Late Archaic–Early Formative period microbotanical evidence for potato at Jiskairumoko in the Titicaca Basin of southern Peru

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The data presented in this paper provide direct microbotanical evidence concerning the early use of potato (*Solanum tuberosum*) within its botanical locus of origin in the high south-central Andes. The data derive from Jiskairumoko, an early village site in the western Titicaca Basin dating to the Late Archaic to Early Formative periods (~3,400 cal y BC to 1,600 cal y BC). Because the site reflects the transition to sedentism and food production, these data may relate to potato domestication and early cultivation. Of 141 starch microremains recovered from 14 groundstone tools from Jiskairumoko, 50 are identified as consistent with cultivated or domesticated potato, based on reference to published materials and a study of wild and cultivated potato starch morphology. Along with macro- and microbotanical evidence for chenopod consumption and grinding tool data reflecting intensive use of this technology throughout site occupation, the microbotanical data reported here suggest the intensive exploitation, if not cultivation, of plant resources at Jiskairumoko. Elucidating the details of the trajectory of potato domestication is necessary for an overall understanding of the development of highland Andean agriculture, as this crop is central to the autochthonous agricultural suite. A paucity of direct botanical evidence, however, has hindered research efforts. The results of the modern and archaeological starch analyses presented here underscore the utility of this method in addressing questions related to the timing, mode, and context of potato origins.

microbotanical starch analysis | *Solanum tuberosum* | plant domestication | south-central Andes | food production

Recent molecular and phytogeographical data indicate the high south-central Andes as the locus of domestication for several crops, including the potato (*Solanum tuberosum*) (1–3). Archaeological evidence from the region pinpoints the Late Archaic (~3,400–2,200 cal y BC) and Terminal Archaic periods (~2,200–1,600 cal y BC) as the time during which the transition from foraging to agro-pastoralism transpired; small-scale farming was in place by the subsequent Early Formative period (~1,600 cal y BC) (4–7).

Despite the centrality of geophytes to the high-elevation crop suite, however, most of their origins remain elusive. Macrobotanical preservation of this class of plants—and the diagnostic utility of macrogeophyte remains—is limited. Accordingly, beginning in the 1960s, Andeanists Towle (8) and Ugent et al. (9, 10) sought to further their insights through microbotanical analysis of starch morphology from macrogeophytes. Their pioneering work foreshadowed the mounting role of microbotanical studies around the world, including the study area (11–18). Following suit, this study contributes direct microbotanical evidence for potato within its botanical hearth at the onset of food production.

The Study Area: Paleoenvironment and Archaeological Context

Jiskairumoko is an open-air village site situated in the central Ilave Valley of the western Titicaca Basin of southern Peru (Fig. S1). At ~3,890 m above sea level, Jiskairumoko nears the uppermost limit of montane agriculture. The site was occupied from the Late/Terminal Archaic to Early Formative periods (6, 19) and valley- and site-level data point to significant socioeconomic change during this time, namely, the advent of camelid management and chenopod cultivation, shifts in mobility related to changing subsistence strategies, and the emergence of socioeconomic differentiation. Survey data point to population increase and settlement aggregation at fewer and bigger sites, like Jiskairumoko, near river terraces during the Terminal Archaic period (6, 20). At Jiskairumoko, evidence for sedentarization includes the circular organization of five pithouse structures, labor-intensive wattle-and-daub architecture, the formalized use of space and maintenance of residential structures, secondary refuse patterning, characteristics of storage areas and grinding tools, and faunal and macrobotanical evidence for occupational duration (6). Moreover, the presence of a gold-bead necklace in a Terminal Archaic burial suggests the emergence of socioeconomic differentiation (6, 19).

Based on Paduano et al.'s (21) study of pollen and charcoal lake core data, Craig et al. (20) observe that the rise in the fine charcoal fraction in the Titicaca Basin after ~2,000 cal y BC "represents the first time in the history of the lake" that fire frequency increased during a more humid period. Craig et al. (20) concur with Paduano et al. (21) that this pattern likely reflects agricultural clearing rather than fires resulting from high aridity and accumulated woody biomass. Together, the archaeological and paleoenvironmental data seem to reflect a dramatic transformation in regional land-use patterns, specifically, the onset of

Significance

The potato is perhaps the most important of the high Andean crops. Cultivated the length of the Andean cordillera and across disparate ecological zones, it is now also a principal global staple. For this study, we analyzed starch microremains recovered from 14 groundstone tools from Late Archaic to Early Formative period contexts at Jiskairumoko, an early village site in the Titicaca Basin of the south-central Andes of Peru. A total of 50 starches were identified as consistent with cultivated potato. These data are significant because they contribute to the empirical foundation for understanding the development of food production in the study area and underscore the utility of starch analysis in addressing questions relating to geophyte domestication and cultivation.

Author contributions: C.U.R. designed research; C.U.R. performed research; C.U.R. analyzed data; C.U.R. and M.S.A. wrote the paper; and M.S.A. designed the field project and led the excavation of Jiskairumoko.

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agro-pastoralism at this time. This study adds to our picture of Titicaca Basin developments by elucidating aspects of geophyte use at Jiskairumoko.

Methods and Materials

Twenty unwashed grinding tools were tested for starch grains; tools encompass the span of Jiskairumoko's occupation and represent distinct morphological types and modes of design (Table S1). Standard protocols were used to process artifacts in order to avoid postexcavation contamination and recover starch grains (*SI Methods and Materials*). Adhering residues were recovered from tools using sonication and starches were extracted using a heavy liquid flotation solution of cesium chloride. An Olympus BHM metallurgical transmitted light microscope equipped with polarization lens and a Nikon Coolpix 990 digital camera was used to analyze and photograph starches. Starch granules were described in terms of a standard set of morphological and metric characteristics (22).

Taxonomic identification of archaeological starch was based on published reference works and a preliminary comparative study (9, 10, 15, 23–30). Reference taxa include Andean pseudocereal, seed, legume, fruit, and geophyte crops like chenopods, amaranth, maize, beans, chiles, manioc, *achira*, oca, ulluco, and potato (9, 10, 15, 16, 23, 25, 28, 30–33). Key objectives of the comparative analysis were to discern the degree to which (*i*) starches from oca, potato, and ulluco are distinctive and (*ii*) starches from wild and cultivated potato differ from one another (Fig. 1). Study results constitute much of the basis for our interpretation of the Jiskairumoko *Solanum*, which are the focus of our discussion of the archaeological starches. A more detailed description of the grinding toolkit, sample processing, microscope analysis, and reference study can be found in *SI Methods and Materials*.

Results

A total of 141 starch grains were recovered from 14 grinding tools; of these, 50 (35%) were identified as potato (*Solanum* sp.) and derive from nine artifacts spanning occupation of the site (Table 1). Radiocarbon dates derive from associated cultural features and are corroborated by architectural characteristics or a lack of evidence for mixing/disturbance (6, 34). In addition to *Solanum*, the starch assemblage includes various distinctive unidentified morphological types, along with *Phaseolus*. Artifacts yielding more than one starch grain have a mix of *Solanum* and other starch types, indicating that the tools were used to process diverse plants, rather than having specialized uses. A pattern of generalized use fits with the somewhat ad hoc morphology of the grinding toolkit, comprising single and multiple concomitant use, expediently and strategically designed, and recycled tools (Figs. S2 and S3 and Table S1).

Non-*Solanum* Archaeological Starches. The Jiskairumoko starch assemblage highlights the necessity for further reference work in this area. Fig. S2 depicts a representative sample of the diverse grain types present; most of these cannot be securely identified at this time, as the focus of this work was identifying *Solanum*. Four to five starches appear consistent with bean (*Phaseolus* sp.), based on size, an oblong-reniform shape, visible lamellae, centric hila, and a pale longitudinal fissure consistent with heat treatment (16, 31) (Fig. S2: *A–B1*, *E*, *E1*, *L*, *L1*; possibly *T* and *T1*); three derive from Late Archaic Tool 57. The presence of *Phaseolus* at Jiskairumoko would not be not surprising, as this taxon has been identified in Andean contexts dating as early as 8,210–6,970 ^{14}C y BP (16, 35).

Andean Geophyte Starch Morphology. With respect to the high-elevation Andean geophytes, maca and añu starches are significantly smaller than those of oca, potato, and ulluco (Table S2) and are easily distinguished based on other traits as well (23, 28, 36). Potato overlaps with—but exceeds—ulluco and oca with respect to size. Unique grain types comprised of a combination of traits typify all three taxa (9, 10, 23, 28, 30, 37); moreover, a comparison of starches from wild and cultivated *Solanum* indicates that these may be distinct from one another (Fig. 1, *SI Methods and Materials*, and Tables S3 and S4).

Archaeological *Solanum*. Based on published data and comparative study results, 50 Jiskairumoko starches were identified as *Solanum*. The archaeological starches are consistent with cultivated potato with regard to 2D and 3D form and polarization, surface, and lamellae characteristics. As illustrated in Figs. 1 and 2 and Fig. S3, symmetrical, oval-ovoid grains predominate (84%), followed by asymmetrical, oblong grains (14%), and a single, asymmetrical, angular grain (2%) (Table S3).

The *Solanum* starches fall within the size range documented for modern, cultivated potato starches; the latter range from 3–100 µm, with a mean of 35 µm, versus wild potato starches, which range from 9–45 µm, with a mean of 28 µm (Table S5). The 38 Late Archaic period *Solanum* grains, for example, range in size from 11–58 µm along the longest axis, with a mean length of 29 µm. However, results of the reference study are inconclusive as to the link between domestication and increased starch grain size in potato (37). In crops such as maize, manioc, and *Capsicum* pepper, a marked increase in starch grain size accompanies domestication (15, 25, 33, 38). By contrast, size differences not correlated with

Table 1. Radiocarbon dates and proveniences for tools yielding *Solanum* starches

Block no./structure/^{14}C dates	Tool ID/provenience	Tool type/subtype/other attributes	No. *Solanum* starch
Late Archaic			
Block 9/Pithouse 1/4,562 ± 73 ^{14}C y BP (AA58476)	Tool 57/x27a8vii	Mano, flat-concave/ basin subtype, recycled from metate	16
	Tool 232/aa28c7vii	Mano, flat-concave, recycled from metate	6
	Tool 1/z26c7vi	Mano, flat-concave	1
	Tool 2/bb27b3vi	Mano, flat-concave	1
	Tool 17/y25c11v	Multiple concomitant use tool (mano, abrader, pecking stone), flat/flat-concave mano, recycled	14
Terminal Archaic			
Block 3/Pithouse 3/3,448 ± 44 ^{14}C y BP (AA43382)	Tool 174/x37c7viiia	Flat-concave metate fragment	1
Early Formative			
Block 4/Rectangular Structure 1/3,410 ± 70 ^{14}C y BP (Beta-97320)	Tool 107/ff22c0av	Mano, flat-concave	1
3,401 ± 45 ^{14}C y BP (AA43375)	Tool 125/hh32d0aiv	Mano, flat-concave	7
3,330 ± 45 ^{14}C y BP (AA43376)	Tool 198/jj30d1iv	Mano, basin	3
3,240 ± 70 ^{14}C y BP (Beta-97321)			
Total no. *Solanum*			50

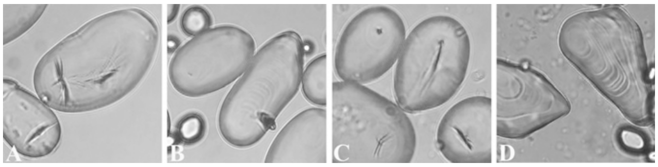

Fig. 1. Modern *Solanum* starch grains from freeze-dried (*A* and *B*) and fresh tubers (*C* and *D*) at 40× magnification. (*A*) Traditional cultivar, *Imilla negra* (size range 9–96 μm, mean length 38 μm); (*B*) traditional cultivar, *Paula* (size range 12–100 μm, mean length 48 μm); (*C*) traditional cultivar, *Paula* (size range 12–75 μm, mean length 41 μm); (*D*) wild ancestor, *Solanum bukasovii* (= *S. candolleanum*) (size data unavailable).

domesticatory status occur among the modern *Solanum* taxa analyzed (Table S5). Factors such as tuber developmental stage/size, growing environment, and taxonomic identity affect starch grain size (39–42); further comparative study of potato starch morphology controlling for these factors may clarify this relationship.

A total of 88% of the Jiskairumoko *Solanum* starches have open hila or fissuring; 36% are partly-gelatinized, damaged (e.g., cracked) or appear "battered" (Fig. 2 *E* and *F* and Fig. S3 *I–L1*). Compared with the profile of modern *Solanum* analyzed, these percentages align more closely with those seen in freeze-dried, rather than fresh, tubers. Specifically, closed hila and an absence of fissures predominate in fresh tubers (wild and domesticated), whereas open hila and fissures predominate in freeze-dried tubers (Table S6). Various experimental studies have found a positive correlation between processing and the increased incidence of wear or damage to starches, including cracking and gelatinization (43–45); the modern *Solanum* data are consistent with such findings.

As Collins and Copeland (46) observe, however, it can be difficult to distinguish anthropogenic wear from that resulting from unknown taphonomic factors when dealing with ancient starches. Assuming, nevertheless, that the damage to the Jiskairumoko *Solanum* starches is in fact a result of culinary processing, given the starches' provenance, we propose that the wear reflects the grinding of the ancient tubers (47), likely for detoxification purposes. Following Johns (48–50), we consider a technology as involved as freeze-drying to have developed later, with the secondary expansion of agriculture into higher elevations and the development of frost-resistant potatoes at that time.

Discussion

Perhaps because of its status as a global staple, Emshwiller (51) observes, the phylogeny of the domesticated potato has been subject to more investigation and debate than that of its Andean geophyte counterparts. Nevertheless, elucidating potato's taxonomy, distribution, and origins has proven challenging. As Johns and Keen (52) observe, high rates of gene flow among wild, weedy, and cultivated potatoes result in the ongoing creation of new taxa (52); this factor and a high degree of morphological variability have made pinpointing the progenitor species and number and places of domestication difficult (53–57).

Until recently, explanations for potato's origins favored multiple, independent domestications of several members of a group of wild taxa known collectively as the *Solanum brevicaule* complex, comprising a northern and southern clade and found in southern Peru, northwestern Bolivia and Bolivia, and northern Argentina, respectively (54, 55, 57–61). Recent phylogenetic research, however, points to a reduction in the number of species in the *S. brevicaule* complex and to a monophyletic origin: the one-time domestication of a single wild ancestor, *Solanum candolleanum* (56, 61–64). The proposed progenitor includes 31 taxa previously identified as distinct species/subspecies and belonging to the northern clade of the *S. brevicaule* complex (56), suggesting that initial domestication transpired somewhere in southern Peru/northwestern Bolivia (2, 56, 65).

In discussing the geography of the potato, Hawkes (55) notes that where *Solanum* species are found today, they have been present since the last glaciation circa 10,000 y ago. Hawkes (55) observes that taxa adapted to cold, high environments—including ancestral *S. candolleanum*—"have been able to extend much further than those restricted to isolated medium altitude valleys"—hence the progenitor's broad distribution throughout southern Peru/northwestern Bolivia. Botanical and paleoenvironmental data indicate that Jiskairumoko residents would likely have encountered *S. candolleanum* in their immediate environment, among other weedy, herbaceous plants (3, 5, 21, 36, 55, 66–69). First, Hawkes (55) documents the occurrence of *Solanum canasense* and *Solanum multidissectum* (both = *S. candolleanum*) in the Department of Puno, Peru, where Jiskairumoko is located. Furthermore, as a pioneer or "camp-follower" species, in the sense of Anderson (70), wild potatoes are especially attracted to—and flourish in—disturbed habitats (71). Of particular interest in this respect are the river terraces associated with Jiskairumoko. The site itself is situated upon a gravel knoll; as described by Rigsby et al. (72) in their documentation of the Ilave Valley's fluvial history, the knoll is a remnant of an ancient river terrace, one of five created as a result of rising and falling lake levels associated with regional paleoclimatic shifts. The terrace upon which Jiskairumoko sits (T5) was created circa 18,000 cal y BP; a nearby lower terrace (T2) was created more recently, ∼2,300 cal y BC (21, 72–74). At the time of Jiskairumoko's occupation, T2 would have been found within the river floodplain and subject to frequent inundation and aggradation resulting from then-current high rainfall and lake levels. Floodplain disturbance would have provided for the increased productivity of camp-followers like potato and chenopods, perhaps setting the stage for their heightened exploitation and experimentation (20).

Macro- and microremain data at Jiskairumoko point to the Late/Terminal Archaic period exploitation of chenopods and

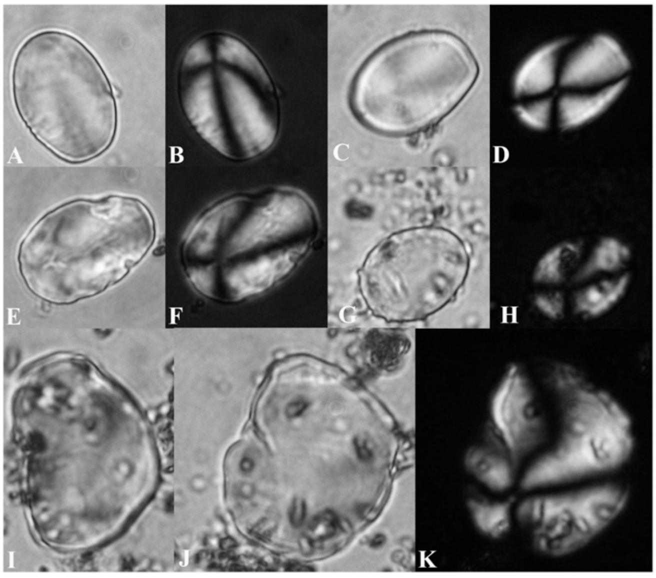

Fig. 2. Jiskairumoko *Solanum* starch grains, transmitted and polarized view: (*A*) T17G21, 23 × 16 μm; (*B*) same grain, polarized; (*C*) T57G03: 23 × 17 μm; (*D*) same grain, polarized; (*E*) T57G22: 25 × 17 μm; (*F*) same grain, polarized; (*G*) T57G30: 19 × 15 μm; (*H*) same grain, polarized; (*I*) T17G22: 34 × 21 μm; (*J*) same grain: alternate view; (*K*) same grain: alternate, polarized view.

potato, respectively. Although both are locally available resources that could have been gathered, from a morphological perspective the data are consistent with domesticated plants. Flotation data for Jiskairumoko are incomplete; however, using scanning electron microscopy, Andrea Murray identified seven chenopods from a Terminal Archaic burial as having thin seed coats, indicating their domesticated status (6). Chevalier's identification of chenopod phytoliths from the dental calculus of Terminal Archaic skeletons corroborates exploitation of this taxon at this time (6, 19). Furthermore, as discussed, the archaeological *Solanum* starch morphology is consistent with that of cultivated potato. A scenario of Late Archaic cultivation fits well with regional paleoenvironmental data, indicating broad-scale agricultural clearing by ~2,000 cal y BC and contemporaneous valley- and site-level data pointing to camelid management, sedentarization, and the advent of socioeconomic inequality, discussed above (6, 19, 21).

As Johns and Alonso (75) relate, however, wild potatoes contain varying levels of glycoalkaloids that cannot be neutralized by heat (cooking) alone, or by simply removing the peel. High-toxicity species, which include ancestral *S. candolleanum*, would have required some extra processing to permit initial, regular exploitation. The authors suggest that domestication of such taxa likely involved selection for a decrease in tuber toxicity. With this in mind, the presence of potato in culinary contexts at Jiskairumoko suggests either that toxicity had already been reduced through domestication or that site residents used some other means to reduce toxicity. Johns (48) proposes a chemical–ecological model in which geophagy (specifically, the consumption of phyllosilicate clays to neutralize glycoalkaloids) facilitated potato's domestication. The chemical profile of Jiskairumoko soils is unknown, such that testing the applicability of the model is not possible at this time. However, as Browman and Gundersen (76) relate, comestible earths have been recovered at archaeological sites in the altiplano, attesting to the antiquity of this practice.

Based on the toxicity of wild potatoes and the recovery of *Solanum* starch from Jiskairumoko groundstone, we propose that these tools were used not only for seed/pseudocereal plants, but may also have figured into the detoxification of potato at Jiskairumoko, perhaps alongside geophagy. As Stahl (77) points out, grinding—along with processes like milling, grating, and pounding (collectively referred to as "comminution")—often play a role in detoxification, as in the ethnographically well-known examples of bitter manioc (*Manihot esculenta*) and acorn (*Quercus* spp.). Furthermore, Johns (49, 50) observes that in making freeze-dried potatoes (e.g., *chuño*, *moray*, *tunta*), freezing causes tuber cell walls to burst, which facilitates the leaching of glycoalkaloids; we submit that grinding could achieve this same end. Although we find no documented examples of raw potato grinding, Cobo (78) reports the making of very fine flour out of rehydrated *chuño*, which was first toasted and then ground; Towle (8) describes a similar process of grinding flour from *moray*: both are added to stews.

At this point, we cannot say with certainty whether the Jiskairumoko *Solanum* derive from cultivated/domesticated or wild potato. Such a determination hinges on future reference work, wherein: (*i*) selection of accessions is informed by the history of study of the genus and most recent taxonomic/phylogenetic treatments; (*ii*) the number of grains studied per taxon and type of morphological characters analyzed take into consideration recent methodological developments and new standards in the field (79–84); (*iii*) variables such as tuber developmental stage/size and growing environment are controlled for; and (*iv*) the morphological implications of hybridization among wild/weedy/domesticated potatoes are understood. Such hybridization is commonplace and Andean farmers today, for example, typically welcome volunteer seedlings. Johns and Keen (52) furthermore suggest that, in the past, at times of crop failure, "weed potatoes would be obvious sources of tubers for food and seed." Just as Bruno and Whitehead (5) consider the macrobotanical ramifications of quinoa crop/weed relationships, so must we develop expectations for the microbotanical repercussions of domesticated potatoes' ongoing relationships with wild/weedy *Solanum*, in the context of both early plant cultivation and later, more established, farming practices.

Conclusions

The results of this study illustrate the utility of starch microbotanical analysis in addressing questions relating to the timing, mode, and context of potato domestication. The data presented here add to the empirical dataset for potato use within its domesticatory hearth during the Late Archaic to Early Formative periods. Moreover, preliminary reference work described here suggests the potential of using a population signature approach to distinguish between domesticated and wild *Solanum* (SI). More comprehensive reference data are necessary to permit full realization of the potential of this method in the study area; such datasets provide the foundation for recent strides made in understanding ancient subsistence regimes around the world (22, 38, 85).

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