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Small is big: The microfossil perspective on human–plant interaction

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The archaeological record contains only scattered and incomplete clues to the scope and complexity of past human behavior, and archaeologists must develop every possible source of useful information. Although much overused of late, the truism that absence of evidence is not evidence of absence holds particular force in archaeology and nowhere more than in the prehistory of human–plant interaction. Until recently, the reconstruction of plant use and domestication has been biased by a necessary dependence on macrobotanical remains preserved in arid environments or through serendipitous carbonization. Microbotanical analyses have proven increasingly valuable in balancing the record. Over the last few decades, phytolith (plant opal silica bodies) and starch grain studies have contributed significantly to the multiproxy reconstruction of past environments, human use of plants, and the pathways of plant domestication (e.g., refs. 1 and 2). This observation is especially true in humid regions, where conditions do not favor the preservation of macrobotanical remains, and in areas where tubers were important sources of plant foods; tubers are soft structures that often are consumed in their entirety, and they tend to leave few macro remains even under optimal preservation conditions. Working in the humid tropics of Central America, Dickau *et al.* (3) demonstrate in this issue of PNAS the power of archaeological starch grain analysis by using this proxy to elucidate the differential movement and adoption of both seed and root crops in western and central Panama beginning $\approx 7,800$ years ago.

Although starch grains and phytoliths have been recognized by scientists for nearly two centuries, the systematic study of these plant microfossils for archaeological purposes dates only to the last three decades (1, 4). Increasingly, archaeobotanists use phytoliths and/or starch grains to identify plants of origin at low taxonomic scale, to distinguish between domesticated and wild species, to differentiate between plant organs producing the microfossils, and to associate plants directly with human activity by recovering starch and phytoliths from artifacts and even human teeth. Recent research by myself and colleagues (5) at the site of Waynuna, in the southern Peruvian highlands, illustrates all of these data types. Although we exca-

vated the site to study Terminal Pleistocene [13,000–11,400 calibrated years before present (cal BP)] coast–highland interaction, Waynuna proved to be Late Pre-ceramic (4,000–3,600 cal BP) in age and thus unsuitable to answer the original research questions. Microfossil analyses turned this “failure” into a source of important new information on the history of Andean plant use. Although the excavations recovered no plant parts visible to the naked eye, analysis of starch grains from midden sediments and stone tools demonstrated the regional presence and processing of domesticated seed (maize, *Zea mays*) and tuber (potato, *Solanum* sp.; arrowroot, *Maranta* sp.) crops a millennium earlier than previous records based on macrobotanical remains had shown (5). Phytoliths provided independent confirmation of the starch identifications. The discovery of both cob and leaf phytoliths in the principal house floor deposit showed that these organs had deteriorated on or near the site and therefore supported an inference that the site’s inhabitants farmed the corn. Detailed examination of the starch grains found that both hard and soft endosperm varieties of maize were present and revealed damage to maize grains typical of grinding rather than natural deterioration.

Phytoliths and starch grains have led to the identification of early agriculture elsewhere in the New World. On the Ecuadorian coast, Piperno and Stothert (6) found phytoliths of wild squashes and gourds (*Cucurbita* spp.) at one site dating to the Terminal Pleistocene and domesticated *Cucurbita* phytoliths dating to the earliest Holocene at the same site and one other. Mean size distinguished wild from domesticated specimens; these results are supported by studies of modern wild and domesticated squash phytoliths. In these sites, phytoliths provided an additional avenue of information as a source of datable organic material. As they form, phytoliths incorporate bits of the parent plant material, which is then preserved from contamination by the silica envelope of the phytolith. With a large enough sample, accelerator mass spectrometer radiocarbon dates can be successfully attained directly from the microfossils.

Working in mid-Holocene sites of the Ecuadorian coastal zone, Pearsall *et al.* (7) have amplified our understanding of early maize types at Real Alto, a site dat-

ing to almost 6,000 years ago. Starch grains indicated both hard and soft endosperm varieties, as at Waynuna a millennium later, whereas phytolith morphology pointed to maize that “combined primitive and derived traits in a way that is not observed in living maize varieties” (ref. 7, p. 438).

Recent microfossil studies at either extreme of the American continents have shed light on different human–plant interactions. Zarrillo and Kooyman (8) used starch grains from two late pre-European stone tools to document long-distance movement of foodstuffs such as maize in the Canadian plains. In Uruguay, Iriarte *et al.* (9) analyzed both starch grains and phytoliths from the 5,000- to 4,000-year-old site of Los Ajos, finding a number of different crop plants such as maize and beans (*Phaseolus* sp.) (9). In the context of regional prehistory, the site is unexpectedly complex in architecture and, as the microfossils demonstrate, unexpectedly early in the adoption of agriculture. Macrobotanical remains of domesticated plants were not recovered at the site. The new data push back the frontier of agriculture and settled village lifeways in the southern cone of South America.

Plant microfossils have led to similar advances in other parts of the world. Recent research by Denham *et al.* (10) at Kuk Swamp in New Guinea used starch grains from tools and phytoliths from site sediments as key parts of a multiproxy effort to track plant use over the Holocene (11,400 cal BP to present). Bananas (*Musa* sp.) and the tuber taro (*Colocasia esculenta*) were intensively exploited by 10,000 cal BP, and the domestication and cultivation of banana had occurred by $\approx 7,000$ years ago. These results challenge the earlier conception of New Guinea as a passive recipient of domesticated plants and the idea of agriculture brought by Austronesian speakers rather than an independent center of plant domestication. At Ohala II in Israel, a well dated Upper Paleolithic site ($\approx 23,500$ – $22,500$ cal BP), Piperno *et al.* (11) showed that wild barley seeds were being processed with a stone

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grinder, constituting the earliest direct evidence thus far for this important kind of activity, which makes seeds more easily digested by the human body (11).

Plants and animals have passed back and forth through Panama, situated at the crossroads of the Americas, since the Isthmus closed and North and South America united ≈ 3 million years ago. Once humans settled the New World, they, too, began traversing this narrow land bridge. Indeed, archaeological sites of all epochs are known, and systematic archaeological surveys, excavations, and analyses of flora, fauna, stone tools, ceramics, and human skeletons during the past 25 years have provided arguably one of the best archaeological records of any Neotropical region (e.g., refs. 12 and 13). Our ability to reconstruct plant exploitation and domestication in ancient Panama, as in other tropical zones, had been hampered by the poor preservation of botanical remains in the humid tropical climate. Microfossil work has opened new doors. Several years ago, Piperno *et al.* (14) identified starch grains from stone tools from 7,800-year-old deposits at the Aguadulce Shelter in Central Pacific Panama as manioc (*Manihot esculenta*), yams (*Dioscorea* sp.), arrowroot, and maize. Combined with previously analyzed phytoliths from Aguadulce and pollen and phytoliths from Panamanian lakes, the starch grain data provided the earliest New World evidence for root-crop cultivation and a mixed economy relying in part on both domesticated seeds and tubers. Maize came from southwestern Mexico, and manioc and arrowroot originated in South America. Thus, it appeared that prehistoric Panamanians adopted these major crops at much earlier times than the previously known and sparse macrobotanical record had suggested.

Dickau *et al.* (3) add much important new information to this picture. Identification of starch grains from early stone tools (Fig. 1) at the site of Cueva de los Ladrones supports the early use of domesticated tubers and maize in Central Pacific Panama, seen at nearby Aguadulce Shelter. Some phytolith studies had been done at similar-age sites in the higher-rainfall, less-seasonal environment of Western Pacific Panama that were excavated >30 years ago by Ranere and Cooke (12, 13),

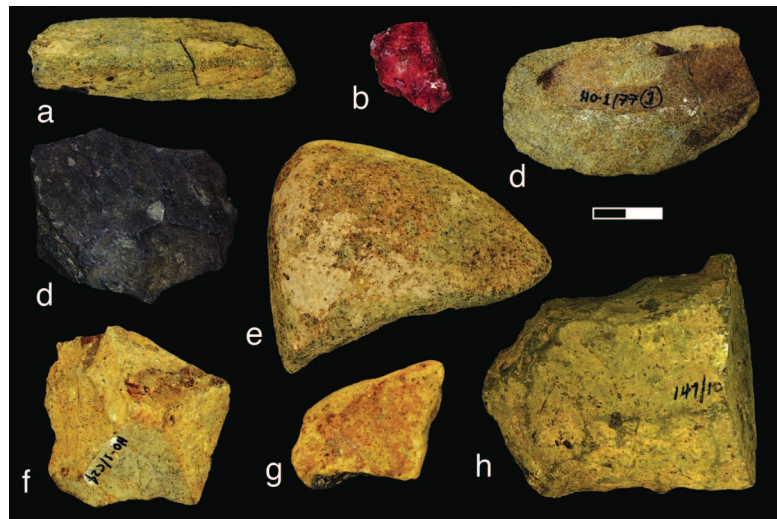


Fig. 1. Stone tools from Panama sites that yielded identifiable starch grains. (a) Handstone from Cueva de los Ladrones with maize starch (site catalogue no. CL82b). (b) Flake knife from Casita de Piedra with arrowroot starch (catalogue no. 101/15). (c) Wedge from Hornito with maize starch (catalogue no. 77-1). (d) Chopper from Casita de Piedra with manioc starch (catalogue no. 52/44). (e) Handstone from Cueva de los Ladrones with maize and yam starch (catalogue no. CL68/1). (f) Chopper from Hornito with maize starch (C24). (g) Grinding-stone base fragment from Cueva de los Ladrones with maize starch (catalogue no. CL68/2). (h) Chopper from Trapiche with yam and maize starch. (Scale bar, 1 cm.) See table 1 in ref. 3 for stratigraphic and chronological contexts. This composite photo was prepared by Aaron O’Dea and Drude Molbo.

but little information on plant use and domestication was available, and starch grain analysis had not been applied. The starch grain research of Dickau *et al.* (3) found maize, root, and tuber starches, such as arrowroot and manioc. The investigators (3) show that, although the trajectory of agricultural development and associated demographic trends differed in highland Western and lowland Central Panama, with intensive forms of slash-and-burn agriculture apparently developing thousands of years earlier in the latter region, many of the same crop plants were adopted in the two regions at approximately the same time. Such kinds of detailed comparisons, essential for explicating the processes that led to full-fledged agricultural economies and social complexity, are probably impossible without the sorts of multiproxy botanical studies that Dickau and others are increasingly undertaking. Alongside the introduced crops, early inhabitants also exploited local wild plants high in important carbohydrate sources such as yams (*Dioscorea* spp.) and *Zamia* spp. Although *Zamia*, a cycad, has long been thought to be

important in pre-Columbian subsistence economies, Dickau *et al.* provide the first empirical evidence from the neotropical mainland affirming this belief.

The results of Dickau *et al.* (3) add to other recent work in northern and southern South America, mentioned previously, indicating that important seed and root crops such as maize, manioc, and arrowroot were well dispersed and used by preceramic societies. Perhaps of greatest anthropological significance, Dickau *et al.* note that the multiple origins of the domesticates that appeared in Panama between $\approx 7,800$ and 7,000 years ago show that crops moved independently of people: diffusion of plants rather than migration of farmers. Given the importance of agriculture in the development of complex societies in the New World and elsewhere and of American domesticates in global subsistence today, we need to understand such pathways to domestication and the adoption of agricultural lifeways in the greatest possible detail. Multiproxy microfossil analyses such as the current Panamanian study (3) offer new insight and balance biases of an imperfectly preserved record. Small is big.

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