Starch grain evidence for the preceramic dispersals of maize and root crops into tropical dry and humid forests of Panama

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The Central American isthmus was a major dispersal route for plant taxa originally brought under cultivation in the domestication centers of southern Mexico and northern South America. Recently developed methodologies in the archaeological and biological sciences are providing increasing amounts of data regarding the timing and nature of these dispersals and the associated transition to food production in various regions. One of these methodologies, starch grain analysis, recovers identifiable microfossils of economic plants directly off the stone tools used to process them. We report on new starch grain evidence from Panama demonstrating the early spread of three important New World cultigens: maize (*Zea mays*), manioc (*Manihot esculenta*), and arrowroot (*Maranta arundinacea*). Maize starch recovered from stone tools at a site located in the Pacific lowlands of central Panama confirms previous archaeobotanical evidence for the use of maize there by 7800–7000 cal BP. Starch evidence from preceramic sites in the less seasonal, humid premontane forests of Chiriquí province, western Panama, shows that maize and root crops were present by 7400–5600 cal BP, several millennia earlier than previously documented. Several local starchy resources, including *Zamia* and *Dioscorea* spp., were also used. The data from both regions suggest that crop dispersals took place via diffusion or exchange of plant germplasm rather than movement of human populations practicing agriculture.

agricultural origins | crop dispersals | Neotropics | starch grain analysis

With the advent of molecular studies directed toward understanding the phylogenetics of various economic plants throughout the world, the domestication hearths of several major crop plants have been identified (e.g., refs. 2–5). However, tracing the dispersal of these domesticates, and the economic transition from foraging to food production by the societies that domesticated or adopted them, remains firmly dependent on the recovery of identifiable archaeobotanical remains. The development and application of microbotanical techniques in archaeology has led to major advances in investigating plant use and subsistence in regions where preservation of macrobotanical remains (seeds, fruits, tubers) is poor. In the Americas, phytoliths, pollen, and most recently starch grains, have provided substantial empirical evidence demonstrating the considerable antiquity of food production and crop dispersals in tropical regions once considered peripheral to agricultural origins. Numerous studies now show that people were experimenting with horticulture and moving domesticated plants around tropical forests by 9500–7500 cal BP,[¶] and that food production concentrating on a few particularly productive cultigens was widespread throughout the Neotropics by 5500 cal BP (6–14).

The Isthmus of Panama forms a relatively narrow landbridge between North and South America, and was the terrestrial route for the dispersal of numerous domesticates. Not surprisingly, some of the earliest evidence for the spread of several crops has been recovered from preceramic sites in central Panama, in the seasonally dry Pacific coastal plain and foothills (6, 8, 9, 15). In this article, we report on starch grain analysis on stone tools from the sites of Cueva de los Ladrones (hereafter, Ladrones) in central Panama, and Hornito, Casita de Piedra, and Trapiche, in the Chiriquí region of western Panama. Our results provide significant evidence for the early dispersals of maize, manioc, and arrowroot through the Isthmus into other parts of the American tropics. They also show that in some regions of the Neotropics with high rainfall and moderately seasonal climates, food production was practiced nearly as early as it was in drier regions with marked seasonality.

Western Pacific Panama

The rockshelters of Casita de Piedra (BO-1) and Trapiche (BO-2) are located in the province of Chiriquí ≈1 km apart at 750 m above mean sea level. Each site is formed by the overhang of large boulders along the west side of the Río Chiriquí canyon (Fig. 1). This area receives 3,000–3,500 mm of rainfall annually (16) and lies within the premontane humid forest zone (17). A drier period occurs between December and April but is less intense than in central Pacific Panama. Excavations by Ranere in 1971 revealed stratified deposits 1.2 m deep at both sites (18). Six radiocarbon dates from Casita de Piedra document occupation from ≈7500 to 3000 cal BP. No ceramics were recovered in the excavated levels. The Trapiche shelter had both preceramic and ceramic occupations. During the preceramic periods, the site was periodically inhabited from ≈6700 to 2300 cal BP based on four radiocarbon dates on charcoal. These preceramic strata were capped by a 15-cm level that contained a small number of Valbuena Ware ceramics, characteristic of the Late Bugaba phase (1550–1350 cal BP) at village sites to the west (19).

Based on the lithic material from these and other sites, Ranere (18) defined two preceramic phases in Chiriquí: the Talamanca phase from 8000 to 5200 cal BP, and the Boquete phase from 5200 to 2100 cal BP. The Talamanca phase was characterized by large bifacially flaked wedges, scraper-planes, choppers, and the use of unmodified flakes of andesite. During the Boquete phase, bifacial wedges disappeared, small tabular wedges became abundant, pestles and polished celts first appear, and wider variety of raw material was used. Edge-ground cobbles, milling-stone bases, and nutting stones were used in both phases. Ranere proposed that the Talamanca phase material represented an exclusively hunting and

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¶All dates given as calibrated years before present (cal BP), calibrated at 2σ by using OxCal 4.0 (1). See Table 1 for original uncalibrated radiocarbon dates (^{14}C yrs BP).

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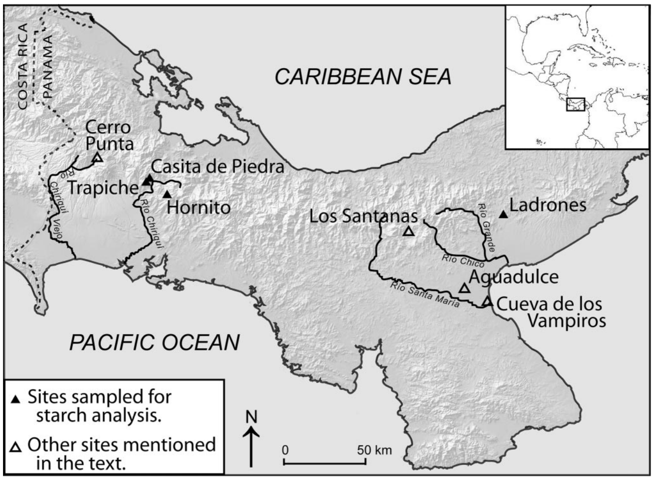

Fig. 1. Location of archaeological sites.

gathering economy but that some domesticated root crops, such as manioc (*Manihot esculenta*), may have been introduced during the Boquete phase. However, no direct botanical evidence for the latter hypothesis was recovered during excavations. Carbonized macro-remains in both Talamanca and Boquete levels were limited to durable plant parts such as *nance* pits (*Byrsonima crassifolia*), *algarrobo* seed fragments (*Hymenaea courbaril*), and palm endocarps and kernels from *Acrocomia aculeata* and *Attalea butyracea* (20). Faunal remains were absent, presumably because they did not preserve.

The Hornito site (HO-1, 640 m above mean sea level) is located ≈12 km southeast of the Casita de Piedra and Trapiche rockshelters, on the southwestern slope of Cerro Hornito (Fig. 1). This shallow open-air site, test-excavated by Cooke in 1976 (21), consists of a single, 10- to 25-cm layer of cultural materials dating to ≈7000 cal BP based on an average of three charcoal dates (22). Typical Talamanca phase ground and flaked tools, made mostly of dark igneous rock, were recovered from the site. Charred macrobotanical remains of *nance*, palms, and legumes were identified by C. E. Smith (23).

Our results from starch analysis on tools from Casita de Piedra, Trapiche, and Hornito [see Table 1 and supporting information (SI) Table 2] not only confirmed Ranere's hypothesis that root crops were used during the Boquete phase but also demonstrated their use in the preceding Talamanca phase. Moreover, our results indicated that maize (*Zea mays*) was processed alongside these root crops in both preceramic phases.

Two root crops originally domesticated outside the Isthmus of Panama were positively identified from the Chiriquí sites. Arrowroot (*Maranta arundinacea*) starch was present on a flake knife (101/15) from the basal levels of Casita de Piedra. Because a radiocarbon date on charcoal of 7661–7261 cal BP was obtained from the same stratigraphic level in an adjacent excavation unit, we infer that arrowroot was in use ≈7400 cal BP near the beginning of the Talamanca phase (Fig. 2*A*). Starch recovered from an edge-ground cobble (132/16) at Trapiche shows that arrowroot continued to be used into the Boquete phase. The second root crop we identified was manioc. It was recovered from a flake chopper (52/44) at Casita de Piedra, recovered midway between charcoal dates of 6881–6325 and 4823–4430 cal BP. We suggest that an age of 5600 cal BP is a reasonable estimate for this tool. A second identification was made on a grinding stone base (69/18) at Casita de Piedra, dating to ≈3600 cal BP (Fig. 2*B*).

We recovered maize starch at all three preceramic sites. It was found on two chopper-like tools (77-1, C24) at Hornito (≈7000 cal BP) (Fig. 2*C*). It was also recovered from stone tools stratified in the Talamanca and Boquete phase levels at Trapiche, and in Boquete phase levels of Casita de Piedra. The starch from these three sites represents the earliest evidence yet recovered for the presence of maize in the region. Carbonized macrobotanical remains from the Cerro Punta valley only date to 1750–1550 cal BP (24). Maize pollen from a sediment core taken from nearby Laguna Volcán is comparable in age. Evidence for extensive forest clearing, however, is apparent from the beginning of this core at 3160–2854 cal BP (25). Across the border in Costa Rica, a lake core from Laguna Zoncho revealed earlier maize pollen (3317–2952 cal BP), associated with markers of substantial forest clearing for cultivation, but lake sediments in this core did not extend back earlier than this date (26).

In addition to exogenous domesticates, we identified starch grains from several local native plant taxa. Our comparisons of the archaeological grains with modern reference collections comprising many (n = 12) species of *Dioscorea* native to Panama indicate that native yams were used during both the Talamanca and Boquete phases. At least two separate species appear to have been processed. One may have been *D. urophylla*, which has distinctive thin, elongated grains (Fig. 2*D*). A species of *Calathea* was used at Casita de Piedra during the Boquete phase (Fig. 2*E*). The domestication and cultivation history of *Dioscorea* and *Calathea* spp. is uncertain. Several members of both genera have been cultivated in house gardens by indigenous groups throughout the Neotropics, without becoming fully domesticated (27). Our data for preceramic Chiriquí suggest that the tubers of these taxa may have been collected either wild from the surrounding environment, or cultivated alongside the introduced crops discussed above in a mixed-species horticultural system.

We recovered *Zamia* starch at Hornito (Fig. 2*F*), and tentatively identified it at Casita de Piedra. Many members of the genus store high quality starch in modified or subterraneous stems, but the presence of neurotoxins requires some type of processing before consumption (28). Although the prehispanic and colonial use of *Zamia* in the Greater Antilles and southern Florida has been well documented (29–31), this is the first archaeobotanical evidence that this genus played a role in the prehispanic economies of mainland Central America. Comparative analysis of species extant in and near Chiriquí suggests the granules on the preceramic tools may derive from either *Z. skinneri* or *Z. fairchildiana*. The lack of archaeological or ethnographic evidence for cultivation suggests that the preceramic inhabitants of Chiriquí collected the plant wild from the surrounding forests.

In addition to starchy subterraneous organs, some of the tools from the Chiriquí sites were used to process seeds from grasses (Poaceae) and legumes (Fabaceae). Species-level identification of these starch grains may be possible in the future through expansion of our comparative collection.

Central Pacific Panama

Ladrones (CL-01) is a rockshelter located in the Pacific foothills of central Panama, ≈25 km from the coast of Parita Bay at 350 m above mean sea level (Fig. 1). The region receives between 1,500 and 2,000 mm of rainfall annually, the majority of which falls between April and December (16). The seasonal distribution of rainfall and prevailing winds contribute to the vegetative classification of the area as dry tropical premontane forest (17). Ladrones was used as a dwelling primarily between 7800 and 2200 cal BP based on six radiocarbon dates from charcoal and shell (32). Features such as hearths and midden deposits suggested that the site was largely used for domestic activities throughout its history. For the purposes of this article, we focus on the preceramic occupation of the site, before the appearance of Monagrillo-style pottery associated with a date of 5736–5314 cal BP at Ladrones (33).

The lithic assemblage of the preceramic levels is comparable to that seen in other sites in central Pacific Panama between 8000 and

Table 1. Starch recovered from tools and associated dates

Site cat. no.	Tool type	Unit	Level	Assoc. date (^{14}C yrs BP)	Calibrated date before present	Poaceae	*Z. mays*	Fabaceae	*Zamia* cf. *skinneri*	*Dioscorea* sp.	*Dioscorea* cf. *urophylla*	*Maranta arundinacea*	*Calathea* sp.	*Manihot esculenta*	Unidentified	Total
Ladrones			3	4800 ± 100	5736–5314											
CL-68/1	Handstone	0	10	≈6600	≈7500	(4)	4(3)			1					7	19
CL-68/2	Base	0	10	≈6600	≈7500		4								2	6
CL-82b	Handstone	01	11	6860 ± 90	7928–7671	(3)	10(5)								10	28
Casita de Piedra			B1	2890 ± 70	3352–2852											
69/2	EGC	4	B3	≈3300	≈3600		(2)	(1)		1			2		191	197
69/18	Base	4	B3	≈3300	≈3600	1(2)	(3)							1	37	44
64/18	Base	3	C2	≈3800	≈4200	3(2)	18	1		2					22	48
76/2	Chopper	5	C2	≈3800	≈4200	2(1)	4(1)		(1)						17	26
			C3	4075 ± 105	4847–4296											
			D3	4085 ± 75	4823–4430											
52/44	Chopper	2	E2	≈5000	≈5600	(1)								4	7	12
87/33	EGC	4	E2	≈5000	≈5600	(4)		(1)	(1)	(1)					14	21
			E4	5795 ± 105	6881–6325											
101/15	Flake knife	5	F3	6560 ± 120	7661–7261							1			1	2
Trapiche			B1	2300 ± 75	2696–2119											
147/10	Chopper	4	C1	3870 ± 75	4518–4086	1(2)	9(2)			16	2				25	57
132/16	EGC	3	D1	≈4000	≈4800	4(1)						2(2)			6	15
153/1	Chopper	5	D2	≈4300	≈4900	4(4)	9								15	32
			E2	4685 ± 85	5602–5071											
			E3	5850 ± 110	6933–6411											
Hornito																
C24	Chopper	C		6270 ± 270 to 5880 ± 260	7666–6554 to 7412–6192	(2)	9								9	20
77-1	Wedge	A		6270 ± 270 to 5880 ± 260	7666–6554 to 7412–6192	(1)	6(3)								11	21
E18	Scraper	E		6270 ± 270 to 5880 ± 260	7666–6554 to 7412–6192				2(2)						3	7

Radiocarbon calibrations made using the OxCal 4.0 program (1). EGC, edge-ground cobble. Numerals represent the number of granules identified from each taxon on a tool. Numerals in parentheses represent tentative identifications. A more complete version of this table appears as SI Table 2.

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5400 cal BP (22). Bipolar reduction of small quartz or agate pebbles produced tabular wedges, burin-like spalls, and small bipointed flakes. Unmodified flakes were commonly used along with more formally produced tools like scrapers, knives, and flakes unifacially retouched as possible projectile points. Unlike most other preceramic sites in Panama, edge-ground cobbles were not recovered; however, the site did yield numerous handstones and flat grinding stones, interpreted as plant processing tools. Remains of nearshore marine fish, shells, and crabs in middens indicate inland transport of coastal resources (32). Macrobotanical remains were uncommon in preceramic levels and were limited to fragments of more durable taxa like *nance*, unidentified palm endocarps, and a possible Sapotaceous seed coat (23, 32). A sediment column taken along the original excavation baseline contained maize pollen near the base of the cultural occupation, dating to ≈7800 cal BP (15). Maize phytoliths were also recovered in the preceramic levels of the column (15).

New starch data from our analysis provide additional evidence that the first preceramic occupants of Ladrones were using maize by 7800 cal BP (Table 1). Four tools from the preceramic levels were sampled for possible starch residues. Maize starch was identified on a ground-stone tool (CL-82b) from the deepest cultural level, Layer 11 in Area 01, just above sterile clay (see ref. 33 for contextual data). A radiocarbon date of 7928–7671 cal BP was obtained on charcoal in Area 2A on top of this sterile clay. Maize starch was also recovered from a handstone fragment (CL-68/1), and a grinding stone base (CL-68/2), both from one level above this, Layer 10 in Area 0. The starch granules recovered from these three tools were irregularly polygonal in shape, with centric hila (Fig. 2*G*). Size ranged from 10 to 24 μm with a mean of 17.4 μm. These features are diagnostic of maize and are consistent with granules derived from hard endosperm varieties of maize (e.g., popcorns, not flour corns) (34).

Starch from a species of yam (*Dioscorea*) was recovered from the handstone (CL-68/1) found in Layer 10 (Fig. 2*H*). This grain was not consistent with the domesticated New World yam, *D. trifida* (*yampi*), which is widely cultivated in Panama today. We propose therefore that the preceramic occupants of Ladrones were using another local (native) yam species, of which several are still used today as an alternative food source.

Discussion

The recovery of starch grains from particular plant species directly off the stone tools used to process them contributes strong empirical evidence on ancient plant use. This has been particularly valuable in environments such as the humid and seasonal tropics, where identifiable macrobotanical remains of all but the most durable taxa do not preserve well in most archaeological contexts. Using starch analysis, we have recovered evidence for the use of several local carbohydrate-rich resources such as *Zamia* and *Dioscorea* spp., which have long been surmised to be important in the subsistence economies of tropical forest inhabitants in the Americas but are rare or invisible in most other archaeobotanical records. Moreover, our results have documented that three domesticated species (maize, manioc, and arrowroot), initially brought under cultivation in distant continental areas, were adopted in Panama by people living in areas with different climatic regimes. Thus, we provide data on patterns of crop dispersals in the Neotropics.

The domestication and spread of maize has been the focus of more research than any other crop in the Americas. Molecular data indicate that domesticated maize (*Z. mays* ssp. *mays*) is genetically closest to, and was therefore likely derived from, a population of teosinte (*Z. mays* ssp. *parviglumis*) found today in the central Balsas River Valley in southwestern Mexico (5, 35). The work of Matsuoka *et al.* (5) on mutation rates in microsatellites suggests that the divergence of teosinte and maize likely occurred sometime around 9,000 cal BP. Archaeobotanical evidence increasingly points toward maize's rapid spread down Central America and into South America. Previous starch, pollen, and phytolith data from the rockshelters of Aguadulce, Los Santanas, and Ladrones demonstrated that maize had reached central Pacific Panama between 7800 and 7000 cal BP (6, 9, 15). Our recovery of starch grains off stone tools found in the basal strata at Ladrones adds further support for the early introduction of maize. To the west, our data show that maize was available in the Chiriquí region of western Panama by at least 7000 cal BP. These dates from Panama are not surprising, given that several studies and different archaeobotanical datasets show that maize reached sites in Colombia and Ecuador between 8000 and 7500 cal BP (6, 11, 12, 36). Views that maize dispersals occurred later (37, 38) are not supported by our starch and other microfossil data from Panama.

Phylogenetic work by Olsen and Schaal (4, 39) indicate that manioc was likely domesticated in the area of southwestern Brazil where its wild progenitor (*M. esculenta* ssp. *flabellifolia*) still grows. Until recently its dispersal history was poorly known, due mainly to its rarity in macrobotanical and phytolith records. Archaeologists became accustomed to inferring its use from certain artifact types [inferences that probably need to be reevaluated (40, 41)]. However, advances in pollen and especially starch grain analyses have markedly increased the direct botanical data available regarding the history of this cultigen. The earliest archaeobotanical evidence in South America comes from the Porce valley of northwestern Colombia at 7500 cal BP (12). Starch from Aguadulce shows that it reached central Panama by 7000 cal BP (10). Our data from Chiriquí provide botanical evidence of the presence and use of manioc in that region by at least 5600 cal BP. We anticipate that future analyses may show that it was available earlier than this, because pollen evidence suggests that it reached the Gulf Coast of Mexico by 6500 cal BP (7). It now seems clear that manioc was moving north from South America into Panama and beyond around the same time that maize was being dispersed southwards through Central America into South America.

Although it is not known exactly where arrowroot was first brought under cultivation, botanists favor the lowland seasonal forests of northern South America (27, 42). In South America, it has been documented in Valdivia period contexts (≈6300–2600 cal BP) in coastal Ecuador (6), and in later period sites in both the lowlands (41) and highlands (43). It is one of the earliest cultigens in both western and central Panama, predating maize and manioc. In central Panama at the coastal site of Cueva de los Vampiros, phytoliths were recovered in preceramic strata dated to 9700 cal BP (32). Arrowroot phytoliths were also identified at Aguadulce in pre-7800 cal BP levels (6), along with those of squash (*Cucurbita* sp.) and lerén (*Calathea allouia*). Our data indicates that arrowroot reached western Panama by at least 7500 cal BP based on the starch recovered from the basal levels of Casita de Piedra. So far it has not been identified from archaeological contexts any farther north along the Central American isthmus.

Our starch data, combined with other archaeobotanical research in Panama, show that the region was a major crossroads for crop dispersals, particularly during the initial stages of agriculture in the New World. At preceramic sites in two ecologically dissimilar areas of Panama, a mix of seed and root crops was used concurrently. These domesticates originated from different locales to the north and south of the Isthmus. They thus appear to be moving independently of one another and independently of technological dispersals like ceramics and metallurgy. This pattern strongly suggests that the main mechanism for crop dispersals into Panama was through diffusion or exchange of germplasm between neighboring groups, rather than a migration of land-hungry agriculturists importing their entire suite of domesticates (32). We believe that the earliest use and spread of domesticated plants in the American tropics was likely among semimobile foragers experimenting with small-scale cultivation near seasonally occupied rockshelters and small clusters of dwellings in forest clearings. The mobility of these

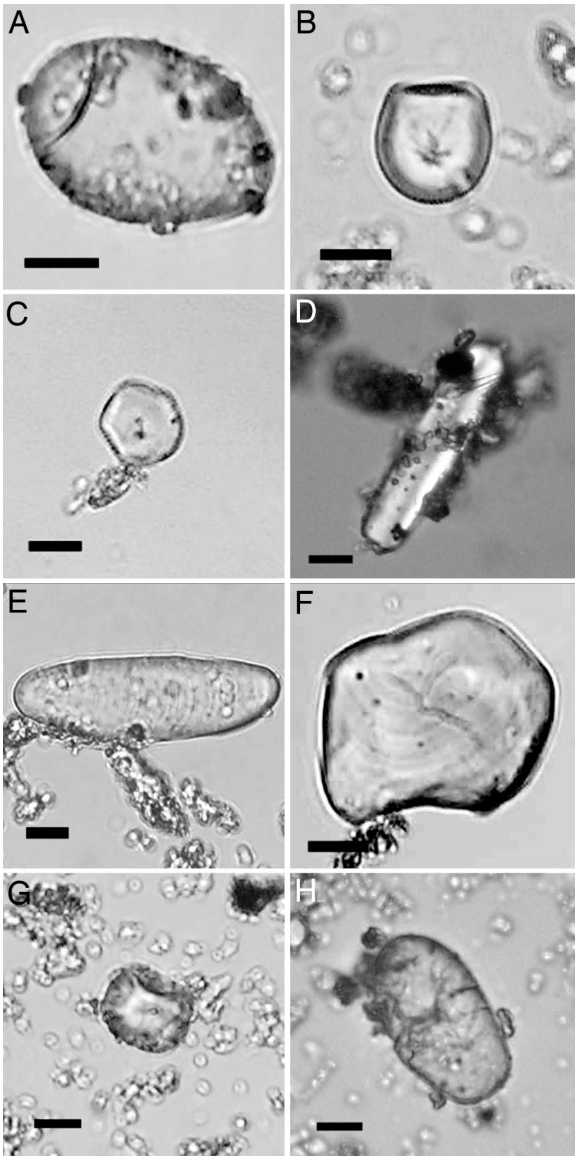

Fig. 2. Selected archaeological starch grains. (*A*) Arrowroot (*Maranta arundinacea*) starch from Casita de Piedra, flake knife 101/15, ≈7400 cal BP. (*B*) Manioc (*Manihot esculenta*) starch from Casita de Piedra, grinding-stone base 69/18, ≈3600 cal BP. (*C*) Maize (*Z. mays*) starch from Hornito, wedge 77-1, ≈7000 cal BP. (*D*) *Dioscorea* cf. *urophylla* starch from Trapiche, chopper 147/10, ≈4300 cal BP (under cross-polarized light). (*E*) *Calathea* sp. starch from Casita de Piedra, edge-battered cobble 69/2, ≈3600 cal BP. (*F*) *Zamia* sp. starch from Hornito, scraper E18, ≈7000 cal BP. (*G*) Maize starch from Ladrones, triangular grinding stone CL-82b, ≈7800 cal BP. (*H*) *Dioscorea* sp. starch from Ladrones, handstone CL-68/1, ≈7500 cal BP. (Scale bar: 10 μm.) Additional examples of starch grains from the sites are provided in supporting information (SI) Figs. 3–8.

first cultivators would have expedited the dispersal of new domesticates.

The transition to farming precipitated by the introduction of domesticates appears to have followed different trajectories in Panama. In western Panama, reconstruction of the vegetation around the Chiriquí rockshelters based on phytoliths from archaeological sediments suggests that the surrounding environment remained mostly forested for the duration of the Preceramic, until ≈2300 cal BP (44). If maize, arrowroot, manioc, and possibly other taxa were planted near the shelters, then this cultivation probably remained at a relatively small scale. Alternatively, these foodstuffs may have been cultivated at lower elevations and subsequently transported or exchanged with the premontane sites. However, we presently lack supporting paleoecological or archaeological evidence for this scenario.

Indications of widespread forest clearing near the Rio Chiriquí rockshelters do not appear until the third millennium cal BP, when arboreal phytoliths decline in abundance, and disturbance taxa like grasses and *Heliconia* increase significantly (44). Further west in Chiriquí, agriculturalists moved into humid montane forests at higher elevations (1,000–2,000 m above mean sea level) also during the third millennium cal BP (45, 25). This migration has been linked to the development of new maize races adapted to cool moist climates (24, 45, 46). These agriculturalists introduced pottery and carefully fashioned *manos* and *metates* into the region. By 1900 cal BP, populations had increased rapidly, nucleating in permanent villages (47, 48).

This sequence differs from the one seen in the seasonally dry areas of central Pacific Panama to the east. In this region, the initial cultivation of domesticated species like arrowroot, squash, and lerén between 9700 and 7800 cal BP is associated with widespread forest clearance by a burgeoning population (6, 8, 49–51). Particulate charcoal in paleoenvironmental records indicates that people took advantage of the strong drying winds in the dry season to facilitate burning. With the arrival of maize and manioc during the eighth millennium cal BP, landscape disturbance increased as cultivation shifted to swidden agriculture (6, 52). Around the time the first (Monagrillo) ceramics appear in central Panama (≈5500 cal BP), the cumulative destruction of the deciduous forest in the Pacific foothills reached a point where even secondary woody taxa became scarce on the landscape (52). By 2500–2200 cal BP, people began nucleating in villages on the coastal plain, dependent on maize and manioc agriculture (33, 46, 53).

Compared with central Pacific Panama, the transition from the initial adoption of domesticated plants to sedentary agricultural village life appears to be less intensive in western Panama. Environmental differences may be partly responsible for this situation. The humid premontane forests around the Chiriquí sites were likely less economical to clear than the seasonally dry deciduous forests of central Panama. Human demographic and cultural history may also be involved. Preceramic population densities may initially have been lower in Chiriquí, where no late Glacial or early Holocene sites have been recorded, than they were in central Panama, where a Paleoindian presence has been documented at several sites (8, 46, 54, 55). In central Panama, there is a 7-fold increase in the number of archaeological sites at 7800 cal BP. In western Panama, only a handful of sites, including Hornito and the Rio Chiriquí rockshelters, are known for the entire preceramic period (up until 3000 cal BP), despite archaeological surveys in search of preceramic occupations. Regardless of these regional differences, our research clearly shows that populations in both western Panama and central Panama had adopted domesticated plants and were practicing food production long before they settled in nucleated villages or made ceramic pots.

Conclusion

The ability of starch grain analysis to identify plant taxa in the unfavorable preservation environments of western and central Panama confirms the importance of this method for establishing the presence of particular plant species, both domesticated and wild, in the subsistence practices of early inhabitants of tropical forests. The domesticated plants recovered from our sites (maize, manioc, and arrowroot) originated in tropical areas outside the Isthmian region, some distance to the north and to the south. Therefore, our research supports other data for early and rapid dispersals of both root and seed crops throughout lowland Neotropical forests, areas that were formerly considered marginal to early food production but are now increasingly understood to have been important centers of early agriculture (6, 7, 12, 56, 57). Differences in the intensity of preceramic food production and land use in western and central Panama show that early tropical forest inhabitants followed different paths toward the establishment of fully agricultural economies.

Materials and Methods

A variety of tools was selected from each site for starch analysis, including both ground stone and flaked stone tools, to cover the widest possible range of plant processing activities. Residue was isolated from microcrevices in the tool surfaces by placing tools in an ultrasonic bath for 5 min. After concentrating the residue, starch was separated by heavy liquid flotation (cesium chloride prepared to a density of 1.79 g/cm^3). Extracted starch was rinsed, concentrated, and then examined under ×400 magnification by using a transmitted light microscope. Identifications were made by using the Neotropical starch comparative collection housed at the Smithsonian Tropical Research Institute, Panama. This collection is comprised of >400 species including domesticates, economic species, and congeneric taxa. Additional comparative material was collected by the first author. For more details, see *SI Materials and Methods*.

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