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

Ruth Dickau*,†, Anthony J. Ranere‡, and Richard G. Cooke§

*Department of Archaeology, University of Calgary, 2500 University Drive NW, Calgary, AB, Canada T2N 1N4; ‡Department of Anthropology, Temple University, 1115 West Berks Street, Philadelphia, PA 19122-6089; and §Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Ancon, Balboa, Republic 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.

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 Rio 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 Boque 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 Boque 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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Table 1. Starch recovered from tools and associated dates

<table>
<thead>
<tr>
<th>Site cat. no.</th>
<th>Tool type</th>
<th>Unit Level</th>
<th>Assoc. date (BP)</th>
<th>Calibrated date before present</th>
<th>Poaceae</th>
<th>Fabaceae</th>
<th>Zamia cf. skinneri</th>
<th>Dioscorea sp.</th>
<th>Dioscorea cf. urophylla</th>
<th>Maranta arundinacea</th>
<th>Calathea sp.</th>
<th>Manihot esculenta</th>
<th>Unidentified</th>
<th>Total</th>
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<tr>
<td>Ladrones</td>
<td>Handstone</td>
<td>0</td>
<td>4800 ± 100</td>
<td>5736–5314</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td>7</td>
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<tr>
<td></td>
<td>Base</td>
<td>0</td>
<td>~6600</td>
<td>~7500</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>2</td>
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<tr>
<td>Casita de Piedra</td>
<td>EGC</td>
<td>B3</td>
<td>~3300</td>
<td>~3600</td>
<td>(2)</td>
<td>(1)</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>191</td>
<td>197</td>
<td>3</td>
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<tr>
<td></td>
<td>Base</td>
<td>C2</td>
<td>~3800</td>
<td>~4200</td>
<td>3(2)</td>
<td>18</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td>2</td>
<td>22</td>
<td>48</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Chopper</td>
<td>5</td>
<td>~3800</td>
<td>~4200</td>
<td>2(1)</td>
<td>4(1)</td>
<td>(1)</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>17</td>
<td>26</td>
<td>2</td>
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<tr>
<td></td>
<td>EGC</td>
<td>E2</td>
<td>~5000</td>
<td>~5600</td>
<td>(1)</td>
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<td></td>
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<td></td>
<td>4</td>
<td>7</td>
<td>12</td>
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<td></td>
<td>Flake knife</td>
<td>F3</td>
<td>~6500</td>
<td>~7661–7261</td>
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<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
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<tr>
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<td>4</td>
<td>~3800</td>
<td>~4518–4086</td>
<td>16</td>
<td>2</td>
<td></td>
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<td>25</td>
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<td></td>
<td>EGC</td>
<td>3</td>
<td>~4000</td>
<td>~4800</td>
<td>(4)</td>
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<td>(1)</td>
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<td>6</td>
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<td>Chopper</td>
<td>5</td>
<td>~4300</td>
<td>~4900</td>
<td>4(4)</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>15</td>
<td>32</td>
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<td></td>
<td>E2</td>
<td></td>
<td>~465 ± 85</td>
<td>~5602–5071</td>
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<td>2</td>
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<td></td>
<td>E3</td>
<td></td>
<td>~5850 ± 110</td>
<td>~6933–6411</td>
<td></td>
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<td></td>
<td>1</td>
<td></td>
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<tr>
<td>Hornito</td>
<td>Chopper</td>
<td>C</td>
<td>6270 ± 270</td>
<td>7666–6554 to 5880 ± 260</td>
<td>(2)</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>20</td>
<td></td>
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<tr>
<td></td>
<td>Wedge</td>
<td>A</td>
<td>6270 ± 270</td>
<td>7666–6554 to 5880 ± 260</td>
<td>(1)</td>
<td>6(3)</td>
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<td>11</td>
<td>21</td>
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<td></td>
<td>Scraper</td>
<td>E</td>
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<td>7666–6554 to 5880 ± 260</td>
<td>(2)</td>
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<td>3</td>
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Radiocarbon calibrations made using the OxCal 4.0 program (1). EGC, edge-ground cobbles. 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.
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-83b) 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 hilum (Fig. 2G). 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., popcorn, not flour corns) (34).

Starch from a species of yam (*Dioscorea*) was recovered from the handstone (CL-68/1) found in Layer 10 (Fig. 2H). 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 Amer-

ica. Previous starch, pollen, and phytolith data from the rockshelters of Aguadulce, Los Santos, 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 Chiriqui 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 Chiriqui 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
first cultivators would have expedited the dispersal of new domestics.

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 \( \approx 2300 \) 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. Alter-
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, material was collected by the first author. For more details, see SI Materials and Methods.

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