

Archaeological evidence of teosinte domestication from Guilá Naquitz, Oaxaca

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Analysis of the three most ancient *Zea mays* inflorescence fragments from Guilá Naquitz, Oaxaca, Mexico shows they did not disarticulate naturally, indicating that agricultural selection of domesticated teosinte was underway by 5,400 ¹⁴C years before the present (about 4,200 dendrocalibrated years B.C.). The cooccurrence of two-ranked specimens with two rows and four rows of grain and numerous additional morphological characteristics of these specimens support hypotheses based on molecular and quantitative genetic analyses that maize evolved from teosinte. Domestication of the wild ancestor of maize occurred before the end of the 5th millennium B.C.

The oldest macrobotanical evidence of the initial phases of maize evolution comes from two Mesoamerican archaeological localities, the valleys of Tehuacán and Oaxaca. These two localities have produced the earliest evidence of maize cultivation by preceramic hunter-gatherers (1–4). Considerable debate about these specimens hinges on their relative antiquity and a detailed analysis and interpretation of their morphology. Morphological comparison of specimens from Oaxaca and Tehuacán combined with the accurate dating of the Guilá Naquitz specimens indicates that efforts to domesticate teosinte were successful at least 700 years before the earliest maize cobs were incorporated into the preceramic refuse of San Marcos Cave in the Tehuacán Valley.

Archaeological specimens of domesticated *Zea* inflorescences (cobs) from Guilá Naquitz were subjected to accelerator mass spectrometry (AMS) radiocarbon dating (1). Two of three specimens were AMS dated at $5,420 \pm 60$ (C9, Fig. 1, specimen b) and $5,410 \pm 40$ (D10) ¹⁴C years B.P. (6,235 calibrated years B.P.). Tests for contemporaneity indicate the two dates can be averaged ($5,412 \pm 33$ years B.P.) because their ages are not significantly different ($t = 0.14$, not significant). The AMS dates on the Guilá Naquitz cobs indicate they are about 730 years older than the most ancient specimens of maize reported from the Tehuacán Valley (2). The two specimens from C9 occurred in the same provenience and presumed depositional unit and were reported to be fragments of one inflorescence (3). Attempts to refit these two specimens were unsuccessful. Statistical comparison with the Tehuacán maize assemblage has been conducted as if the two specimens from C9 were from different inflorescences. The morphological characteristics of the Guilá Naquitz cobs support accumulating genetic evidence that demonstrates the ancestor-descendant relationship hypothesized for teosinte and maize and document further some of the genetic differences that distinguish the inflorescences of wild and domesticated *Zea* (5–7).

Materials and Methods

Morphological Differences Between Maize and Teosinte Inflorescences. The maize ear (the cob plus its attached grains) is distinguished from the teosinte female inflorescence by morphological characteristics that confer selective disadvantage for surviving in the wild. Maize has a rigid, polystichous (3- to 12-ranked) rachis with tenaciously attached grains that require human intervention for dispersal and propagation. The teosinte

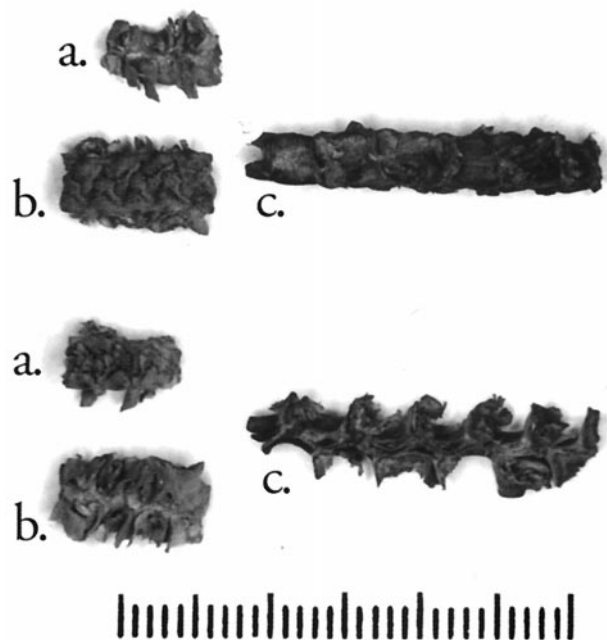


Fig. 1. Photograph of three Guilá Naquitz archaeological cobs. Specimens a and b from C9. Cob apex is at left (*Upper*) or at right (*Lower*). All three specimens have two ranks of cupules. Specimens a and b have a single spikelet per node, i.e., a single grain per cupule. Specimen a (*Upper*) shows abaxial side (away from axis), whereas specimen b (*Upper*) shows adaxial (toward axis) side of bilaterally symmetrical distichous inflorescence. Specimen a (*Lower*) shows one rank of spikelets on abaxial side, whereas specimen b (*Lower*) shows abaxial side. Perpendicular orientation of lower glumes of two-rowed specimens is visible in specimens a and b (*Lower*). Specimen c is the distichous four-rowed specimen from D10. The alternate arrangement of opposing rachids, shallow cupules, and the perpendicular to reflexed lower glumes are visible in *Lower*, whereas paired spikelets and open cupules are visible in *Upper*. Specimens are actual size. (Scale = 6 cm.)

female inflorescence, on the other hand, is distichous (two-ranked) and naturally disarticulates, disseminating a single grain in each cupulate fruitcase. Each rachis segment or rachid in the maize ear bears a pair of fertile grain-bearing spikelets at the base of a cupule (the indurate invagination of each rachis segment) that are oriented perpendicular to the rachis axis. The teosinte inflorescence, in contrast, has a single grain-bearing spikelet per rachid that is oriented parallel to the rachis and is partially enclosed by the lateral margins of the invaginated rachis segment. Teosinte grains are thus protected inside the fruitcase formed by the invaginated rachid and lower glume when they are individually dispersed (7–9). In many grain crops, the first step

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in domestication resulted from human selection for a rachis that did not naturally disarticulate. Once this rigid-rachis phenotype had been fixed genetically, human selection and agroecosystem creation and maintenance led to an increase in grain size (10–12). The predicted initial evolutionary changes documented for other grain crops such as barley and wheat are evident in the early inflorescence fragments of *Zea mays* encountered at Guilá Naquitz.

Results

Morphology of Early *Zea* Inflorescences at Guilá Naquitz. All three specimens from Guilá Naquitz have a nondisarticulating rachis. Breaks in the rachis near the inflorescence apex occur through the internode instead of at the node (Fig. 1), which indicates that the plants bearing these inflorescences were domesticated and depended on human dispersal and propagation. All three inflorescences are also distichous (two-ranked); one fragment (Fig. 1, specimen c, D10) has four rows of grain (two-ranked with two rows per rank), and the other two have two rows of grain (two-ranked with one row per rank; Fig. 1, specimens a and b, C9). Like teosinte, the two-rowed specimens are two-ranked (distichous) and possess a single grain-bearing spikelet per rachis segment. The single four-rowed specimen is like maize, because it has paired spikelets on each rachis segment. The stratigraphic and temporal association of these cobs with distinct morphologies suggests that the Guilá Naquitz specimens represent domesticated plants that were subject to human selection for paired spikelets, that is, ears with four or more rows of grain.

The lower glume of each spikelet in the two-rowed inflorescence fragments (C9) is perpendicular to the rachis, short, dull, soft, and flexible in contrast to the rachis, which is mottled, shiny, rigid, and very indurate. The single grain-bearing spikelets alternate on the axis and are oriented at an approximately 45° angle to each other instead of being opposed at 180° as in the four-rowed specimen (Fig. 1, specimens b and c). The rachis segments are very short in comparison to the female inflorescence of both the presumed ancestor, teosinte, and modern descendants, extant Mexican maize races. Rachis segments are approximately one-half as long as those of the shortest of the extant Mexican maize races, Mexican annual teosintes, and teosinte homozygous for *tg1* (7, 13, 14). Cupules of the two-rowed specimens are as wide as they are long and very shallow (Fig. 2; refs. 4 and 15). The two-rowed cobs from Guilá Naquitz are similar to those of teosinte, because each rachis segment has a single spikelet; the rachis is distichous and has a mottled, smooth, and shiny surface; and because both are indurate and possess alternately stacked rachis segments. These cobs differ from teosinte by having spikelets oriented perpendicularly to the rachis, very short and shallow cupules, and a nondisarticulating rachis.

The four-rowed inflorescence is similar to four archaeological cobs from the Tehuacán valley, three from San Marcos, and one from Coxcatlán cave. The rachis of this Guilá Naquitz cob is distichous, but each rachis segment has two grain-bearing spikelets per node; one is sessile, and the other is distinctly pedicellate, a characteristic of maize. The lower glumes are indurate but less so than those of the two other specimens at Guilá Naquitz (Fig. 1, *Lower*, specimen c). Rachis internodes alternate, the spikelets of one rank alternating with spikelets of the opposing rank. Rachis internodes are twice as long but only as wide as the internodes of the two-rowed specimens (Figs. 1 and 2). The cupules are shallow, seeming to be flat and slightly reflexed at the apex. This single cob from Guilá Naquitz, like the few aforementioned specimens from Tehuacán, possesses three of four derived morphological attributes characteristic of the female inflorescence of maize: a rigid rachis, paired grain-bearing spikelets, and spikelets oriented perpendicularly to the axis. This specimen is distichous like teosinte; thus, it lacks the fourth

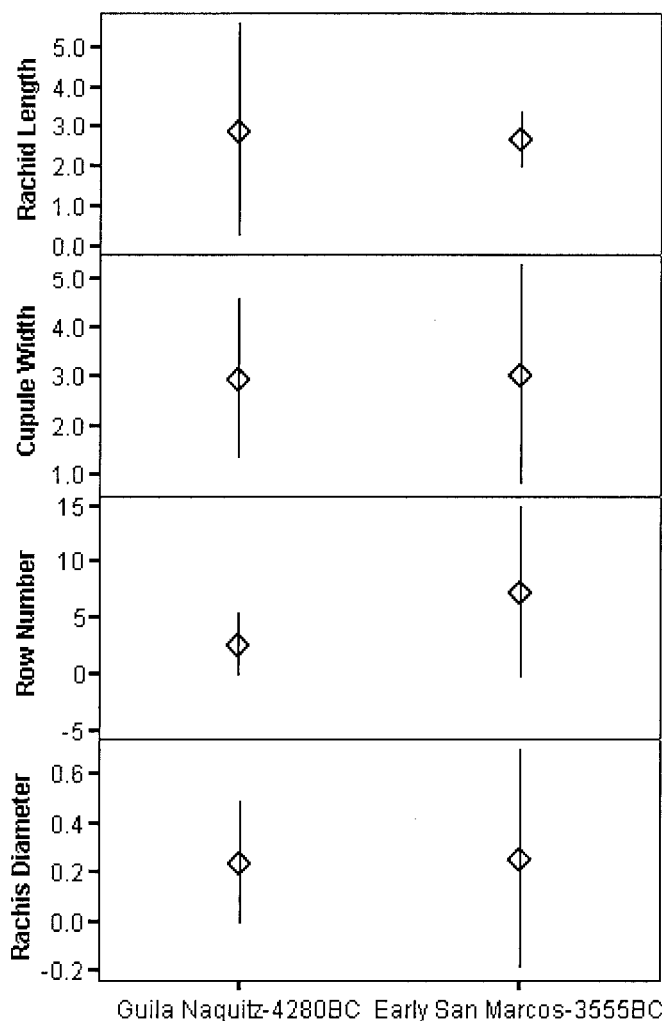


Fig. 2. Morphometric comparison of the three archaeological specimens from Guilá Naquitz on left with the three earliest archaeological specimens from San Marcos cave, Tehuacán Valley, Puebla, Mexico on right. Rachid length and cupule width are in millimeters; rachis diameter is in centimeters; diamonds indicate mean; error bars represent the 95% confidence interval.

derived characteristic, polystichy. The other two cobs from Guilá Naquitz share only two of these derived characteristics: a rigid rachis; and a perpendicular orientation of spikelets to the rachis.

Discussion

Early Evolution of Maize. By 5,400 ¹⁴C years B.P., human cultivators had made genetic changes in teosinte that resulted in a nondisarticulating rachis, a reduced rachid length, spikelets reoriented perpendicularly to the rachis, and opened cupulate fruitcases, which exposed the grain. The precise genetic focus of human selection on teosinte is not obvious from the phenotypes of the archaeological specimens. However, inferences based on existing genetic evidence suggest that at least two genetic loci were subject to human manipulation at this early date (8, 16–18). The teosinte branched locus (*tb1*) has demonstrated effects on the condensation of lateral branches and the rachis segments of inflorescences located on lateral branches in maize and teosinte. The rachis segments of the Guilá Naquitz specimens are remarkably short, as short as the earliest maize from the San Marcos cave, and considerably shorter than any extant teosinte or Mexican land race. The teosinte glume architecture locus (*tg1*) controls the development of the cupulate fruitcase and the

degree of glume induration in teosinte and maize. The fact that the glumes of all three cob fragments from Guilá Naquitz seem flexible and less indurate than the rachis or the glumes of teosinte suggests that this locus was the focus of human selection after or simultaneously with shortened rachis internodes and a rigid rachis phenotype. The cooccurrence of two-rowed and four-rowed distichous inflorescences at Guilá Naquitz suggests that these and other genetic factors had not yet reached fixation and that modifiers had not yet accumulated to stabilize the maize-like phenotype with paired spikelets.

Conclusion

A comparison of the morphological characteristics of three cobs from Guilá Naquitz with the three earliest specimens from San Marcos Cave (4,750 ¹⁴C years B.P.) indicates the two populations are not distinguishable on statistical grounds (Fig. 2). Hence, by 5,400 ¹⁴C years B.P. and for the ensuing 700 years, human selection seems to have focused on stabilizing the distichous, nondisarticulating, naked-grained phenotype and on increasing the number of grain-bearing spikelets per node from one to two. The morphological similarity of the Guilá Naquitz and earliest Tehuacán specimens (Fig. 2) suggests that human intentionality sought to maintain or increase the productivity of this grain crop.

This evidence does not reject the possibility that human use of teosinte focused on something other than grain (19) but does suggest that by the 6th millennium before the present era, humans were focusing their subsistence activities on maintaining readily harvestable grain-producing inflorescences. These few inflorescence fragments also suggest that propagation of domesticated teosinte during this time period relied on a human subsistence and settlement system with a degree of permanence that allowed teosinte to evolve dependence on human land management practices over the course of the growing and harvest season.

Dates of ca. 4,700 ¹⁴C yr. B.P. for the earliest Tehuacán Valley maize cobs, together with the Guilá Naquitz dates on domesticated teosinte, suggest that earlier evidence of human manipulation of teosinte awaits discovery in Mesoamerican archaeological deposits.

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