and differentiation of phytoliths from maize and wild

791   grasses: use of morphological criteria. Amer. Anti. 49, 361–383.

792   Piperno, D.R., 1985. Phytolith taphonomy and distributions in archaeological sediments from

793   Panama. J Archeol Sci 12:246-267.

794   Piperno, D.R., 1988. Phytolith Analysis: An Archaeological and Geological Perspective.

795   Academic Press, San Diego.

796   Piperno, D.R., 1989. The occurrence of phytoliths in the reproductive structures of selected

797   tropical angiosperms and their significance in tropical paleoecology, paleoethnobotany, and

798   systematics. Rev. Palaeobot. Palyn. 61, 147–173.

799   Piperno, D.R., 2006. Phytoliths: A Comprehensive Guide for Archaeologists and

800   Paleoecologists. AltaMira Press, New York.

801   Piperno, D.R., 2009. Identifying crop plants with phytoliths (and starch grains) in

802   Central and South America: a review and an update of the evidence. Quat. Int.

803   193, 146–159.

804   Piperno, D.R., 2011. The origins of plant cultivation and domestication in the New World

805   tropics. Curr. Anthropol. 52(S4), S453–S470.

806   Piperno, D.R., Pearsall, D.M., 1993. Phytoliths in the reproductive structures of maize and

807   teosinte: implications for the study of maize evolution. J. Archaeol. Sci. 20, 337–362.

808   Piperno, D.R., Pearsall, D.M., 1998a The Silica Bodies of Tropical American Grasses:

809   Morphology, Taxonomy, and Implications for Grass Systematics and Fossil Phytolith

810   Identification. Smithsonian Contrib. Bot. Number 85, pp. 1-40.

811   Piperno, D.R., Pearsall, D.M. ,1998b. The Origins of Agriculture in the Lowland Neotropics.

812   Academic Press, San Diego.

813   Piperno, D.R., Stothert, K.E., 2003. Phytolith evidence for early Holocene *Cucurbita*

814   domestication in southwest Ecuador. Science 299, 1054–1057.

815   Piperno, D.R., Dillehay, T., 2008. Starch grains on human teeth reveal early broad crop diet

816   in northern Peru. Proc. Natl Acad Sci USA 105,19622–19627.

36

817   Piperno, D.R., Andres, T.C., Stothert, K.A., 2000. Phytoliths in *Cucurbita* and other

818   Neotropical Cucurbitaceae and their occurrence in early archaeological sites from the lowland

819   American tropics. J. Archaeol. Sci. 27, 193–208.

820   Piperno, D., Holst,I., Wessel-Beaver,L., Andres,T.C., 2002. Evidence for the control of

821   phytolith formation in *Cucurbita* fruits by the *hard rind* (*Hr*) genetic locus: archaeological and

822   ecological implications. Proc. Nat. Acad. Sci. USA 99,10923–10928.

823   Piperno, D.R., Clary, K.H., Cooke, R.G., Ranere, A.J., Weiland, D., 1985. Preceramic maize

824   in Central Panama: phytolith and pollen evidence. Amer. Anthro. 87, 871–878.

825   Piperno, D.R., Ranere, A.J., Holts, I., Iriarte, J., Dickau, R., 2009. Starch grain and phytolith

826   evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico.

827   Proc. Natl. Acad. Sci. U.S.A. 106, 5019–5024.

828   Pohl, M.D., et al., 1996. Early agriculture in the Maya lowlands. Lat. Amer. Anti. 7, 355-372.

829   Portillo, M., Valenzuela, S., Albert, R.M., 2012. Domestic patterns in the Numidian site of

830   Althiburos (northern Tunisia): The results from a combined study of animal bones, dung and

831   plant remains. Quat. Int. 275, 84–96.

832   Power, R.C., Rosen, A.M., Nadel, D., 2014. The economic and ritual utilization of plants at

833   the Raqefet Cave Natufian site: The evidence from phytoliths. J. Anthropol. Archaeol. 33, 49–

834   65.

835   Qin, L., 2012. Archaeobotany research and expectation on Chinese argiculture origin, in:

836   School of Archeaology and Museology Peking University, The Center of the Study of Chinese

837   Archaeology in Peking University (Eds.), Archaeological Research, Cultural Relics Press,

838   Beijing, pp. 260–315 (in Chinese).

839   Radomski, K., Neumann, K., 2011. Grasses and Grinding Stones: Inflorescence Phytoliths

840   from Modern West African Poaceae and Archaeological Stone Artifacts. In: Fahmy, A.,

841   Kahlheber, S., D'Andrea, A.C. (Eds.),Windows on the African Past: Current Approaches to

842   African Archaeobotany. Africa Magna Verlag, Frankfurt, pp. 153–166.

843   Ranere, A.J., Piperno, D.R., Holst, I., Dickau, R., Iriarte, J., 2009. The cultural and

844   chronological context of early Holocene maize and squash domestication in the Central Balsas

845   River Valley, Mexico. Proc. Natl. Acad. Sci. USA 106, 5014–5018.

846   Rosen, A.M., 1992. Preliminary identification of silica skeletons from Near Eastern

847   archaeological sites: An anatomical approach, in: Rapp, G.R., Mulholland, S.C. (Eds.), Phytolith

848   Systematic. Plenum Press, New York, pp. 129–147.

849   Rosen AM., 2010. Natufian plant exploitation: Managing risk and stability in an environment

850   of change. Eurasian Prehistory 7, 117-131.

851   Rosen, A.M., Weiner, S., 1994. Identifying ancient irrigation: A new method using opaline

852   phytoliths from emmer wheat. J. Archaeol. Sci. 21, 125–132.

853   Shillito, L.M., 2011a. Simultaneous thin section and phytolith observations of finely

854   stratified deposits from Neolithic catalhoyuk, Turkey: Implications for paleoeconomy and Early

855   Holocene paleoenvironment. J. Quat. Sci. 26, 576–588.

856   Shillito, L.M., 2011b. Taphonomic observations of archaeological wheat phytoliths from

857   Neolithic Catalhöyük, Turkey, and the use of conjoined phytolith size as an indicator of water

858   availability. Archaeom. 53, 631–641.

859   Thompson, R.G., Hart, J.P., Brumbach, H.J., Lusteck, R., 2004. Phytolith evidence for

860   twentieth-century BP maize in northern Iroquoia, Northeast Anthropol. 68, 25-40.

861   Thompson, R.G., 2006. Documenting the presence of maize in Central and South America

862   through phytolith analysis of food residues, in: Zeder M.A., Bradley, D.G., Emshwiller, E.,

863   Smith, B.D., (Eds.). Documenting Domestication: New Genetic and Archaeological Paradigms.

864   University of California Press, Berkeley, pp 82–98.

865   Tubb, H.J., Hodson, M.J., Hodson, G.C., 1993. The inflorescence papillae of the Triticeae: a

866   new tool for taxonomic and archaeological research. Ann. Bot. 72, 537–545.

867   Tsartsidou, G., Lev-Yadun, S., Albert, R.-M., Miller-Rosen, A., Efstratiou, N., Weiner, S.,

868   2007. The phytolith archaeological record: strengths and weaknesses evaluated based on a

869   quantitative modern reference collection from Greece. Jour. Archaeol. Sci. 34, 1262–1275.

870   van Heerwaarden, J., Doebley, J., Briggs, W.H., Glaubitz, J.C., Goodman, M.M., Sánchez

871   González, J.J., Ross-Ibarra, J., Gaut, B.S., Eguiarte, L. 2011. Genetic signals of origin, spread,

872   and introgression in a large sample of maize landraces. Proc. Nat. Acad. Sci. USA 108,1088–

873   1092.

874   Vrydaghs, L., Ball, T.B., Volkaert, H., Vand den Houwe, I., Manwaring, J., De Langhe, E.

875   2009. Differentiating the volcaniform phytolith of bananas: Musa acuminata, in: Denham, T., De

876   Langhe, E., Vrydaghs, L. (Eds.), Ethnobot. Res. Appl. Special Issue: History of Banana

877   Domestication, 7, 239–246.

878   Vrydaghs, L.,De Langhe, E., 2003. Phytoliths: An opportunity to rewrite history, in: INIBAP

879   Annual Report 2002. International Network for the Improvement of Banana and Plantain,

880   Montpellier, France, 14–17.

881   Wang, C., Lu, H., 2012. Research progress of fan shaped phytoliths of rice and relevant

882   issues. Quat. Sci. 32, 269–281 (in Chinese).

883   Wang, Y.J., Lu, H.Y., 1993. The Study of Phytoliths and its Applications. China Ocean

884   Press, Beijing (in Chinese).

885   Weisskopf, A. Harvey, E. Kingwell-Banham, E. Kajale, M. Mohanty, R. Fuller, D.Q., 2014.

886   Archaeobotanical implications of phytolith assemblages from cultivated rice systems, wild rice

887   stands and macro-regional patterns. J. Archaeol. Sci. 51, 43–53.

888   Weisskopf, A. Qin, L. Ding, J. Ding, P. Sun, G. Fuller, D.Q. Applying phytoliths to the

889   reconstruction of rice agriculture: From wet to dry and back again in the Neolithic Lower

890   Yangtze. Antiquity (in press)

891   Wilcox, G. 2007. The adoption of farming and the beginnings of the Neolithic in the

892   Euphrates valley: cereal exploitation between the 12th and 8th millennia cal BC, in:Colledge, S.,

893   Connelly, J. (Eds.), The Origins and Spread of Domestic Plants in Southwest Asia and Europe.

894   University College London Institute of Archaeology Publications. Walnut Creek, CA: Left Coast

895   Press, Inc., pp. 21–36.

896   Wilson, S.M., 1985. Phytolith analysis at Kuk, an early agricultural site in Papua New

897   Guinea. Archaeol. Ocean. 20, 231–238.

898   Wu, Y., Jiang, L., Zheng, Y., Wang, C., Zhao, Z., 2014. Morphological trend analysis of rice

899   phytoliths during the early Neolithic in the Lower Yangtze. J. Archaeol. Sci. 49, 326–331.

900   Yang, X., Zhabng, J., Perry, L., Ma, Z., Wan, Z., Li, M., Diao, X., Lu, H., 2012a. From the

901   modern to the archaeological: Starch grains from millets and their wild relatives in China. J.

902   Archaeol. Sci. 39, 247–254.

903   Yang, X., Wan, Z., Perry, L., Lu, H., Wang, Q., Zhao, C., Li, J., Xie, F., Yu, J., Cui, T.,

904   Wang, T., Li, M., Ge, Q., 2012b. Early millet use in northern China, Proc. Natl. Acad. Sci. 109,

905   3726–3730.

906   Yang, X., Ma, Z., Li, Q., Perry, L., Huan, X., Wan, Z., Li, M., Zheng, J., 2014. Experiments

907   with Lithic Tools: Understanding Starch Residues from Crop Harvesting, Archaeometry 56,

908   828–840.

909   Zarrillo, S., Pearsall, D.M., Raymond, J.S., Tisdale, M.A., Quon, D.J., 2008. Directly dated

910   starch residues document early formative maize (*Zea mays* L.) in tropical Ecuador. Proc. Natl.

911   Acad. Sci. USA 105,5006–5011.

912   Zhang, J.P., Lu, H.Y., Wu, N.Q., Yang, X.Y., Diao, X.M., 2011. Phytolith Analysis for

913   Differentiating between Foxtail Millet (*Setaria italica*) and Green Foxtail (*Setaria viridis*), PLoS

914   ONE 6, e19726.

915   Zhao, Z., Piperno, D.R., 2000. Late Pleistocene/Holocene Environments in the middle

916   Yangtze River Valley, China and rice (*Oryza sativa*) domestication: The phytolith evidence.

917   Geoarchaeology 15, 203–222.

918   Zhao, Z.J., 1998. The Middle Yangtze region in China is one place where rice was

919   domesticated: phytolith evidence from the Diaotonghuan Cave, Northern Jaingxi. Antiquity 72,

920   885–897.

921   Zhang, J.P., Lu, H.Y., Wu, N.Q., Qin, X.G., Wang, L., 2013. Palaeoenvironment and

922   agriculture of ancient Loulan and Milan on the Silk Road. The Holocene 23, 208–217.

923   Zhao, Z.J., Pearsall, D.M., Benfer, R.A., Piperno, D.R., 1998. Distinguishing rice (*Oryza*

924   *sativa* poaceae) from wild Oryza species through phytolith analysis, II: Finalized method. Econ.

925   Bot. 52, 134–145.

926   Zheng, Y.F., Dong, Y.J., Matsui, A., Udatsu, T., Fujiwara, H., 2003. Molecular genetic basis

927   of determining subspecies of ancient rice using the shape of phytoliths, J. Archaeol. Sci. 30,

928   1215–1221.

929 **Figure Captions**

930 Fig. 1. Typical cross-shaped phytolith three-dimensional structures from maize, teosinte, and

931 non-*Zea* grasses. Maize produces high proportions of Variant 1 (mirror-image) cross-shapes

932 while many wild grasses produce high proportions of other types unlike maize. Balsas teosinte,

933 maize's wild progenitor, produces many Variant 2 cross-shapes in its leaves unlike maize. From

934 Piperno, 2006.

935 Fig. 2. Wavy-top (top, bottom left) and ruffle-top rondels (bottom, right) from maize. Ruffle-

936 top rondels occur much more frequently in teosinte than maize. From Piperno, 2006.

937 Fig. 3. The various kinds of non-rondel phytoliths found in teosinte fruitcases. Those

938 diagnostic of teosinte are in the center (a, oblong, one-half decorated; b, elongated spiney; c,

939 elongated with one wavy and one serrated edge). Phytoliths a-f occur in some non-*Zea* grasses,

940 but they like the others are always produced in teosinte and can be used to rule out its presence if

941 absent from samples. The phytoliths range in size from about 10 (phytolith f) to 35 µM in

942 diameter (phytolith b). From Piperno, 2006.

943 Fig. 4. *Tripsacum* fruitcase phytoliths. Unlike those of teosinte or maize, they have serrated

944 edges and ridges across the top. From Piperno, 2006.

945 Fig. 5. Scalloped phytoliths from the domesticated species *Cucurbita moschata*. Wild squash

946 phytoliths have the same morphology but are often much smaller than in domesticates. From

947 Piperno, 2006.

948 Fig. 6. Scalloped phytoliths from bottle gourd. Unlike in *Cucurbita*, scallops are irregularly-

949 shaped and one hemisphere of the phytolith is flat and undecorated. Size ranges from 64 to 112

950 µM. From Piperno, 2006.

951 Fig. 7. Seed phytoliths from arrowroot. From Piperno, 2006.

42

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

953   Fig. 9. An articulated aggregation of inflorescence bract phytoliths from *Triticum*

954   *aestivum* showing the long cell wave patterns and papillae characteristic of *Triticum* sp. Photo by

955   Arlene M. Rosen from modern plant phytolith reference collection at ICREA, University of

956   Barcelona, courtesy of Rosa M. Albert.

957   Fig. 10. An articulated aggregation of inflorescence bract phytoliths from *Hordeum*

958   *vulgare* showing the long cell wave patterns and papillae characteristic of *Hordeum* sp. Photo by

959   Arlene M. Rosen from modern plant phytolith reference collection at ICREA, University of

960   Barcelona, courtesy of Rosa M. Albert.

961   Fig. 11. Drawing of a papilla. Domesticated grasses have a consistent papilla diameter found

962   throughout the multi-cell, as measured by the outer ring of the papillae, while wild 'weed' grass

963   will exhibit a range of papillae diameters. From Piperno, 2006; originally reprinted from Tubb et

964   al. (1993).

965   Fig. 12. Undulated patterns and ending structures of epidermal long cells in the upper lemma

966   and palea for the two millet species. Ω-undulated pattern (A) and wavy type (C) of ending

967   structure in *S. italic*; η-undulated pattern (B) and finger type (D) of ending structure in *P.*

968   *miliaceum*.

969   Fig. 13. Double-peaked glume cell phytoliths from *Oryza*. From Piperno, 2006. Originally

970   re-printed from Zhao et al., 1998.

971   Fig. 14. Comparison of the scale-like decorations on bulliform phytoliths in domesticated and

972   wild rice. Modified from Fujiwara (1976).

973   Fig. 15. Seed phytoliths from *Musa acuminata* subsp. *banksii* (left) and *Ensete*, right. From

974   Piperno, 2006; originally courtesy of Carol Lentfer.

43

975   Fig. 16. Seed phytoliths from *Musa ingens*. From Piperno, 2006; originally courtesy of Carol

976   Lentfer.

977   Fig. 17. A comparison of leaf phytoliths from *Ensete* and *Musa*. From Piperno, 2006. The

978   schematic drawings were originally from Mbida Mindzie et al., 2001 and the photographs were

979   courtesy of Carol Lentfer.

980

981

982

983

984

985

986

987

988

989

990

991

992

993

994

995

996

997

Table 1. Crop Plant Phytolith Production and Levels of Taxonomic Specificity

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

Southern and Southeast Asia			
***_Musa_ spp.[SG-G] (bananas)	High High	Genus 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; llerén 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 con-generic 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 Panicoid 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.

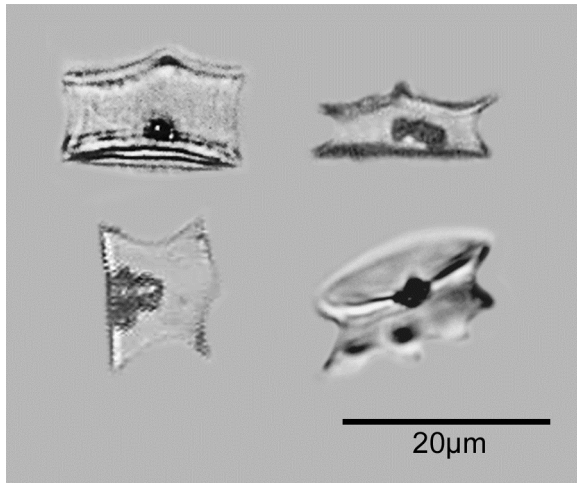Table 2. Discrimination of *S. italica* and *P. miliaceum*

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

Leaf Cross-shaped bodies 3-D Variants
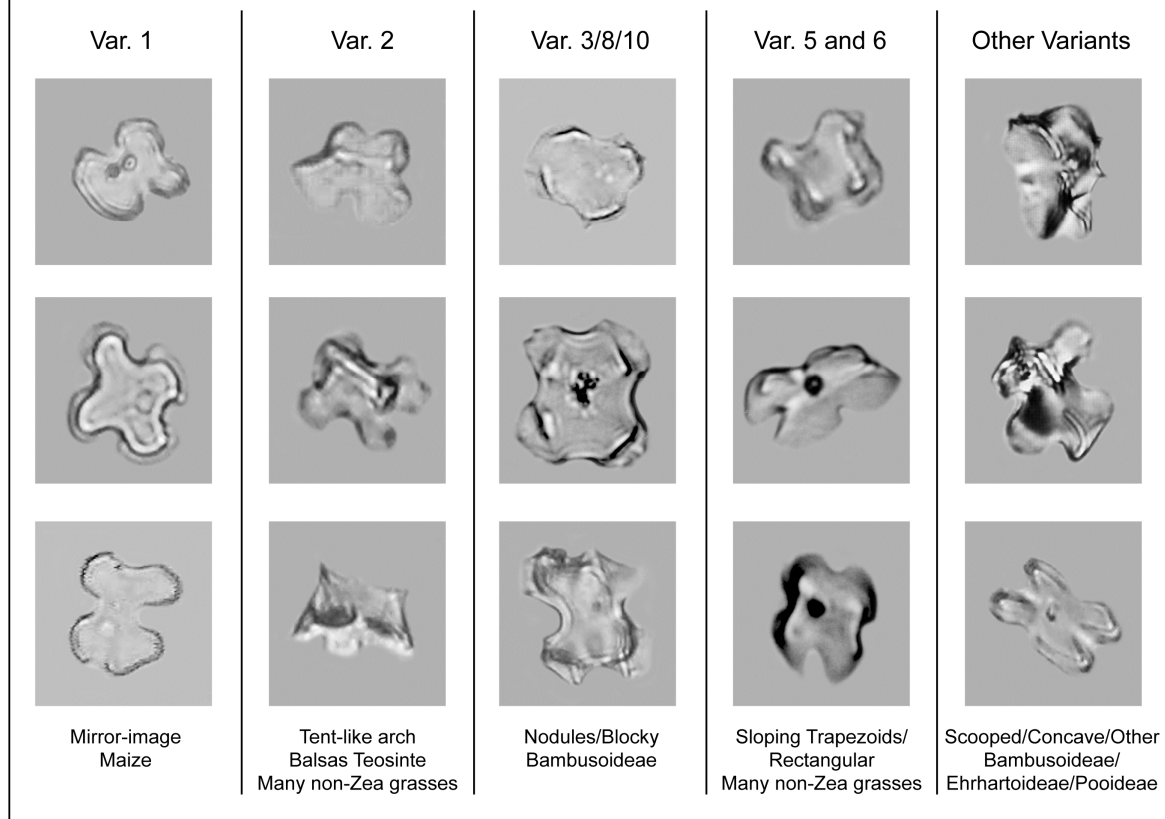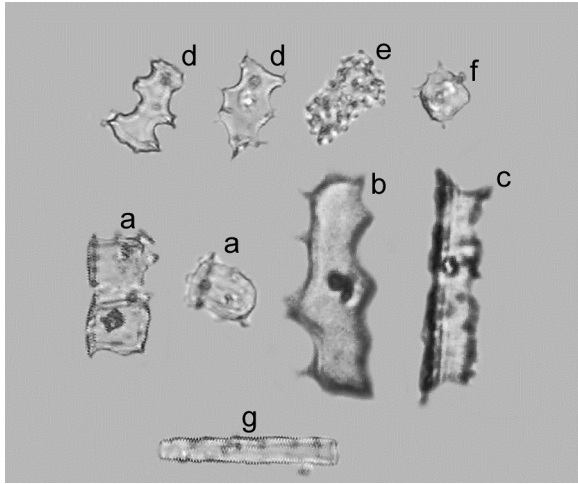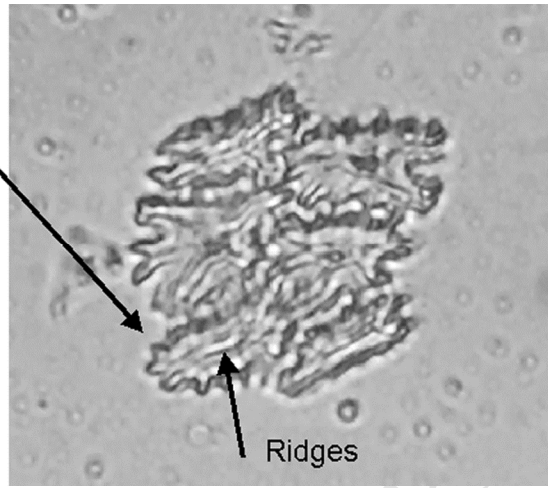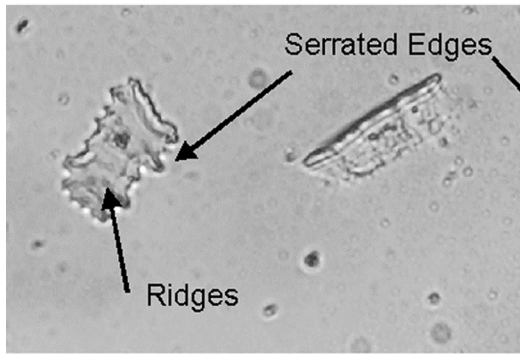
Var. 1	Var. 2	Var. 3/8/10	Var. 5 and 6	Other Variants
Mirror-image Maize	Tent-like arch Balsas Teosinte Many non-Zea grasses	Nodules/Blocky Bambusoideae	Sloping Trapezoids/ Rectangular Many non-Zea grasses	Scooped/Concave/Other Bambusoideae/ Ehrhartoideae/Pooideae

20μm

Domesticated rice   Wild rice

scale-like decorations

40 μm

20 µm

MUSA

CONE SHAPE PART

BASAL PART

longitudinal view

polar view

ENSETE

CONE SHAPE PART

BASAL PART

longitudinal view

polar view
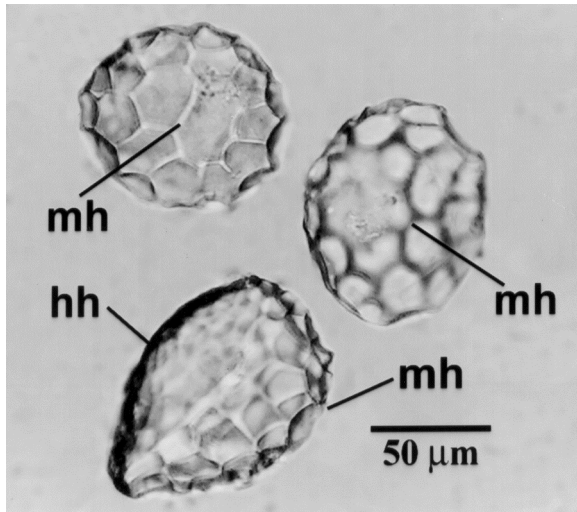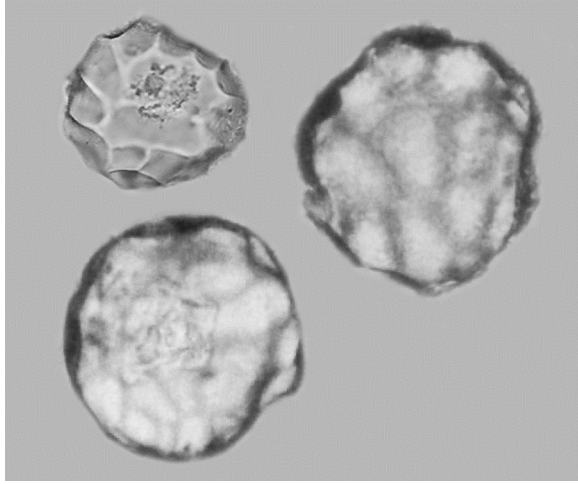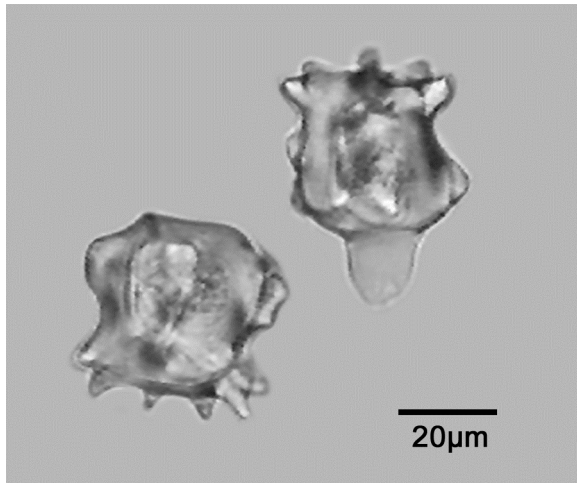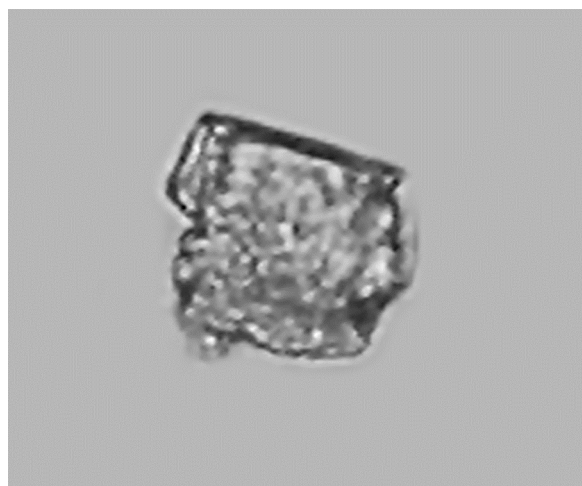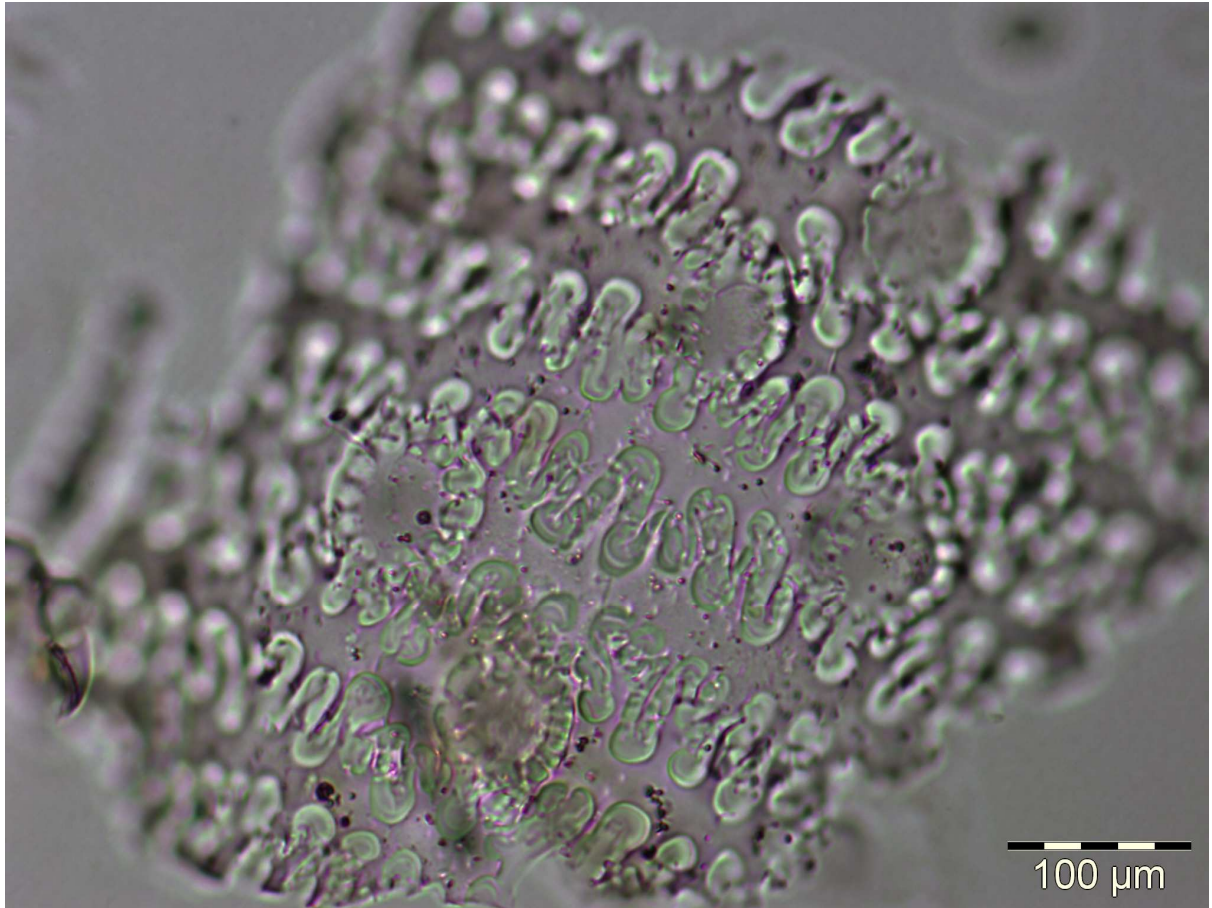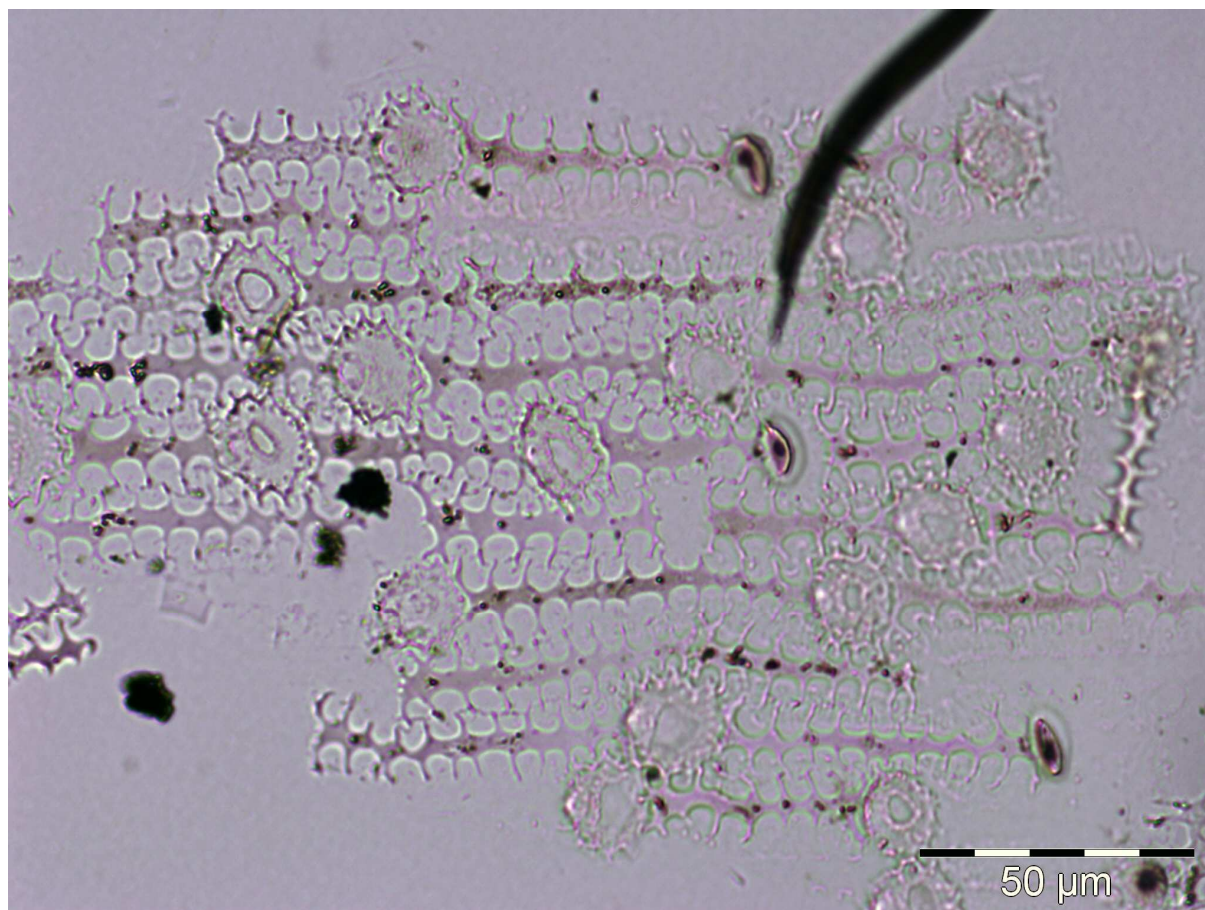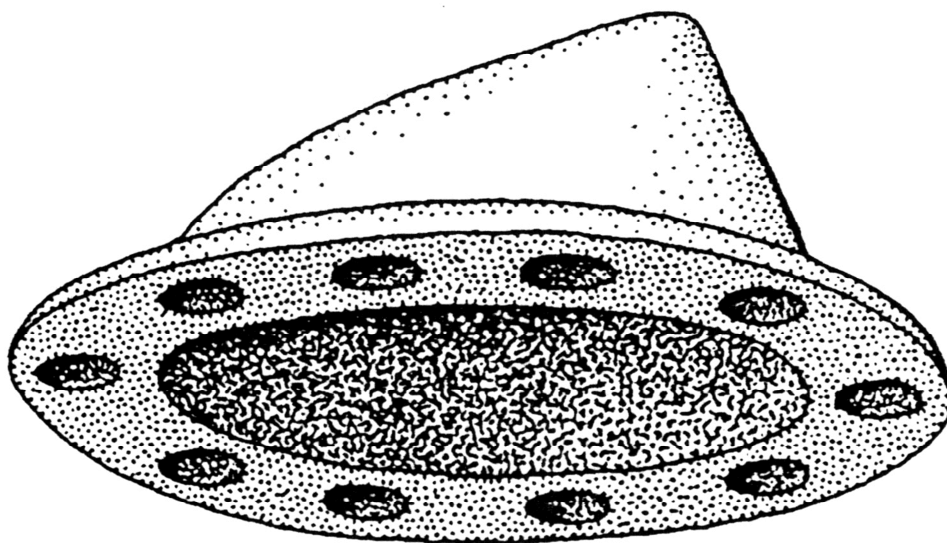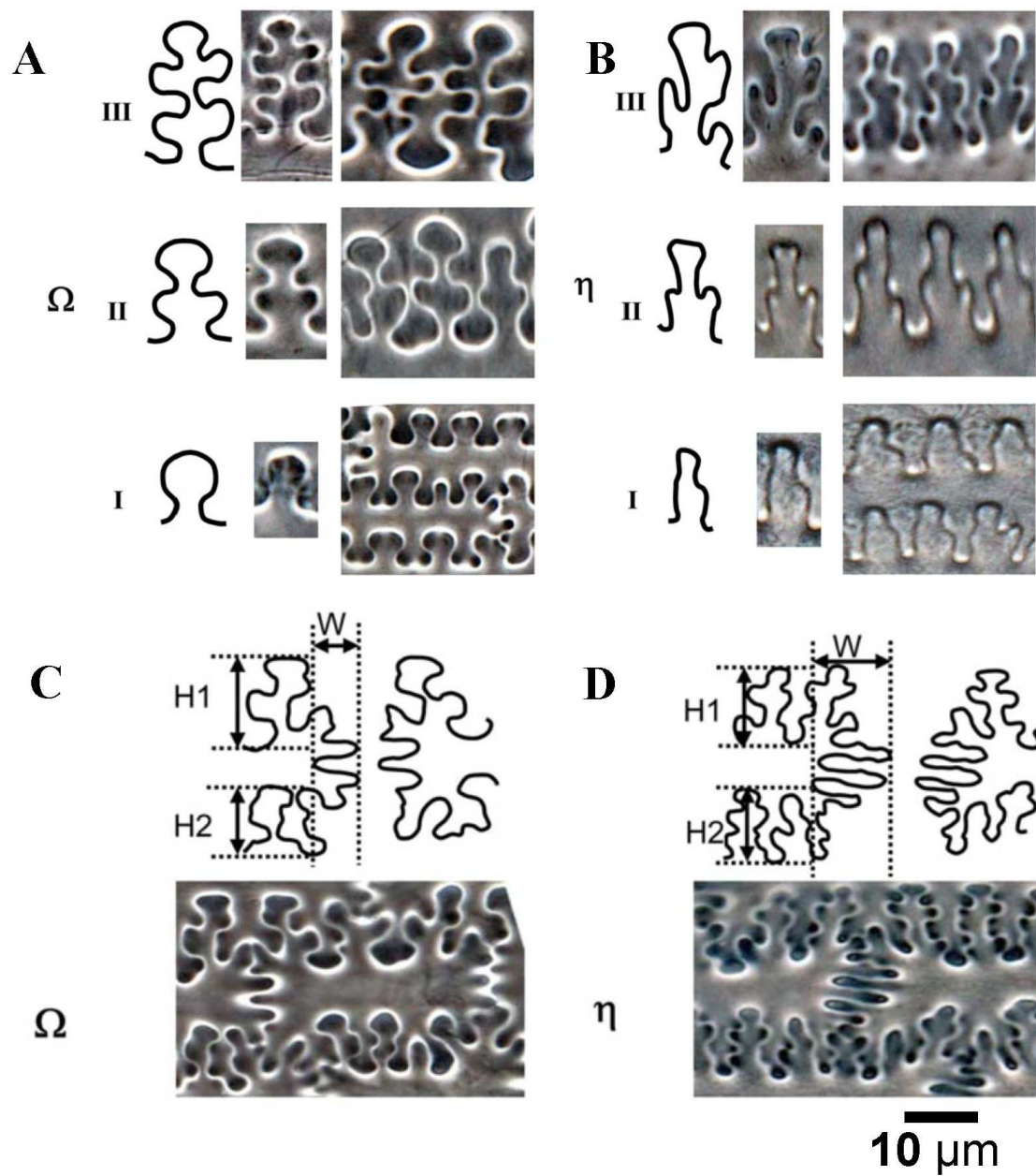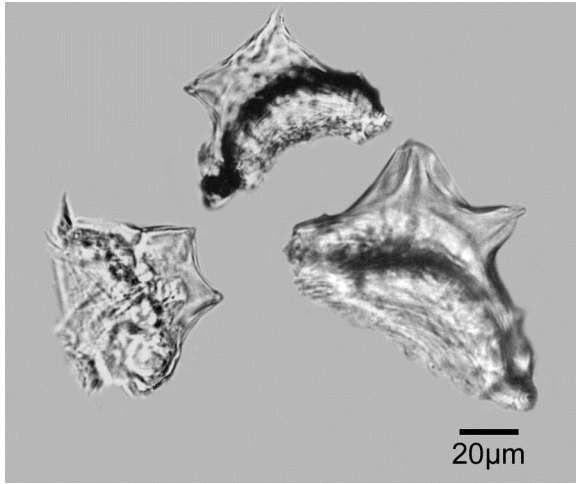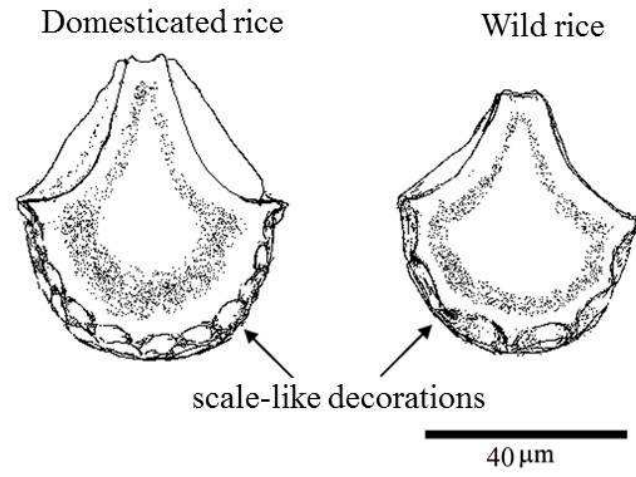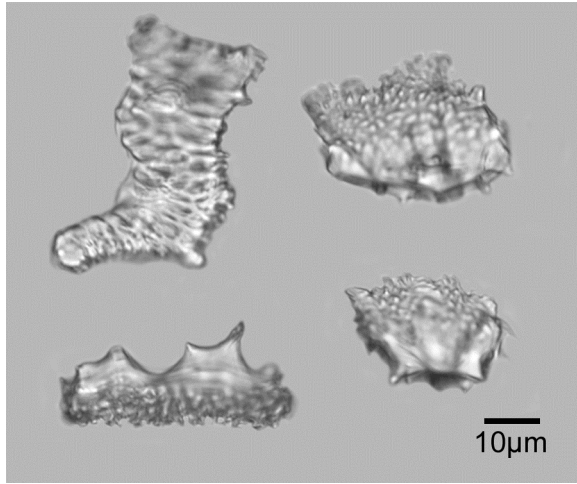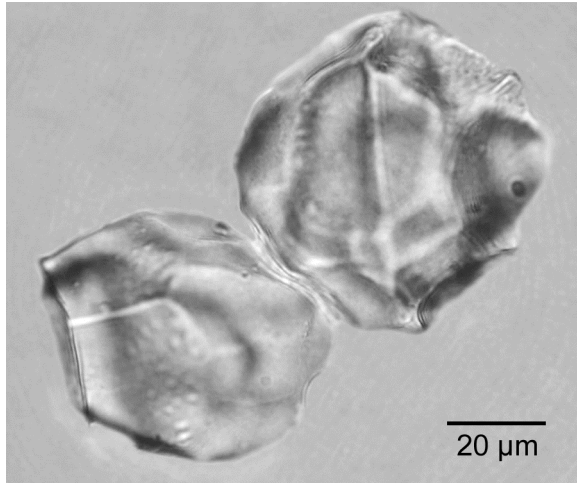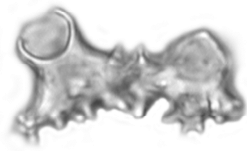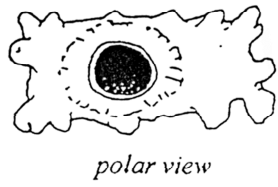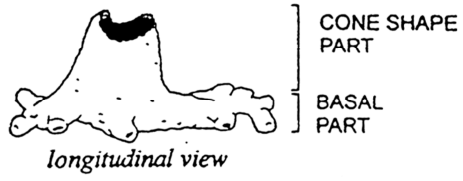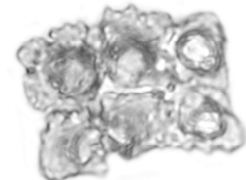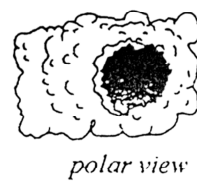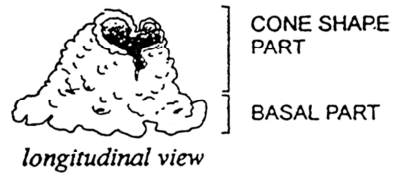
3.1.tif

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.