Phytolith Evidence for Early Holocene *Cucurbita* Domestication in Southwest Ecuador

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Cucurbita **(squash and gourd) phytoliths recovered from two early Holocene archaeological sites in southwestern Ecuador and directly dated to 10,130 to 9320 carbon-14 years before the present (about 12,000 to 10,000 calendar years ago) are identified as derived from domesticated plants because they are considerably larger than those from modern wild taxa. The beginnings of plant husbandry appear to have been preceded by the exploitation of a wild species of** ***Cucurbita*** **during the terminal Pleistocene. These data provide evidence for an independent emergence of plant food production in lowland South America that was contemporaneous with or slightly before that in highland Mesoamerica.**

The transition from hunting and gathering to agriculture was one of the most important economic and social passages of human prehistory, and the topic has long been a focus of archaeological research. Studies in dry highland regions of Mesoamerica show that plant domestication had occurred by 9000 years before the present (yr B.P.) (about 10,000 calendar years ago) (*1*, *2*). However, empirical research in the lowland Neotropics, long hypothesized to have been another independent center of agricultural origins (*3*), has been impeded by the poor preservation of plant remains. Here we describe early plant domestication in Ecuador using an analysis of phytoliths: microscopic siliceous remains of plants that survive in humid environments over long periods of time (*4*).

The early Holocene Las Vegas preceramic culture of coastal Ecuador is known from 34 sites on the Santa Elena Peninsula (*5*, *6*). Excavations at the type site, OGSE-80 (hereafter site 80) have produced evidence for a broad-spectrum subsistence strategy involving terrestrial, estuarine, and mangrove environments, and fairly sedentary occupations dated from about 10,000 to 6600 ^{14}C yr B.P. (about 11,300 to 7300 calendar years ago) (*5*–*7*). Traces of a terminal Pleistocene human presence are found stratified underneath a part of the Las Vegas midden. Cultural materials are sparse in these deep levels, but three ^{14}C determinations on shell and charcoal from this zone range from 10,840 ± 410 yr B.P. to 10,300 ± 240 yr B.P. (about 13,800 to 11,000 calendar years ago) (*5*, *6*).

M5 A4-67 (site 67) is another Las Vegas site located 15 km further inland than site 80 (*6*). Midden contents (chipped stone tools, shells, fish bones, and deer bones) support the idea that this is a habitation site. ^{14}C dates range from ~10,800 to 7250 yr B.P. (Table 1 and table S1) and indicate that occupations at sites 67 and 80 were contemporaneous (*8*). Although seeds, roots, and nuts were not preserved at sites 80 and 67 and pollen grains are rare, phytoliths were abundant.

At site 80, we found the presence of *Cucurbita* fruit phytoliths throughout the Las Vegas occupation, and we suggested that wild *Cucurbita* was exploited during the latest Pleistocene and domesticated by ~9000 yr B.P. (*6*, *7*, *9*). However, our interpretations hinged on this single site, and our chronology was based on dating the carbon isolated from tens of thousands of phytoliths of different sizes and taxonomic classes occurring in the same samples with *Cucurbita* (*7*–*9*). The dates were closely comparable to those from associated shell and charcoal but were not as precise as ^{14}C analysis of individual macrofragments of domesticated plants might have been.

In the present study, we isolated and studied *Cucurbita* phytoliths in three additional sediment samples from the terminal Pleistocene occupation at site 80, as well as 12 samples representing the earliest to latest cultural activity at site 67 (*4*, *8*). Ten samples from site 67 were from a column sample removed from a deep stratigraphic cut, Unit 1, which was located well away from burials; the remaining two were recovered from undisturbed contexts in other portions of the site as the excavations proceeded. To assess the status of the *Cucurbita* remains as wild or domesticated, we used a large modern reference collection comprising 157 mature fruits from 115 different populations, land races, and varieties from most known wild and all domesticated species of *Cucurbita*. We examined 18 fruits from 18 different populations of wild and semi-domesticated varieties from the only known *Cucurbita* native to Ecuador, *Cucurbita ecuadorensis* (*10*–*12*). We dated archaeological *Cucurbita* remains using refined methods of phytolith ^{14}C study (*8*) (figs. S1, A and B).

All archaeological sediment samples yielded spherical scalloped phytoliths specific to the fruit rinds of the genus *Cucurbita* (*7*, *9*, *13*, *14*). An increase in mean and maximum size above those recorded in modern wild plants is a standard criterion for separating wild from domesticated macrobotanical remains (such as seeds and peduncles) of *Cucurbita* archeologically (*2*). Our data show that size criteria are useful in phytolith studies, because mean and maximum phytolith length and thickness in modern wild species are substantially smaller than in domesticated varieties (Fig. 1, A and B). There is also a clear relation between phytolith size and fruit size (Fig. 1C). The sensitivity of phytolith size to domestication can also be seen in individual fruits from wild taxa (*C. argyrosperma* ssp. *sororia* and *C. pepo* ssp. *fraterna*) that exhibit signs of introgression with domesticated species, such as nonbitter flesh. These fruits have somewhat larger phytoliths than do wild examples, with no such evidence of domesticated germ plasm (Fig. 1, A and B, arrows). Moreover, fruits from different wild species and populations sampled over wide geographic areas have similar sizes.

Phytoliths with a mean length of about 82 to 86 μm or longer and a mean and maximum thickness of at least 68 and 90 μm, respectively, are contributed only by semi-domesticated *C. ecuadorensis* fruits at least 14 cm in height or 16 cm in diameter. A maximum phytolith thickness of 100 μm or more was seen only in a *C. ecuadorensis* fruit that was 14 cm in height and 18 cm in diameter, and similarly in the largest fruits of *C. moschata* and *C. ficifolia* studied, with diameters of 17 to 25 cm and heights of 21 to 36 cm (*15*). Phytoliths of such sizes also distinguish all other domesticated from wild taxa and provide a secure baseline for identifying domesticated varieties of archaeological *Cucurbita* in Ecuador.

In three different terminal Pleistocene samples from site 80, where ^{14}C ages on charcoal and shell range between 10,840 ± 410 yr B.P. and 10,300 ± 240 yr B.P., phytolith size is indicative of a wild species of *Cucurbita* (Table 1 and table S1). In the three deepest samples from Unit 1 at site 67 [between 70 and 100 cm beneath the surface(b.s.)], where phytoliths are dated at or somewhat before 10,820 ± 250 yr B.P., phytolith size likewise falls within or close to the upper ends of the means and ranges of wild species. Because no other wild species of *Cucurbita* has been located in Ecuador, the evidence suggests that a wild form of *C.*

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ecuadorensis was present on the landscape and used by the pre–Las Vegas people.

Previous analyses of site 80 indicated that *Cucurbita* phytoliths with sizes substantially exceeding those found in modern wild specimens made their first appearance near the base of the Las Vegas–phase midden in the 110- to 120-cm level of Unit E8-9 (*6*, *7*, *9*). Our initial determination of phytolith age in this sample from a phytolith extract overwhelmingly represented by grass phytoliths isolated from the fine (5 to 20 μm) and coarse (20 to 50 μm) silt was 9080 ± 60 yr B.P. (*7*, *9*) (Table 1, box). Our new results indicate that this date is somewhat too young. Where *Cucurbita* phytoliths are large (with a mean length of 80 μm or more) and numerous, they can be consolidated in large numbers nearly entirely in the sand fraction of a sample, in such a way that few other types of phytoliths are present. We were thus able to segregate about 70% of all the *Cucurbita* phytoliths from Unit E8-9, 110- to 120-cm level. Carbon isolated from approximately 550 domesticated-sized *Cucurbita* phytoliths and 3200 large grass phytoliths concentrated from the sand yielded a date of 10,130 ± 40 ^{14}C yr B.P. (Table 1, box) (*8*).

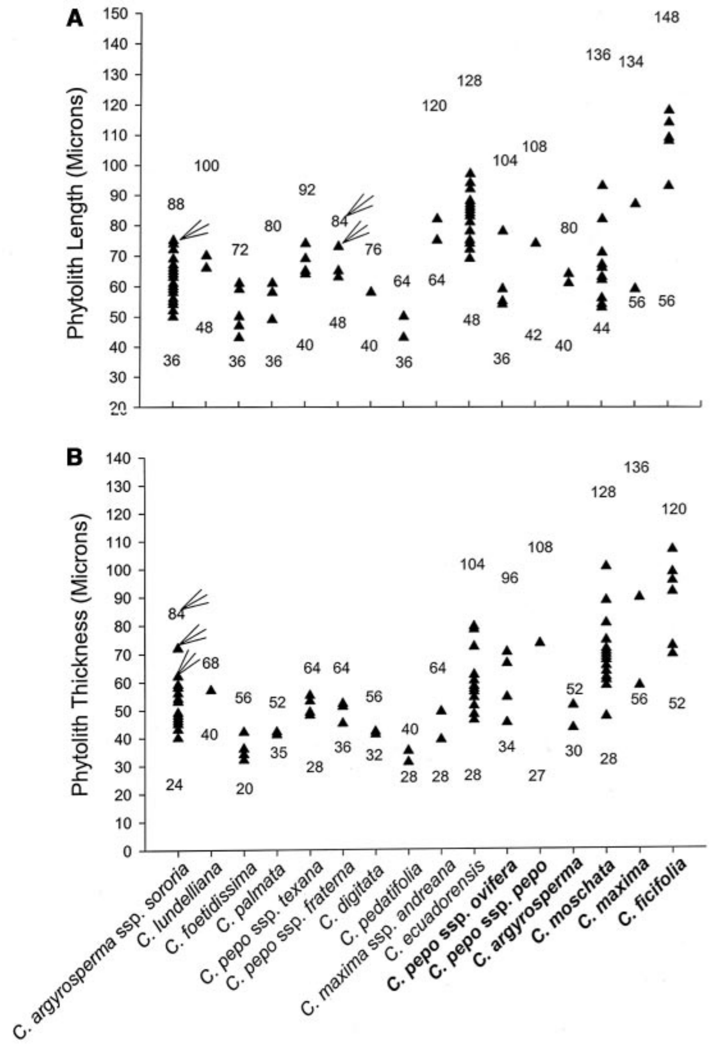
Another date on an isolate of coarse silt phytoliths from this sample, in which the remainder of the *Cucurbita* occur, was 9320 ± 250 yr B.P. Hence, an age of between ~10,100 and 9300 yr B.P. can be assigned to the appearance of a domesticated *Cucurbita*. A new date of 7990 ± 40 yr B.P. on the fine silt (5- to 20-μm) phytolith fraction (Table 1, box), in which no *Cucurbita* phytoliths occur (these were never observed in any fine silt fractions), is younger than that of the coarse silt and sand isolates, thus revealing some variability in the micromovement of phytoliths of different sizes in sediments. Because a previous age determination of 9740 ± 60 yr B.P. on phytoliths from Unit F8-9, 110- to 120-cm level, was carried out on fine and coarse silt phytoliths (here 90% of *Cucurbita* phytoliths occur in the coarse silt), the true age of the *Cucurbita* in this level near the base of the midden is probably older, an inference which is suggested by their size as well (Table 1).

The results from site 67 are similar. In the Unit 1 column samples, the earliest *Cucurbita* phytoliths that are identifiable as derived from a domesticated species occur from 60 to 70 cm b.s. Those from this and stratigraphically higher levels segregate almost entirely in the sand, but they are less densely distributed than in site 80, and separate sand isolations from individual levels could not be dated. Coarse silt phy-

Table 1. Phytolith age and size at Las Vegas sites OGSE-80 and M5A4-67. Under "sample number (*n*)," the first number indicates phytolith length and the second indicates thickness. In the "sample provenience" column, fs is fine silt, cs is coarse silt, and s is sand. All site 80 samples are listed in cm beneath datum (b.d.). Unit 1 column samples from site 67 are listed in cm b.s.; the others are in cm b.d. The date of 3810 ± 40 yr B.P. from site 67 at 3 to 10 cm b.s. is consistent with the presence of a few ceramic sherds dating to the late Valdivia period in superficial contexts at this site. Size ranges for phytolith length and laboratory numbers for radiocarbon dates are available as supporting material on *Science* Online.

^{14}C yr. B.P. phytoliths	Dendrocalibrated calendar yr B.P. 2 SD age range	Mean phytolith length (μm)	Mean phytolith thickness (μm)	Range of thickness (μm)	Sample number (*n*)	Sample provenience, cm b.s. or b.d.
			Site OGSE-80			
7170 ± 60*	8105 to 8095 and 8055 to 7860	94*	78*	64–95	12, 6	GH8-9, 105–110 fs+cs
10130 ± 40	12120 to 11560	86*	68*	42–93	66, 32	E8-9, 110–120, s
9320 ± 250†	11210 to 9900	–	–			E8-9, 110–120, cs
9080 ± 60*	10365 to 10325 and 10275 to 10170	–	–			E8-9, 110–120, fs+cs
7990 ± 220†	9480 to 8370	–	–			E8-9,110–120, fs
9740 ± 60*	11225 to 11095 and 10915 to 10895	72*	55*	36–76	51, 45	F8-9, 110–120, fs+cs
		65‡	55	41–80	9, 3	C113, 210
		72‡	56	36–72	14, 10	CH112, 230
		69‡	59	36–84	16, 9	C112, 268
			Site M5A4-67, Unit 1 column sample			
3810 ± 40	4350 to 4330 and 4300 to 4090	86	70	56–84	15, 13	3–10, fs+cs
5900 ± 40	6780 to 6650					3–10 + 20–30, s
–		88	77	52–96	16, 16	10–20
5910 ± 40	6790 to 6650	–	–			20–30, fs+cs
7250 ± 190†	8400 to 7760	88	73	55–92	18, 15	20–30, cs
–		90	75	44–96	18, 14	30–40
8070 ± 160†	9450 to 8530	(Few *Cucurbita* phytoliths are present)				40–50, fs+cs
8240 ± 170†	9540 to 8650	–	–	–		50–60 + 60–70, cs
		88	75	46–104	24, 19	50–60
		83	72	48–100	16, 14	60–70
10,820 ± 250†	13420 to 11950	79	68	40–84	32, 17	70–80, fs+cs
		77	63	44–80	24, 17	80–90
		73	63	44–74	13, 6	90–100
			M5A4-67, other samples			
	–	86	71	44–100	48, 35	Unit E3, 60–90
8980 ± 40	10220 to 10140 and 10000 to 9960	83	70	48–92	33, 27	Unit E4,110–120, fs+cs+s

*Phytolith date and size data reported previously in (*7*). All phytolith dates were obtained using accelerator mass spectrometry (AMS). †date was obtained with the microsample-AMS ^{14}C phytolith method (*8*). ‡Associated with terminal Pleistocene dates on charcoal and shell of 10,840 ± 410, 10,300 ± 240, and 10,500 ± 130 ^{14}C yr B.P. (13,790 to 10,870 calendar years ago).



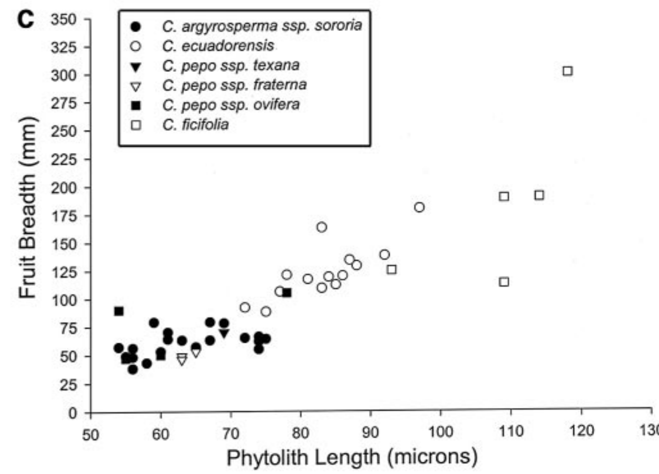


Fig. 1. (**A**) Length and (**B**) thickness of scalloped phytoliths in nine wild, six domesticated, and one semidomesticated species of *Cucurbita*. Names of domesticated species are shown in bold print. Each triangle represents the mean phytolith size from an individual fruit, usually from a separate population, for which at least 50 phytoliths were measured. Numbers above and below the triangles are size ranges recorded for each species. For detailed information on the localities where these plants were collected or grow, see (*14*). (**C**) Relationship between phytolith length and fruit breadth for three wild, two domesticated, and one semidomesticated species of *Cucurbita*. Pearson's correlation coefficient = 0.88; $P < 0.001$.

toliths combined from 50 to 60 and 60 to 70 cm b.s. of Unit 1 have an age of 8240 ± 170 yr B.P. An earlier Holocene age is therefore likely for the 60- to 70-cm b.s. *Cucurbita* remains, a scenario supported by a 8980 ± 40 yr B.P. age on a phytolith assemblage containing domesticated *Cucurbita* from Unit E4, 110- to 120-cm level.

The 5900 ± 40 yr B.P. phytolith age from a combination of equal amounts of sand fraction phytoliths from 3 to 10 and 20 to 30 cm b.s. of Unit 1, where coarse silt phytolith ages were 3810 ± 40 and 7250 ± 190 B.P., respectively, accurately reflects a mixture of phytoliths from these two time periods. This finding further indicates that downward displacement of larger-sized phytoliths is negligible, because it should have resulted in a much younger age determination for the phytoliths combined from 3 to 10 and 20 to 30 cm.

The morphologies of the *Cucurbita* phytoliths documented at sites 80 and 67 closely conform to those from modern wild and semidomesticated *C. ecuadorensis*, and the earliest Holocene domestication probably resulted from the husbandry of a local wild *C. ecuadorensis*. Some land races of *C. moschata*, including those collected in southwest Ecuador (*10*), contribute phytoliths whose size and morphological characteristics make them indistinguishable from semi-domesticated *C. ecuadorensis.* Therefore, contribution from both *C. ecuadorensis* and *C. moschata*, with postulated origins in tropical lowland Colombia (*16*), should not be ruled out, particularly during the later stages of the Las Vegas preceramic occupations. In addition to *Cucurbita*, phytoliths from the bottle gourd (*Lagenaria siceraria*) and *Calathea allouia*, a root crop used casually today in indigenous neotropical horticulture, are present at sites 80 and 67 as early as ~9300 yr B.P. (*7*, *9*).

Our findings indicate that an intensification of plant use in broad-spectrum foraging economies, leading to plant food production, arose independently in tropical northern South America shortly after the termination of the Pleistocene. Seeds of *Cucurbita* spp. are oil- and protein-rich and were favored by some of the latest foragers and earliest farmers in Mesoamerica (*1*, *2*) and South America. Our data also indicate that Las Vegas horticulture prepared the way for the intensification of agriculture based on major seed and root crops during the early ceramic Valdivia period (beginning ~5500 yr B.P.) in coastal Ecuador (*5*, *17*, *18*). The domestication of local varieties of *Cucurbita* in southwest Ecuador supports views (*19*) that in South America there was no single center of agricultural origins.

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12. Despite extensive searches, no other wild *Cucurbita* has been found in Ecuador (*10*, *11*). *C. ecuadorensis* is believed to have been at least semi-domesticated and used more commonly in the past than it is at the present time (*10*, *11*). Many free-living populations, which are common in dry forest and along streams and road banks, have small (~8 to 10 cm long) and bitter fruits. Vines found today in house gardens, where they are grown or maintained and consumed by humans or more commonly fed to domestic animals, have fruits with sizes of domesticated species (from 12 to 14 cm long and 12 to 18 cm in diameter) and other domesticated characteristics, such as nonbitter flesh, nonlignified rinds, and considerable variability in color and pattern (*10*).
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15. Phytoliths are placed in fruit rinds in such a way that they straddle the interface between the hypodermis and the outermost stone (lignified) cells. Phytolith thickness is greatly influenced by how large the stone cells are. Domesticated fruits make longer and larger stone cells than do wild fruits, hence phytolith thickness is also a sensitive indicator of domestication (*14*).
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20. Supported by the Smithsonian Tropical Research Institute and the Museo Antropológico, Banco Central del Ecuador (Guayaquil).

Supporting Online Material

www.sciencemag.org/cgi/content/full/299/5609/1054/DC1

Materials and Methods

Fig. S1

Table S1

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Materials and Methods

Site 67 Sampling

The column samples from the wall of Unit 1 from Site 67 that are labeled 80 to 90 cm b.s. correspond to the portion of the midden with the most dense concentration of shell, bone, stone artifacts, fire-altered stone, and bits of burnt earth. This midden deposit is at least 40 cm thick and has no visible stratigraphy. The column sample was excavated in artificial 10 cm levels within this midden. The 7890 ± 70 date on shell, sampled at about the same depth as the column sample from the wall, is 3000 ^{14}C yrs. younger than the phytolith date from the 80 to 90 b.s. column sample. The difference probably reflects the deposition of shell in highly compressed midden characterized by horizontal heterogeneity.

Phytolith Analysis and Dating

Phytoliths were isolated from modern plants and archaeological sediments using standard methods of analysis (ref. *4* in the print manuscript). As described therein, discrete separations of phytoliths from fine silt, coarse silt, and sand fractions of sediment were achieved by gravity sedimentation and wet sieving over a 270 mesh geological screen.

Conventional and accelerator mass spectrometry (AMS) analysis of the carbon-14 trapped within phytoliths was originally described and applied to sediment phytoliths from archaeological and paleoecological contexts in North America (*S1-S3*). We dated phytolith samples by AMS using refinements of these methods developed by Darden Hood of the Beta-Analytic Inc. radiocarbon laboratory, Miami, Florida and DRP, which allow age determinations on smaller numbers of phytoliths, including reasonably discrete separations of *Cucurbita*. Phytoliths for ^{14}C study were isolated from 5 to 10 grams of sediment using the following modifications to standard methods:1) sterile test tubes were used for all steps, 2) oxidation in a solution of concentrated HNO3 and $KClO_3$ was preceded by a 10 minute warm bath in 10% KOH to enhance removal of humic acids, and 3) after phytoliths were removed from sediment by chemical flotation, they were washed and re-heated in concentrated HNO3 and $KClO_3$ to ensure removal of any organic material that might be clinging to surficial crevices. Before submission to the radiocarbon facility, a sub-sample was weighed and then mounted on a microscope slide, and all phytoliths were counted and identified. The number of phytoliths dated was estimated by extrapolation to the sample weight combusted and graphitized at the radiocarbon laboratory.

Once at the radiocarbon facility, phytolith samples were combusted to carbon dioxide in a closed chemistry line under active oxygen flow. Tin was added to the samples prior to combustion so that upon application of heat, the temperature of combustion would elevate to +1400 C via the exothermic reaction between tin and oxygen. This temperature completely melted the phytoliths and thoroughly combusted the target organic carbon within them. Comparisons of SEM photos taken before and after combustion demonstrating an almost pure separation of phytoliths before and only melted silica afterward, confirmed this result (Figs. S1A and B).

In cases where available carbon was below about 250 micrograms after combustion, the small volume of evolved sample CO2 was measured and then diluted with a known quantity of radiocarbon dead CO2 (called the Micro-sample AMS or MS-AMS). This step ensured that enough graphite, about 0.5 to 1 mg, was available for a standard AMS analysis with appropriate fractionation correction. The fraction of sample gas within the diluted gas was calculated as a "dilution factor" to use in the final data calculation. The sigma on the date was derived by combining the counting errors and uncertainties in the dilution step.

Validation of the dating was performed by analyzing a known age reference standard in conjunction with each unknown sample analysis. The reference sample used was TIRI wood "B" (Belfast Pine) with a consensus age of 4503 ± 6 B.P. The standard was analyzed using approximately the same quantity of carbon as the unknown sample and was diluted with the same gas used to dilute the unknown sample. All wood dilution results were in very close agreement with the known age of the reference sample.

Fig. S1. (**A**) The nearly pure separation of phytoliths that was submitted for carbon-14 study from the fine and coarse silt fraction of Vegas Site M5A4-67, Unit 1, 40-50 cm beneath surface. (**B**) The same preparation of phytoliths as above after combustion at Beta Analytic Inc. radiocarbon facility showing how the phytoliths are completely melted, liberating the carbon within them for carbon-14 study. The carbon that was isolated from this treatment returned an age of 8070 ± 160 B.P.

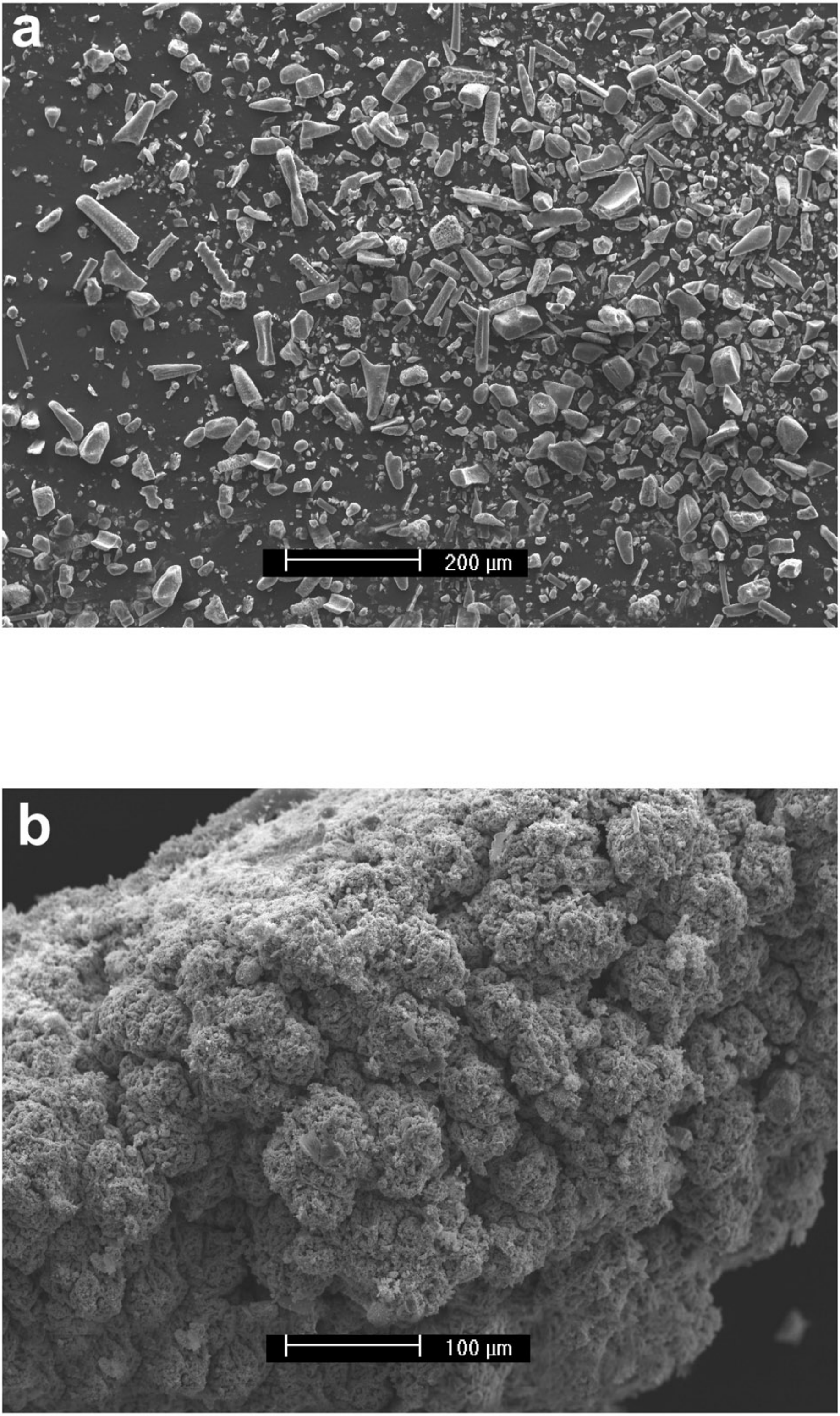
a
200 µm
b
100 µm

Table S1. Phytolith Age and Size in Vegas Sites OGSE-80 and M5A4-67

^{14}C yr. B.P. Phytoliths	Dendrocalibrated, cal-BP 2 S.D. age range	Lab number	Phytolith Length µm	Range	Phytolith Thickness µm	Range	*n*	Sample Provenience cm beneath surface/datum
Site OGSE-80								
7170 ± 60*	8105 to 8095 and 8055 to 7860	UCR-3282; CAMS-14216	94*	64-116	78*	64-95	12, 6	GH8-9, 105-110 fs+cs
10130 ± 40	12120 to 11560		86*		68*	42-93	66, 32	E8-9,110-120, s
9320 ± 250**	11210 to 9900		-		-			E8-9, 110-120, cs
9080 ± 60*	10365 to 10325 and 10275 to 10170		-		-			E8-9, 110-120, fs+cs
7990 ± 220**	9480 to 8370		-		-			E8-9,110-120, fs
9740 ± 60*	11225 to 11095 and 10915 to 10895	UCR-3284; CAMS-14218	72*	48-108	55*	36-76	51, 45	F8-9, 110-120, fs+cs
			65	56-92	55	41-80	9, 3	C113, 210
			72	56-106	56	36-72	14, 10	CH112, 230
			69	40-108	59	36-84	16, 9	C112, 268

Samples from C113, CH112, and C112 are associated with dates on charcoal and shell of 10,840 ± 410, 10,300 ± 240, and 10,500 ± 130 ^{14}C yr. B.P. (13,790 to 10,870 calendar years ago).

^{14}C yr. B.P. Phytoliths	Dendrocalibrated, cal-BP 2 S.D. age range	Lab number	Phytolith Length µm	Range	Phytolith Thickness µm	Range	*n*	Sample Provenience cm beneath surface/datum
Site M5A4-67, Unit 1 Column Sample								
3810 ± 40	4350 to 4330, 4300 to 4090	Beta-168374	86	64-104	70	56-84	15, 13	3-10, fs+cs
5900 ± 40	6780 to 6650	Beta-169266	-	-	-	-	-	3-10 + 20-30 s
	-	-	88	64-104	77	52-96	16, 16	10-20
5910 ± 40	6790 to 6650	Beta-168269	-	-	-	-	-	20-30, fs+cs
7250 ± 190**	8400 to 7760	Beta-167241	88	68-108	73	55-92	18,15	20-30, cs
-			90	58-116	75	44-96	18, 14	30-40
8070 ± 160**	9450 to 8530	Beta-161403	Few *Cucurbita* phytoliths are present					40-50, fs+cs
8240 ± 170**	9540 to 8650	Beta-170223	-	-	-	-	-	50-60 + 60-70, cs
	-	-	88	52-104	75	46-104	24,19	50-60
	-	-	83	56-108	72	48-100	16, 14	60-70
10,820 ± 250**	13420 to 11950	Beta-167239	79	45-112	68	40-84	32,17	70-80, fs+cs
	-	-	77	48-104	63	44-80	24,17	80-90

-		-	73	54-88	63	44-74	13, 6	90-100
M5A4-67, Other Samples								
-		-	86	64-112	71	44-100	48, 35	Unit E3, 60-90
8980 ± 40	10220 to 10140 and 10000 to 9960	Beta-167242	83	52-116	70	48-92	33, 27	Unit E4,110-120, fs+cs+s

*Phytolith date and size data reported previously in ref. 9 of the print manuscript. **MS-AMS ^{14}C phytolith method. fs=fine silt, cs=coarse silt, s=sand. Under sample number (*n*), the first is for phytolith length and the second is for thickness. All Site 80 samples are in cm beneath datum (b.d.). Unit 1 column samples from Site 67 are in cm beneath surface (b.s.); the other two are in cm. b.d. The date of 3810 ± 40 B.P. from 3-10 b.s. of Site 67 is consistent with the presence of a few ceramic sherds dating to the late Valdivia period in superficial contexts at this site.

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