Documenting plant domestication: The consilience of biological and archaeological approaches

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For more than a million years our distant ancestors were hunter–gatherers, relying exclusively on the gathering of wild plants and the hunting of wild animals for their food. Then, between 10,000 and 5,000 years ago, dramatic changes took place in this longstanding way of life, as human societies in more than a half dozen regions of the world, including Mexico, independently domesticated a variety of different plants and animals (1, 2). These early domesticates, and the agricultural economies subsequently based on them, marked a major turning point in the history of the earth and our species, in that they formed the lever with which humans have relentlessly transformed the earth and its terrestrial ecosystems. Not surprisingly, this "Neolithic Revolution" has attracted increasing attention from both biologists and archaeologists in the more than five decades that have passed since the pioneering field research on agricultural origins by Vavilov, Braidwood, and MacNeish (1). No longer open to easy and universal explanation as a rapid and straightforward transition between adaptational steady states, the developmental shift from hunting and gathering to agriculture has in the past several decades blossomed out into a set of long-unfolding and fascinatingly complex, regional scale developmental puzzles. The most dramatic recent advances in understanding these diverse and extended regional transformations center on documenting the domestication of individual species and involve a consilience and cross-illumination of biological and archaeological approaches. In this issue of PNAS, two articles provide a welcome new addition in this area of research, while also underscoring how much is still to be learned about the initial domestication of maize, and more generally, about agricultural origins in Mexico. Piperno and Flannery (3) report on the oldest maize (*Zea mays* ssp. *mays)* cobs yet recovered from Mexico, describing their archaeological context and reporting direct accelerator mass spectrometer (AMS) radiocarbon age determinations. In a companion piece, Benz (4) provides a detailed description of the cobs and documents initial morphological changes associated with domestication, including the development of a nonbrittle, rigid rachis and an associated loss of natural disarticulation and seed dispersal.

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Cross-illuminating, if often uncoordinated, biological and archaeological approaches to documenting domestication are methodologically straightforward and address the basic questions of when, where, and from what progenitor population(s) a domesticate was derived. Comprehensive genetic profile comparisons, on the one hand, have revealed the identity and geographical range of present-day wild progenitor populations of a number of important domesticated plants and animals (1), including cattle (5), einkorn wheat (6), and the maize-beans-squash trinity (7–9). At the same time, archaeobotanists have substantially expanded baseline documentation of the often microscale morphological markers that can be used to distinguish between the reproductive propagules of wild and domesticated plants in archaeological contexts (1–4), whereas zooarchaeologists are focusing on the age and sex profile changes that reflect human management of newly domesticated herd animals (10). In addition, direct small sample AMS radiocarbon dating is now routinely used to establish the unequivocal temporal placement of these early domesticates (1, 3). These biological and archaeological research efforts can converge to yield remarkable results. Genetic fingerprinting, for example, recently pinpointed the present-day location of the wild progenitor populations that gave rise to domesticated einkorn wheat (6). These wild stands of einkorn are situated only about 200 km from the site of Abu Hureyra, which has yielded the earliest evidence of initial domestication of this important cereal grain 9,500 years ago. Similarly, the earliest evidence for the initial domestication of the summer squash lineage of *Cucurbita pepo* in eastern North America 5,000 years ago comes from the Phillips Spring site in Missouri, located less than 60 km north of where its genetically fingerprinted wild Ozark gourd ancestor still grows today (9).

The paired articles in this issue of PNAS document that biological and archaeological approaches to determining where and when maize was initially domesticated in Mexico are now separated by about 400–500 km (3, 4). The two direct AMS radiocarbon dates reported on very primitive maize cobs from Guilá Naquitz cave, situated just east of the city of Oaxaca in the southern highlands of Mexico at an elevation of 1,926 m above sea level, push back the initial domestication of maize to sometime before *ca.* 6,300 calibrated calendar years ago, about eight centuries earlier than previously documented. These Guilá Naquitz cobs were recovered 400–500 km east of the present-day central Balsas river valley habitat of the subspecies of annual teosinte (*Zea mays* ssp. *parviglumis*), which has been identified as the wild ancestor of maize (7). MacNeish and Eubanks (11), see this separation as significant and as supporting their recent theory (following Mangelsdorf) that maize was derived at a higher elevation setting in the southern highlands of Mexico, closer to the earliest archaeological maize, and not solely from an annual subspecies of the wild grass teosinte, but as a hybrid of two wild grasses—a perennial subspecies of teosinte (*Zea diploperennis*), and a species of *Tripsacum*. Ge-

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See companion articles on pages 2101 and 2104.

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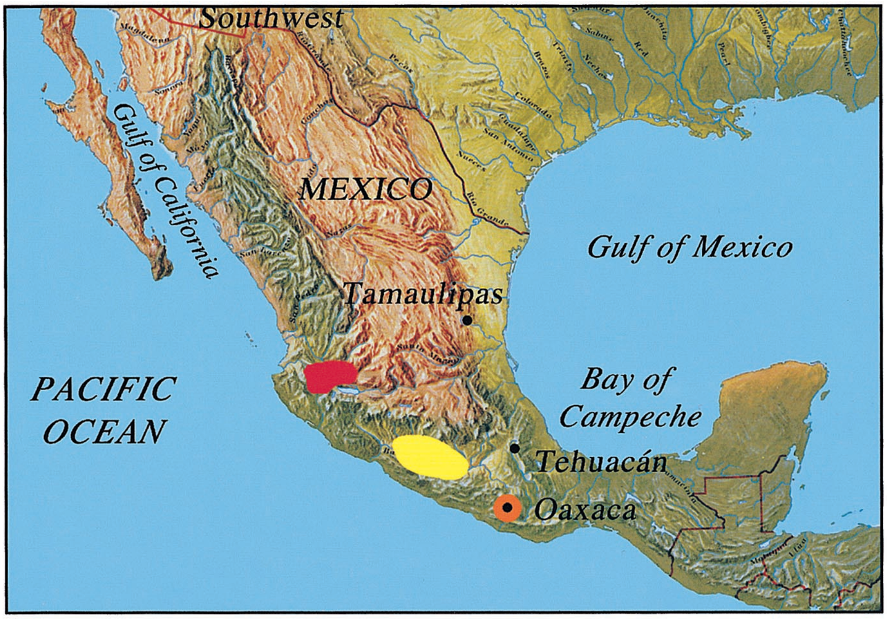

	Oaxaca 17°	Tehuacán 18°30'	Tamaulipas 23°	Southwest 32°
BEAN	2100	2300	1300	2200
MAIZE	6300	5500	4300	3500
SQUASH	10,000	7,900	6300	3500

Fig. 1. Map of Mexico showing the present-day geographical range of the wild progenitor populations of the domesticated common bean (red) (8) and maize (yellow) (7), as well as the area where wild pepo squash was likely initially brought under domestication, based on archaeological evidence (orange) (14, 15). Also shown are the three areas (Tamaulipas, Tehuacán, Oaxaca) where dry caves have yielded much of the available evidence regarding the early pre-Columbian history of these three major crop plants. The associated chart indicates when domesticated common bean, maize, and pepo squash initially appear in the archaeobotanical sequences of Oaxaca, Tehuacán, and Tamaulipas, which along with the Southwest United States form a south to north transect (note degrees north latitude designations). Expressed in calibrated calendar years ago, the dates of initial appearance of these three major crop plants in these four regions are based on direct AMS radiocarbon age determinations (1, 3, 4, 13–15). The age determination for the initial appearance of pepo squash in Tehuacán is based on an AMS date of 7,100 ± 50 ^{14}C yr B.P. (β123040)—about 7,900 calendar years ago, obtained on seed 201 from Coxcatlán Cave (square 148, level 11, zone XIV).

netic research over the past three decades, however, has overwhelmingly established an annual subspecies of teosinte as the solitary wild ancestor of maize (12). The 400- to 500-km gap between the present-day range of the wild ancestor of maize and the earliest maize cobs in the archaeological record also could be narrowed if the present-day, or more importantly, the Middle Holocene, geographical range of the wild ancestor of maize could be identified as extending further east toward Guilá Naquitz. This is certainly a good possibility, given the ongoing discovery of new populations of *Zea mays* ssp. *parviglumis,* in many locations, including Oaxaca, in recent years. The possibility that the wild progenitor populations from which maize was domesticated had a more extensive range in the past is not mutually exclusive with a third explanation for this 400- to 500-km separation—that *Zea mays* was initially brought under domestication by societies situated closer to the currently documented central Balsas range of wild ancestor teosinte populations at some time before 6,300 calendar years ago (1, 3, 4, 7), and was only later introduced into the nearby low-level food production economy of groups in the valley of Oaxaca. Thus in the process of identifying the wild ancestor of maize and delimiting its present-day geographical range, genetic research has both provided a potential answer to the question of where maize was initially domesticated and indicated to archaeologists where they could seek even older archaeobotanical evidence, which would both confirm the spatial context of domestication and establish when this important crop plant was first grown.

In stark contrast, substantially larger gaps still exist between what biological and archaeological approaches can tell us, so far, about the initial domestication of each of the other two major crop plants of Mexico—the common bean (*Phaseolus vulgaris*) and a species of squash (*C. pepo*). Gepts (8) has identified wild *P. vulgaris* populations near Guadalajara, in the west-central Mexican state of Jalisco, as the progenitor source of the domesticated common bean cultivars of Mexico, based on a shared S-type phaseolin seed protein. The earliest directly dated common beans in the archaeological record of Mexico, however, date to only 2,300 calibrated calendar years ago and come from Coxcatlán Cave in the Tehuacán Valley, more than 700 km southeast of Guadalajara (13). Here again, genetic research to identify and define the current range of wild progenitor *P. vulgaris* populations also points to where archaeologists should seek earlier archaeobotanical evidence of initial domestication of the common bean. With squash (*C. pepo*), in contrast, the situation is reversed. Although the wild ancestor of *C. pepo* in Mexico has yet to be identified, seeds of a domesticated *C. pepo* dating to 10,000 calibrated calendar years ago from Guilá Naquitz Cave (14, 15) both indicate a very early domestication of this plant and serve to point biologists to the southern highlands of Mexico in their search for any surviving wild progenitor populations. Pepo squash, of course, is only one of many domesticates, both in Mexico and throughout the world, for which genetic profiling has yet to establish, to the extent possible, the identity and present-day geographical range of wild progenitor populations.

On the archaeological research side, similarly, all of the recent reanalysis and direct AMS redating of early domesticates in long-curated museum collections, including the important new reports in this issue of PNAS (3, 4), underscore how much excavation still remains to be done to fill in the sizable gaps that exist in the archaeological record of early food production economies over a broad area of Mexico. Much of what is known about the early history of Mexico's three major pre-Columbian crop plants (squash, maize, and beans) in fact comes from a total of only five dry caves excavated in the 1950s and 1960s in three separate regions—Tamaulipas (Romero's and Valenzuela's Caves near Ocampo) (16); the Tehuacán Valley (Coxcatlán and San Marcos Caves)

(17); and Oaxaca (Guilá Naquitz) (1, 3, 4, 14, 15) (Fig. 1).

Even though the caves of Tamaulipas, Tehuacan, and Oaxaca represent only three scattered data points on a vast and largely uncharted developmental landscape, the direct AMS-determined date of first appearance of pepo squash, maize, and the common bean in their respective archaeobotanical sequences does form an interesting, if overly simplistic, geotemporal matrix, particularly if the likely geographical ranges of their wild ancestors are used as starting points, and the arrival of these three crops in the American Southwest is added to the north. Piperno and Flannery's AMS dates on maize from Guilá Naquitz (3) fills the last empty cell in this matrix. Biological and archaeological evidence, respectively, indicates that pepo squash and maize were likely first brought under domestication in southern (Oaxaca) and southwestern (central Balsas) Mexico. Available archaeobotanical evidence supports these starting points in that both domesticates first enter the matrix at the southern end (Oaxaca), close to their likely areas of origin, and each then moves north, over time appearing sequentially in Tehuacán, Tamaulipas, and the southwestern United States (Fig. 1). The matrix sequence for *P. vulgaris*, while less clear, is not incompatible with dispersal from a west Mexican (Jalisco) area of origin. The common bean enters the matrix at the south end (Oaxaca), the middle (Tehuacán), and the north (Southwest) at about the same point in time, and appears only much later in Tamaulipas. The matrix also suggests that pepo squash, maize, and the common bean may have had quite different rates of dispersal across Mexico, with maize, for example, consistently moving much more quickly through the matrix than pepo squash.

Perhaps most significant, however, is the clear temporal separation of the initial domestication and subsequent dispersal of pepo squash, maize, and the common bean. Pepo squash was brought under domestication first in southern Mexico 10,000 years ago, and accompanied by bottle gourd (*Lagenaria siceraria)* was subsequently dispersed north into Tehuacán by 7,900 years ago, reaching all of the way north into Tamaulipas by 6,300 years ago. Maize did not enter the matrix at the southern end until about the same time that squash and bottle gourd radiated as far north as Tamaulipas. Interestingly, maize moved north much faster than pepo did, consistently closing the temporal gap until both crops entered the Southwest by about 3,500 years ago. Both pepo squash and maize, in turn, were domesticated and dispersed north across Mexico, into the Southwest, well before the common bean enters the matrix.

Although future archaeological research in western Mexico will quite likely extend the early history of domesticated maize and the common bean further back in time, there will probably not be much temporal overlap in the initial domestication and subsequent dispersal of the three major crop plants. The initial domestication of pepo squash, maize, and the common bean in Mexico thus comes into focus, I would suggest, as an additive sequence of spatially and temporally distinct pulses, occurring over a span of perhaps 6,000 years or more. Pepo squash was domesticated first in Oaxaca by hunting-gathering groups about 10,000 years ago. When maize was brought under domestication in the central Balsas region perhaps 3,000 years later, it was in all likelihood by low-level food-producing societies that had already been growing pepo squash for more than 1,000 years. Similarly, when the common bean was initially domesticated in Jalisco several thousand years later, it was probably added into well-established farming economies based on pepo squash and maize, as well as on other crops yet to be fully documented and directly dated.

Although certainly open to considerable expansion and refinement, the simple three-crop geo-temporal matrix presented in Fig. 1 does provide an initial, reliable, temporal, and spatial context for more focused consideration of causality and the cultural contexts of change along a time transgressive developmental transition that spanned a full 6,000 years in Mexico, from initial plant domestication around 10,000 years ago, to the subsequent first appearance around 4000 B.P. of village-based farming economies in which domesticates made a substantial dietary contribution (18). It also underscores the extent to which the timing, rate, and sequence of such agricultural transitions varied across different regions of the world. The four major indigenous crop plants of eastern North America, for example, all were brought under domestication in a relatively small area over a span of perhaps only 500–1,000 years. In the Near East, in contrast, a larger set of higher-potential plant and animal species (e.g., barley, wheat, goat, sheep, pig, cattle) were brought under domestication in different places at different times, but with much more temporal and spatial overlap than was the case in Mexico, leading to a far more complex and rapidly unfolding developmental mosaic (1). Clearly, regional scale and species-specific research should provide richly diverse and productive avenues of inquiry for biologists and archaeologists alike for decades to come.

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1. Smith, B. D. (1998) *The Emergence of Agriculture* (Scientific American Library, New York).
2. Piperno, D. R. (2000) *Nature (London)* **407,** 894–897.
3. Piperno, D. R. & Flannery, K. V. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 2101–2103.
4. Benz, B. F. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 2104–2106.
5. Bradley, D. G., MacHugh, D. E., Cunningham, P. & Loftus, R. T. (1996) *Proc. Natl. Acad. Sci. USA* **93,** 5131–5135.
6. Heun, M., Schäfer-Pregl, R., Klawan, D., Castagna, R., Accerbi, M., Borghi, B. & Salamini, F. (1997) *Science* **278,** 1312–1314.
7. Doebley, J. (1990) *Econ. Bot.* **44,** 6–27.
8. Gepts, P. (1998) in *The Origins of Agriculture and Crop Domestication*, eds. Damania, A. B., Valkoun, J. & Qualset, C. O. (Genetic Resources Conservation Program, Univ. of California, Davis), pp. 198–209.
9. Decker-Walters, D., Walters, T., Cowan, C. W. & Smith, B. (1993) *J. Ethnobiol.* **13,** 55–72.
10. Zeder, M. & Hesse, B. (2000) *Science* **287,** 2254–2257.
11. MacNeish, R. S. & Eubanks, M. E. (2000) *Lat. Am. Antiq.* **11,** 3–20.
12. Bennetzen, E., Buckler, V., Chandler, J., Doebley, J., Dorweiler, B., Gaut, B., Freeling, S., Hake, E., Kellogg, R. S., Poethig, V., *et al*. (2001) *Lat. Am. Antiq.*, in press.
13. Kaplan, L. & Lynch, T. (1999) *Econ. Bot.* **53,** 262–268.
14. Smith, B. D. (1997) *Science* **276,** 932–934.
15. Smith, B. D. (2000) in *Cultural Evolution*, eds. Feinman, G. & Manzanilla, L. (Plenum, New York), pp. 15–60.
16. Smith, B. D. (1997) *Lat. Am. Antiq.* **8,** 342–383.
17. MacNeish, R. S. (1967) in *Environment and Subsistence, Vol 1: The Prehistory of the Tehuacan Valley*, ed. Byers, D. (Univ. Texas Press, Austin), pp. 290–309.
18. Smith, B. D. (1998) *Science* **279,** 1651–1652.