

## Origin Matters: Lessons from the Search for the Wild Ancestor of Maize

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The wild ancestry of maize has long been a puzzle. Maize shows extraordinary phenotypic and genetic diversity with no obvious morphological similarity to any of its wild relatives. Beadle's teosinte hypothesis, which regards teosinte as the sole wild ancestor of maize, has become widely accepted as the most probable model of maize evolution based on taxonomic, genetic, and other types of evidence. Molecular studies have refined the teosinte hypothesis by identifying a particular form of teosinte, *Zea mays* ssp. *parviglumis*, as the direct ancestor of maize. Maize and teosinte therefore provide a typical case in which modern molecular genetic analyses, in the absence of obvious morphological similarity, have been critical for distinguishing the exact ancestor of a crop from other close wild relatives. Furthermore, a recent microsatellite-based study shows that all extant pre-Columbian maize landraces arose from *Z. mays* ssp. *parviglumis* roughly 9,000 years ago through a single domestication event in the central Balsas River drainage (southern Mexico). That model, showing that maize is a domesticated form of *Z. mays* ssp. *parviglumis*, provides a logical, practical framework for investigations of the genetic mechanisms that drove maize domestication and diversification. This points up the importance of knowing exact origins in studies that use crops and their wild relatives as models. An overview of the progress in genetic and evolutionary studies is presented herein to clarify the identity of the wild progenitor of maize. Implications of recent findings on the origin of maize diversity are discussed.

**Key Words:** crop evolution, diversity, domestication, evolutionary genetics, introgression, teosinte, *Zea*.

### Introduction

“The study of domestic productions will rise immensely in value. A new variety raised by man will be a far more important and interesting subject for study than one more species added to the infinitude of already recorded species.” C. Darwin, *The Origin of Species*

Since the beginnings of agriculture, humans in both the Old and New Worlds have domesticated crops. Today, in many parts of the world, we rely on such crops for our daily sustenance. All domesticated crops, which are thought to have arisen from their wild ancestors during the previous 10,000 to 4,000 years (Smith 1998), have useful properties not found in their wild relatives. For example, the large, nutritious, delicious fruits of domesticated crops differ markedly from the small, sour or bitter, sometimes poisonous, fruits of their wild relatives. Cereal crops have non-brittle spikes that remain intact at maturity, a characteristic absent in their wild counterparts, which greatly facilitates collecting the mass of small grains at harvest. These and other remarkable properties of crops are indicative of the fine adap-

tations that have occurred in agro-ecological environments.

Crops provide not only valuable foods but also important models for evolutionary studies. The genetic forces of mutation, selection, and genetic drift have significant roles in the process of domestication and diversification. One merit of using crops as model materials is availability of the many wild ancestral species that can be used for studies as living materials. With wild ancestors as the starting point of evolution on the one hand and their domesticated counterparts as the goal of evolution on the other, the interplay of mutation, selection, and genetic drift in the rise of a novel biological entity can be studied in depth by means of comparative analyses. Because mutation, selection, and genetic drift are important factors in the process of speciation and other evolutionary events that occur under natural conditions, comparative studies of crops and their wild ancestors should provide insights into the genetic mechanisms that underlie natural evolutionary processes.

Moreover, comparative studies of crops and their wild ancestors are relevant to plant breeding. Crops differ from their wild ancestors in their expression of traits of agronomic importance. Knowledge of the mechanisms that control the expression of agronomic traits should provide a basis for further improvements of crops. In this regard, identifying the genes for agronomic traits is of great interest as the expression of agronomic traits usually is controlled genetically.

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Recent studies show that comparative analyses of crops and their wild ancestors are useful for this purpose. Genes that control important agronomic traits have been identified in maize (Doebley and Stec 1991, 1993, Doebley *et al.* 1997) and tomato (Alpert *et al.* 1995, Frary *et al.* 2000) by QTL analyses of the crops and their wild ancestors. Furthermore, the agronomic gene functions can be analyzed by comparing the expression patterns in crops and their wild relatives (Doebley *et al.* 1997, Hubbard *et al.* 2002).

Because the progenitor-descendent relationship defines the framework of comparison, knowledge of the exact identity of the wild ancestor is essential for successful comparative studies of crops and their wild ancestors. There is high probability that wild ancestral species still exist in the modern world given the relatively recent divergence of domesticated crops from their wild ancestors. This does not, however, mean that wild ancestral species are always identifiable, rather their identities may be confusing. Extensive genetic and evolutionary studies are needed to establish conclusively the identities of wild ancestor plants, as well as the conventional methods that integrate botanical, geographical, historical, linguistic, and anthropological evidence (Vavilov 1926).

In this paper, I will review recent advances in the identification of the wild ancestor of maize, a New World crop. Maize and its close wild relatives, the teosintes, show extreme morphological differences. This has long puzzled investigators. The wild ancestry of maize was a matter of heated debate in the 1970s and early 1980s (see Doebley 2001). The relationship of maize to teosinte became the focus of important research, in which modern molecular genetic analyses were pivotal, in the absence of obvious morphological similarity, in distinguishing the exact ancestor of a crop from other close wild relatives. Recent findings of molecular studies have provided a logical, practical framework for further studies of the genetic mechanisms that drove maize domestication and diversification by shedding light on early episodes of maize evolution. This points up the importance of knowing exact origins in studies of crops and their wild relatives as models. To better understand the issues involved in the origin of maize, I begin with an outline of the current taxonomic status of maize and teosinte, then provide an overview of the progress of genetic and evolutionary studies on the clarification of the identity of the progenitor of maize. Lastly, I discuss the implications of recent findings on the origin of maize diversity.

In my view, the story of the search for the wild ancestor of maize provides many interesting, suggestive, educational chapters for those who study crop origins. The reader is referred to Doebley (2001) for anecdotal episodes.

## Maize and teosinte

Maize (*Zea mays* ssp. *mays*) is a New World cultigen that taxonomically belongs to the genus *Zea*. The genus *Zea* contains wild annual and perennial species native to Mexico

and Central America. Teosinte is the common name for the wild taxa of *Zea*. In the current system of classification (Doebley and Iltis 1980, Iltis and Doebley 1980, Doebley 1990a), *Zea* is divided into two sections, *Luxuriantes* and *Zea* (Table 1). Sect. *Luxuriantes* comprises three annual or perennial species: *Z. diploperennis* (diploid, perennial), *Z. perennis* (tetraploid, perennial), and *Z. luxurians* (diploid, annual). Of these, *Z. diploperennis* and *Z. perennis* have very narrow distributions in the state of Jalisco, Mexico, whereas populations of *Z. luxurians* are distributed in Guatemala, Honduras and Nicaragua. Recently, Iltis and Benz (2000) elevated the Nicaraguan populations of *Z. luxurians* to species status as *Z. nicaraguensis* Iltis & Benz (but see Fukunaga *et al.* 2005). Morphologically, Sect. *Luxuriantes* appears more primitive than sect. *Zea* (Doebley and Iltis 1980).

Sect. *Zea* consists of a single diploid annual species, *Z. mays*. Morphologically, *Z. mays* is highly polymorphic and comprised of three wild and one cultivated subspecific taxa: ssp. *huehuetenangensis* (wild) ssp. *mexicana* (wild), ssp. *parviglumis* (wild), and ssp. *mays* (cultigen). In addition to morphological differences, each wild subspecies of *Z. mays* has a distinct geographic distribution (Fig. 1). Subspecies *huehuetenangensis* is native to western Guatemala. Both ssp. *mexicana* and ssp. *parviglumis* are native to Mexico, but ssp. *mexicana* is found in the highlands of central and northern Mexico, whereas ssp. *parviglumis* primarily is found in Central Balsas and the Pacific slope from southern Guerrero to Jalisco.

The hierarchical system of classification of *Zea* (Table 1), based mainly on the morphology of the male inflorescence (tassel) and its spikes, shows that teosinte actually is a diverse group of distinct biological entities, each of which has distinct key morphological features. This system is supported by ecogeographical and molecular evidence (Doebley 1990a, Buckler and Holtsford 1996, Fukunaga *et al.* 2005), indicating that it reflects the evolutionary relationships of the taxa in this genus. Furthermore, as an important factor bearing on questions surrounding the origin of maize, the taxonomy of *Zea* indicates that of the various types of

**Table 1.** The taxonomy of *Zea* according to Doebley and Iltis (1980), Iltis and Doebley (1980) and Doebley (1990a)

Section <i>Luxuriantes</i> Doebley & Iltis
<i>Zea diploperennis</i> Iltis, Doebley & Guzman
<i>Zea perennis</i> (Hitchc.) Reeves & Mangelsdorf
<i>Zea luxurians</i> (Durieu & Ascherson) Bird
Section <i>Zea</i>
<i>Zea mays</i> L.
ssp. <i>mexicana</i> (Schrad.) Iltis
Race Chalco
Race Central Plateau
Race Nobogame
ssp. <i>parviglumis</i> Iltis & Doebley
ssp. <i>huehuetenangensis</i> (Iltis & Doebley) Doebley
ssp. <i>mays</i>

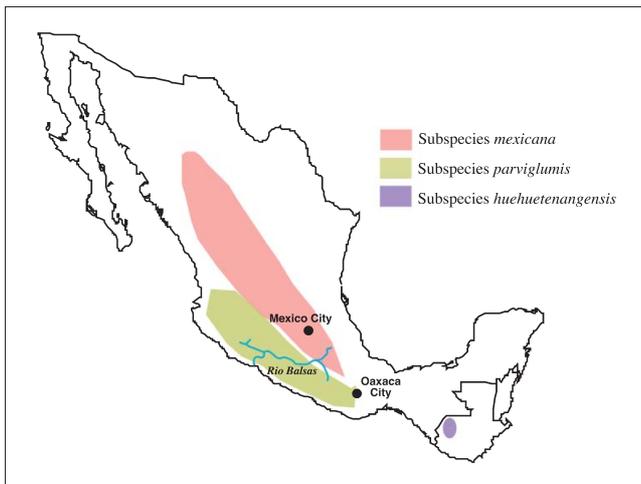


Fig. 1. Distribution of wild taxa of *Z. mays*.

teosinte the three annual ones, ranked as subspecies of *Z. mays* (*ssp. huehuetenangensis*, *ssp. mexicana* and *ssp. parviglumis*), have particularly close morphological similarities to maize (*ssp. mays*), the two Mexican annual teosintes (*ssp. mexicana* and *ssp. parviglumis*) being the most similar (Doebley 1990a). The taxonomy of *Zea*, therefore, points to Mexican annual teosintes as candidates for the wild ancestor of maize.

### The teosinte hypothesis

Maize and teosinte are alike in overall appearance. Both are tall, robust, broad-leaved grasses, but the long tasselled lateral branches of teosinte differ from the short ear (female inflorescence)-tipped lateral branches of maize. The general similarity between maize and teosinte had been noted by 18th and 19th century botanists, leading some to consider teosinte a plausible candidate for the ancestor of maize (see Beadle 1980). The ears of maize and teosinte, however, differ so markedly that one would not be easily convinced that maize arose from teosinte through domestication in the last ca. 10,000 years (see Doebley 2001 for photos). For example, the small ear of teosinte bears ca. 5–10 kernels, each of which is enclosed in a stone-hard cupulate fruitcase. In contrast, the gigantic ear of maize bears hundreds of naked kernels immediately ready for human consumption. Moreover, the teosinte ear disarticulates for dispersal at maturity, whereas the maize ear remains intact at harvest.

In contrast to the profound differences in ear morphology, genetically maize and teosinte are very close. Maize and some teosinte types could hybridize, producing viable, fully fertile hybrids (Collins 1919, Beadle 1932), evidence that they are the same biological species. According to Beadle (1932), the maize hybrid with the “Florida” form of teosinte (*Z. luxurians*) shows partial sterility due to irregular chromosome pairing in meiosis, whereas the hybrid with the Mexican annual form of teosinte (*Z. mays ssp. mexicana*) shows regular chromosome pairing and full fertility. These

findings indicate that maize is simply a domesticated form of teosinte despite the number of morphological differences.

Conflicting morphological and genetic observations have led to two different views on the origin of maize. In one, teosinte is the ancestor, as indicated by the cytogenetic evidence that maize and some teosintes are the same biological species (Beadle 1939). In that view, the small teosinte ear underwent radical transformation to the gigantic maize ear through domestication during the last 10,000 years. In the second view, teosinte is not the ancestor because morphological differences seemingly are too great to believe that they arose in the last 10,000 years (e.g., Mangelsdorf and Reeves 1938, 1939). In that view, one would have to search for the progenitor of maize outside of *Zea* or assume that the progenitor had become extinct. Furthermore, this second view requires explanations for why maize and some types of teosinte came to have such a close cytogenetic relationship.

Beadle (1939, 1978, 1980) proposed “the teosinte hypothesis” in which he regarded teosinte the sole progenitor of maize based on experimental, anthropological, archaeological, geographical, and linguistic evidence. In his famous experiment to show the genetic basis of the maize-teosinte morphological difference, he grew 50,000 maize-teosinte  $F_2$  plants and found that about one in 500  $F_2$  individuals had either the maize or teosinte type ear. This indicated that as few as four or five gene changes would account for the differences in ear morphology. The genetics underlying maize-teosinte ear morphology differences therefore seemed simple enough to conclude that maize arose from teosinte through domestication.

In this context, Doebley and Stec (1991, 1993) used QTL mapping to assess the maize-teosinte morphological difference in a maize-teosinte  $F_2$  population and confirmed that five or six regions of the genome have strong effects on the difference in traits. Furthermore, Doebley’s group successfully identified a candidate gene, *teosinte branched1* or *tb1*, as one of their QTLs and confirmed by complementation tests that the QTL and *tb1* are allelic. The *tb1* mutant of maize, which has long lateral branches tipped by tassels, resembles teosinte in its plant architecture, indicative that the *tb1* gene functions in the control of apical dominance. The *tb1* gene was cloned and shown by comparative nucleotide sequence variation analyses of the maize and teosinte alleles to have been under selection during domestication (see Doebley 2004). This *tb1* gene is one of the earliest examples of cloned QTL genes in plants and animals.

The teosinte hypothesis was supported by a broad range of biological evidence published from the 1970s to 1990s and has been accepted as the most probable model of the evolution of maize. In contrast, hypotheses based on teosinte not being the ancestor of maize [e.g., “the tripartite hypothesis” or “the wild maize hypothesis”, Mangelsdorf and Reeves (1938, 1939), Mangelsdorf (1974)] have lost major scientific backing due to lack of supportive evidence (Bennetzen *et al.* 2001).

Of studies that provide supporting evidence for the

teosinte hypothesis, molecular genetic studies that utilized protein (i.e., isozyme) and DNA markers to assess the genetic similarity of maize and teosinte have added further important details regarding the origin of maize (see Doebley 1990a). Morphologically, the Mexican annual teosintes (*Z. mays* ssp. *mexicana* and *Z. mays* ssp. *parviglumis*) are closest to maize (*Z. mays* ssp. *mays*) (see above). Isozyme and DNA marker-based studies have shown that, of the two Mexican annual teosintes, *Z. mays* ssp. *parviglumis* is indistinguishable from maize at the molecular level, whereas *Z. mays* ssp. *mexicana* is close, but distinct, evidence that *Z. mays* ssp. *parviglumis* is the direct wild ancestor of maize. These findings are particularly striking because the growth form of *Z. mays* ssp. *mexicana* (sparsely tillered and robust) appears more maize-like than that of *Z. mays* ssp. *parviglumis* (highly tillered and grassy) (see Mangelsdorf 1974 for photos). In any event, the published molecular evidence has further refined the teosinte hypothesis by showing *Z. mays* ssp. *parviglumis* to be the top candidate for the unknown direct wild progenitor of maize despite its having a less maize-like appearance than *Z. mays* ssp. *mexicana*.

### Maize domestication: single or multiple independent events?

Extraordinary phenotypic and genetic diversity exists in the maize landraces developed by pre-Columbian agriculturists. Kernels vary in color from white to yellow, orange, red, bronze, light blue, and dark purple, and in size from beadily small to coin large. Ears have a unique series of shapes, varying from the finger-short ears of popcorns to the forearm-long ears of North American varieties and grenade-shaped ones of Andean varieties. As to plant architecture, the dwarf variety grown by the Hopi in the southwest USA grows to about 1 m, whereas the tall tropical variety, whose hard stalks are used as building material in traditional Latin American villages (Weatherwax 1954 for photos), reaches 7 m.

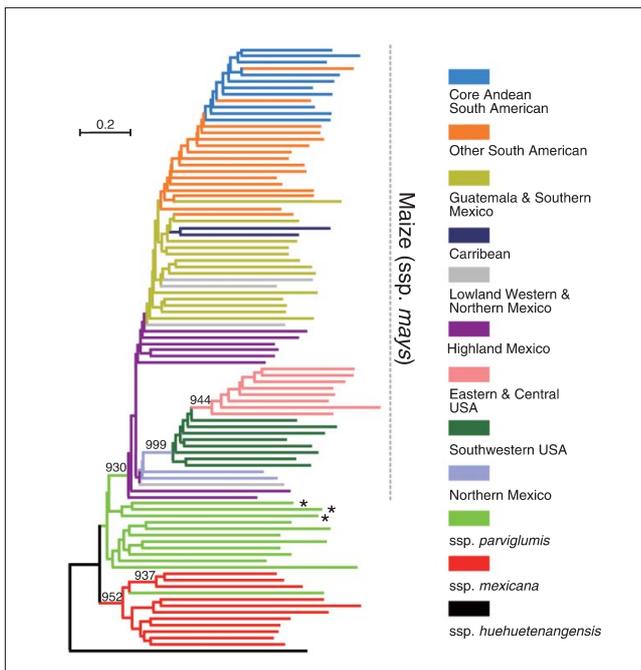
The theoretical framework of the teosinte hypothesis (Beadle 1939, 1978, 1980) provides the basis for two different evolutionary models of the origin of the morphologically and genetically diverse pre-Columbian maize landraces. The first assumes a single domestication event as the starting point of maize evolution, followed by rapid racial diversification (the single domestication model). This model has its roots in the notion that, during the process of domestication, teosinte must have gone through a series of very rare mutations that eventually led to its transformation to maize (Doebley 1990c, see Iltis 2000). In contrast, the second model assumes multiple domestication events as the origin of maize diversity because of the remarkable morphological and genetic variability of teosinte populations (the multiple domestication model). For example, based in part on variation in the patterns of maize ear shape, Galinat (1988) concluded that distinct ancestral types of the annual teosintes in different Mexican regions were the starting points for at least two independent domestications of maize. Likewise, based on

the diversity of chromosome knob patterns among the annual teosintes and maize landraces, Kato (1984) inferred that multiple domestications occurred independently in several Mexican regions.

Domestication is not necessarily rare historically. Humans seem to have independently appreciated and developed domestic uses of the same or similar wild plants and animal species in separate regions from time to time. As for crops, cytogenetic and molecular genetic studies have indicated multiple domestication origins for rice (Cheng *et al.* 2003), barnyard millet (Yabuno 1962), bean (Sonnante 1994), cotton (Wendel 1995), and squash (Decker 1988), but a single domestication origin for wheats (Heun *et al.* 1997, Özkan *et al.* 2002). As for animals (Bruford *et al.* 2003 for review), molecular phylogenetic studies have indicated multiple domestication events for cattle, sheep, pigs, water buffalo, and goats (MacHugh and Bradley 2001, Luikart *et al.* 2001, Larson *et al.* 2005), but a common origin from a single gene pool for all extant dog populations (Savolainen *et al.* 2002).

A possible way to test whether morphologically and genetically diverse maize landraces originated from teosinte due to single or multiple independent domestication events is to perform phylogenetic analyses, using a large number of molecular markers, on a comprehensive sample set of a maize (*Z. mays* ssp. *mays*) and the wild taxa of *Z. mays* (ssp. *huehuetenangensis*, ssp. *mexicana*, and ssp. *parviglumis*). To obtain a reliable phylogeny for out-crossing taxa requires construction of an average tree of the genome by means of a large number of marker loci. Such analyses should provide a highly resolved intraspecific phylogeny by incorporating the large amount of genome-scale information on genetic variation that exists for *Z. mays*.

On the basis of these considerations, Matsuoka *et al.* (2002) analyzed the genetic diversity of maize and the *Z. mays* teosintes at 99 microsatellite loci that give broad coverage of the maize genome. Using these 99 microsatellites, they genotyped 193 pre-Columbian maize landrace plants that originated in cool, eastern North America, the deserts of New Mexico and Arizona, the highlands and lowlands of Mexico and Guatemala, the Caribbean Islands, equatorial lowland South America, and areas of the high Andes Mountains, as well as 71 *Z. mays* teosinte plants that represented the full geographic and ecological ranges of ssp. *huehuetenangensis* (Guatemala, 4 plants), ssp. *mexicana* (Mexico, 33 plants) and ssp. *parviglumis* (Mexico, 34 plants). The microsatellite-based phylogeny of the 264 plants showed all maize in a single monophyletic lineage derived from ssp. *parviglumis* (Fig. 2). In a bootstrap analysis, the maize clade appeared in 930 of 1000 bootstrap samples, indicative that statistically the single domestication model for maize is far more likely than the multiple domestication one. These findings furnish genetic evidence for the single domestication origin of maize. It should be noted, however, that the actual domestication process may have been more complex than is assumed by the single domestication model.



**Fig. 2.** Microsatellite-based intraspecific phylogeny of *Z. mays* (Matsuoka *et al.* 2002). In this phylogeny, 264 individual plants were pooled in 95 ecogeographic groups (2–4 plants/group). The monophyletic clade for maize landraces is indicated by the dashed gray line. Asterisks show positions of the central Balsas populations of *ssp. parviglumis* that are basal to maize. Numbers on branches are values from 1,000 times bootstrap resampling. Only values larger than 900 are shown.

Although large-scale microsatellite-based analyses have provided a highly resolved intraspecific phylogeny, they may not have been capable of distinguishing cases such as those of neighboring communities that separately cultivated teosinte and occasionally traded seeds during the early stages of maize domestication.

In the microsatellite-based phylogeny (Matsuoka *et al.* 2002), three populations of *Z. mays ssp. parviglumis* are particularly closely allied with maize (Fig. 2). Previously, these populations had been identified by isozyme analyses as being the most similar to maize (Doebley 1990c). All are from a relatively small area in the central region of the Balsas River drainage (southern Mexico) (see Matsuoka *et al.* 2002 for maps). The central Balsas River drainage therefore has been designated the cradle of maize domestication on the assumption that the current *Z. mays ssp. parviglumis* distribution does not markedly differ from what it was at the time of maize domestication.

### Dating maize domestication

Given that it arose from teosinte through a single domestication event, when was maize domesticated? Archaeological studies show that the oldest, very primitive, maize cob from highland Mexico is about 6,250 years old, indicative that artificial selection of maize was practiced at that

time (Piperno and Flannery 2001, Benz 2001, see also Jaenicke-Després *et al.* 2003). The actual domestication of maize therefore must have occurred before that date.

Matsuoka *et al.* (2002) attempted the molecular dating of maize domestication from microsatellite variation data. Microsatellite dating utilizes a type of genetic distance that incorporates rates and patterns of microsatellite mutation (Goldstein *et al.* 1995, Zhivotovsky and Feldman 1995). This method is free of external calibration of the molecular clock, thereby enabling genetic absolute dating that is independent of archaeological data. Matsuoka *et al.* (2002) estimated that the extant Mexican maize and *Z. mays ssp. parviglumis* diverged 9,188 years ago (95% confidence limits 5,689–13,093 years ago). This should be considered as representing the upper estimation limit for the time of maize domestication because the sample of *Z. mays ssp. parviglumis* may not have contained direct descendants of the exact population that gave rise to maize. This molecular date for maize domestication is consistent with the age of the oldest maize cob and with the archaeological view that initial crop domestication in Mexico dates to no earlier than 10,000 B.P. (Smith 1998, 2001).

### Maize diversification and spread throughout the Americas

Logical inferences from the single domestication model include the diverse array of extant maize landraces being the product of rapid racial diversification after domestication. Details of the genetic mechanism that generated maize's great morphological and genetic diversity have yet to be studied (see below), but microsatellite-based phylogeny (Fig. 2) has provided insight into the historical course of the diversification and spread of maize throughout the Americas. Firstly, the oldest extant maize landraces seem to be those from highland Mexico as they are basal to all the other landraces. This is in striking agreement with the fact that so far the oldest known maize cob is from an archaeological site in the highland city of Oaxaca, Mexico (Piperno and Flannery 2001, Benz 2001), indicative that early racial diversification first occurred in the Mexican highland. Secondly, from its early racial diversification in the Mexican highland, maize seems to have taken two routes in its dispersion throughout the Americas. One runs south through the western and southern lowlands of Mexico into Guatemala, the Caribbean Islands, the lowlands of South America, and the Andes Mountains. The other extends northward through western and northern Mexico into the southwestern USA, then into the eastern USA and Canada. The route for the northward spread is consistent with previous morphological and archaeological inferences that eastern US landraces with their long and narrow ears were derived from southwestern US landraces (Galinat and Campbell 1967).

## Perspective

### *Importance of knowing exact origins*

Beadle's teosinte hypothesis is supported by a broad range of biological evidence and has been accepted as the most probable model for the evolution of maize (Bennetzen *et al.* 2001). Findings of molecular studies have refined the hypothesis by identifying *Z. mays* ssp. *parviglumis* as the direct ancestor of maize (Doebley 1990a). Furthermore, recent molecular phylogeny findings show that all the extant pre-Columbian maize landraces arose from *Z. mays* ssp. *parviglumis* roughly 9,000 years ago through a single domestication event in the central Balsas River drainage (southern Mexico) (Matsuoka *et al.* 2002).

This model, showing that maize is a domesticated form of *Z. mays* ssp. *parviglumis* (the parviglumis-maize model), provides a logical, practical framework by which to assess in depth questions regarding the population genetics of maize domestication. For example, investigations of the effects on today's maize diversity of bottlenecks and selection during domestication have greatly advanced our understanding of maize evolution (Doebley 2004). In addition, the parviglumis-maize model has been the analytical basis for developing an evolutionary method for identifying genes of agronomic importance that were targets of artificial selection during maize domestication (Vigouroux *et al.* 2002). It is expected that genetic diversity at loci controlling traits of agronomic importance is much decreased due to selective sweep during domestication, whereas unselected loci may retain degrees of genetic diversity comparable to those found for loci in ancestral species. The newly developed evolutionary method (Vigouroux *et al.* 2002) compares the genetic diversity of maize and teosinte at the genome level and searches for maize loci with decreased genetic diversity (i.e., candidate genes for agronomic traits) relative to homologous teosinte loci. Because the cloning of genes that control agronomic traits is a major interest in plant breeding, this method should have wide-range future applications as the availability of maize genome sequence information increases (but see Innan and Kim 2004, Vigouroux *et al.* 2005). In consequence, recent progress in the evolutionary genetics of maize points up the importance of knowing exact origins in studies that use crops and their wild relatives as models.

### *Implications of the origin of maize diversity*

The molecular phylogeny showing a single domestication origin of maize (Matsuoka *et al.* 2002) points to the extraordinary phenotypic diversity of extant maize landraces being the product of rapid racial diversification after domestication. In contrast to our recent progress in understanding the genetic process involved in the incipient stages of maize domestication, relatively little is known about the genetic mechanism that drove subsequent the rapid racial diversification of maize.

One genetic factor that may have contributed significantly to maize's racial diversity is introgression because it

has the potential to create novel phenotypes by incorporating alleles from outside populations through hybridization. Because *Zea* species are all outcrossing, introgression can occur between maize and teosinte as well as between maize races. Field observations have shown that *Z. luxurians* only rarely hybridizes with maize, that *Z. mays* ssp. *mexicana* forms frequent hybrids with maize, and that *Z. mays* ssp. *parviglumis* mostly is isolated from maize by temporal and spatial factors (Wilkes 1977). Molecular findings indicate that although extensive introgression is unlikely under natural conditions introgression does occur between maize and teosinte at low levels in both directions (i.e., from teosinte to maize and from maize to teosinte) (Doebley 1990b, Fukunaga *et al.* 2005). In addition, because Mexican farmers have always exchanged maize seeds beyond community boundaries (Louette *et al.* 1997), introgression between maize races also may have affected maize diversification.

In parallel with cumulative documentation of introgression, details of the genetic and ecological backgrounds needed for introgression (e.g., cross-compatibility and phenology) are being addressed (Kermicle and Allen 1990, Evans and Kermicle 2001, Baltazar *et al.* 2005). These studies will deepen our understanding of the effect of introgression on maize diversity. Nevertheless, introgression is not the sole factor involved in the process of maize diversification. Rather, the extraordinary phenotypic and genetic diversity of maize landraces should be viewed as reflections of complex interactions between maize, teosinte, and humans in the agro-ecological environment (Perales *et al.* 2005). To better understand the origin of maize diversity, interdisciplinary studies are required that integrate biological, anthropological, and environmental approaches.

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## Literature Cited

- Alpert, K.B., S. Grandillo and S.D. Tanksley (1995) *fw2.2*: a major QTL controlling fruit weight is common to both red- and green-fruited tomato species. *Theor. Appl. Genet.* 91: 994–1000.
- Baltazar, B.M., J.J. Sanchez-Gonzalez, L. Cruz-Larios and J.B. Schoper (2005) Pollination between maize and teosinte: an important determinant of gene flow in Mexico. *Theor. Appl. Genet.* 110: 519–526.
- Beadle, G.W. (1932) Studies of *Euchlaena* and its hybrids with *Zea*. I. Chromosome behavior in *Euchlaena mexicana* and its hybrids with *Zea mays*. *Z. Abst. Vererb.* 62: 291–304.
- Beadle, G.W. (1939) Teosinte and the origin of maize. *J. Hered.* 30: 245–247.
- Beadle, G.W. (1978) Teosinte and the origin of maize. In "Maize Breeding and Genetics" Walden, D.B. (ed.), Wiley, New York.

- p. 113–128.
- Beadle, G.W. (1980) The ancestry of corn. *Sci. Am.* 242: 112–119.
- Bennetzen, J., E. Buckler, V. Chandler, J. Doebley, J. Dorweiler, B. Gaut, M. Freeling, S. Hake, E. Kellogg, R. Scott Poething, V. Walbot and S. Wessler (2001) Genetic evidence and the origin of maize. *Latin Amer. Antiq.* 12: 84–86.
- Benz, B.F. (2001) Archaeological evidence of teosinte domestication from Guilá Naquitz, Oaxaca. *Proc. Natl. Acad. Sci. USA* 98: 2104–2106.
- Bruford, M.W., D.G. Bradley and G. Luikart (2003) DNA markers reveal the complexity of livestock domestication. *Nature Rev. Genet.* 4: 900–910.
- Buckler, IV, E.S. and T.P. Holtsford (1996) *Zea* systematics: ribosomal ITS evidence. *Mol. Biol. Evol.* 13: 612–622.
- Cheng, C., R. Motohashi, S. Tsuchimoto, Y. Fukuta, H. Ohtsubo and E. Ohtsubo (2003) Polyphyletic origin of cultivated rice: based on the interspersed pattern of SINEs. *Mol. Biol. Evol.* 20: 67–75.
- Collins, G.N. (1919) Structure of the maize ear as indicated in *Zea-Euchlaena* hybrids. *J. Agric. Res.* 17: 127–135.
- Decker, D.S. (1988) Origin(s), evolution, and systematics of *Cucurbita pepo* (Cucurbitaceae). *Econ. Bot.* 42: 4–15.
- Doebley, J. (1990a) Molecular systematics of *Zea* (Gramineae). *Maydica* 35: 143–150.
- Doebley, J. (1990b) Molecular evidence for gene flow among *Zea* species. *BioScience* 40: 443–448.
- Doebley, J. (1990c) Molecular evidence and the evolution of maize. *Econ. Bot.* 44 (3 Suppl.): 6–27.
- Doebley, J. (2001) George Beadle's other hypothesis: one-gene, one-trait. *Genetics* 158: 487–493.
- Doebley, J. (2004) The genetics of maize evolution. *Annu. Rev. Genet.* 38: 37–59.
- Doebley, J.F. and H.H. Iltis (1980) Taxonomy of *Zea* (Gramineae). I. A subgeneric classification with key to taxa. *Am. J. Bot.* 67: 982–993.
- Doebley, J. and A. Stec (1991) Genetic analysis of the morphological differences between maize and teosinte. *Genetics* 129: 285–295.
- Doebley, J. and A. Stec (1993) Inheritance of the morphological differences between maize and teosinte: comparison of results for two F<sub>2</sub> populations. *Genetics* 134: 559–570.
- Doebley, J., A. Stec and L. Hubbard (1997) The evolution of apical dominance in maize. *Nature* 386: 485–488.
- Evans, M.M.S. and J.L. Kermicle (2001) *Teosinte crossing barrier 1*, a locus governing hybridization of teosinte with maize. *Theor. Appl. Genet.* 103: 259–265.
- Frary, A., T.C. Nesbitt, S. Grandillo, E. Knaap, B. Cong, J. Liu, J. Meller, R. Elber, K.B. Alpert and S.D. Tanksley (2000) *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit size. *Science* 289: 85–88.
- Fukunaga, K., J. Hill, Y. Vigouroux, Y. Matsuoka, J. Sanchez, G.K. Liu, E.S. Buckler and J. Doebley (2005) Genetic diversity and population structure of teosinte. *Genetics* 169: 2241–2254.
- Galinat, W.C. (1988) The origin of corn. In "Corn and Corn Improvement" Agronomy Monograph no. 18, 3rd edition Sprague, G.F. and J.W. Dudley (eds.), American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Publishers, Madison, p. 1–31.
- Galinat, W.C. and R.G. Campbell (1967) The diffusion of eight-rowed maize from the Southwest to the Central Plains. *Mass. Agric. Exp. Station Monogr. Ser.* 1: 1–16.
- Goldstein, D.B., A. Ruiz Linares, L.L. Cavalli-Sforza and M.W. Feldman (1995) Genetic absolute dating based on microsatellites and the origin of modern humans. *Proc. Natl. Acad. Sci. USA* 92: 6723–6727.
- Heun, M., R. Schäfer-Pregl, D. Klawan, R. Castagna, M. Accerbi, B. Borghi and F. Salamini (1997) Site of einkorn wheat domestication identified by DNA fingerprinting. *Science* 278: 1312–1314.
- Hubbard, L., P. McSteen, J. Doebley and S. Hake (2002) Expression patterns and mutant phenotype of *teosinte branched 1* correlate with growth suppression in maize and teosinte. *Genetics* 162: 1927–1935.
- Iltis, H.H. (2000) Homeotic sexual translocations and the origin of maize (*Zea mays*, Poaceae): a new look at an old problem. *Econ. Bot.* 54: 7–42.
- Iltis, H.H. and J.F. Doebley (1980) Taxonomy of *Zea* (Gramineae). II. Subspecific categories in the *Zea mays* complex and a generic synopsis. *Am. J. Bot.* 67: 994–1004.
- Iltis, H.H. and B.F. Benz (2000) *Zea nicaraguensis* (Poaceae), a new teosinte from Pacific Coastal Nicaragua. *Novon* 10: 382–390.
- Innan, H. and Y. Kim (2004) Pattern of polymorphism after strong artificial selection in a domestication event. *Proc. Natl. Acad. Sci. USA* 101: 10667–10672.
- Jaenicke-Després, V., E.S. Buckler, B.D. Smith, M.T.P. Gilbert, A. Cooper, J. Doebley and S. Pääbo (2003) Early allelic selection in maize as revealed by ancient DNA. *Science* 302: 1206–1208.
- Kato, Y., T.A. (1984) Chromosome morphology and the origin of maize and its races. In "Evolutionary Biology" Vol. 17, Hecht, M.K., B. Wallace and G.T. Prance (eds.), Kluwer Academic Press, Dordrecht, p. 219–253.
- Kermicle, J.L. and J.O. Allen (1990) Cross-incompatibility between maize and teosinte. *Maydica* 35: 399–408.
- Larson, G., K. Dobney, U. Albarella, M. Fang, E. Matisoo-Smith, J. Robins, S. Lowden, H. Finlayson, T. Brand, E. Willerslev, P. Rowley-Conwy, L. Andersson and A. Cooper (2005) Wild-wide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* 307: 1618–1621.
- Louette, D., A. Charrier and J. Berthaud (1997) In situ conservation of maize in Mexico: genetic diversity and maize seed management in a traditional community. *Econ. Bot.* 51: 20–38.
- Luikart, G., L. Gielly, L. Excoffier, J.-D. Vigne, J. Bouvet and P. Taberlet (2001) Multiple maternal origins and weak phylogenetic structure in domestic goats. *Proc. Natl. Acad. Sci. USA* 98: 5927–5932.
- MacHugh, D.E. and D.G. Bradley (2001) Livestock genetic origins: goats buck the trend. *Proc. Natl. Acad. Sci. USA* 98: 5382–5384.
- Mangelsdorf, P.C. (1974) Corn: its origin, evolution and improvement. Harvard University Press, Cambridge. p. 11–52.
- Mangelsdorf, P.C. and R.G. Reeves (1938) The origin of maize. *Proc. Natl. Acad. Sci. USA* 24: 303–312.
- Mangelsdorf, P.C. and R.G. Reeves (1939) The origin of Indian corn and its relatives. *Texas Agric. Exp. Station Bulletin* 574: 1–315.
- Matsuoka, Y., Y. Vigouroux, M.M. Goodman, J. Sanchez, G.E. Buckler and J. Doebley (2002) A single domestication for maize shown by multilocus microsatellite genotyping. *Proc. Natl. Acad. Sci. USA* 99: 6080–6084.
- Özkan, H., A. Brandolini, R. Schäfer-Pregl and F. Salamini (2002) AFLP analysis of a collection of tetraploid wheats indicates the

- origin of emmer and hard wheat domestication in southeast Turkey. *Mol. Biol. Evol.* 19: 1797–1801.
- Perales, H.R., B.F. Benz and S.B. Brush (2005) Maize diversity and ethnolinguistic diversity in Chiapas, Mexico. *Proc. Natl. Acad. Sci. USA* 102: 949–954.
- Piperno, D.R. and K.V. Flannery (2001) The earliest archaeological maize (*Zea mays* L.) from highland Mexico: new accelerator mass spectrometry dates and their implications. *Proc. Natl. Acad. Sci. USA* 98: 2101–2103.
- Savolainen, P., Y. Zhang, J. Luo, J. Lundeberg and T. Leitner (2002) Genetic evidence for an East Asian origin of domestic dogs. *Science* 298: 1610–1613.
- Smith, B.D. (1998) The emergence of agriculture. *Scientific American Library*, New York. p. 1–47.
- Smith, B.D. (2001) Documenting plant domestication: the consilience of biological and archaeological approaches. *Proc. Natl. Acad. Sci. USA* 98: 1324–1326.
- Sonnante, G., T. Stockton, R.O. Nodari, V.L. Becerra Velásquez and P. Gepts (1994) Evolution of genetic diversity during the domestication of common-bean (*Phaseolus vulgaris* L.) *Theor. Appl. Genet.* 89: 629–635.
- Vavilov, N.I. (1926) Centers of origin of cultivated plants. In “N. I. Vavilov origin and geography of cultivated plants” Dorofeyev, V.F. (ed.), Cambridge University Press, Cambridge. p. 22–135.
- Vigouroux, Y., M. McMullen, C.T. Hittinger, K. Houchins, L. Schulz, S. Kresovich, Y. Matsuoka and J. Doebley (2002) Identifying genes of agronomic importance in maize by screening microsatellites for evidence of selection during domestication. *Proc. Natl. Acad. Sci. USA* 99: 9650–9655.
- Vigouroux, Y., S. Mitchell, Y. Matsuoka, M. Hamblin, S. Kresovich, J.S.C. Smith, J. Jaqueth, O.S. Smith and J. Doebley (2005) An analysis of genetic diversity across the maize genome using microsatellites. *Genetics* 169: 1617–1630.
- Weatherwax, P. (1954) Indian corn in old America. The Macmillan Company, New York. p. 113–120.
- Wendel, J.F. (1995) Cotton. In “Evolution of Crop Plants” Smartt, J. and N. Simmonds (eds.), Longman, London, p. 358–366.
- Wilkes, H.G. (1977) Hybridization of maize and teosinte, in Mexico and Guatemala and the improvement of maize. *Econ. Bot.* 31: 254–293.
- Yabuno, T. (1962) Cytotaxonomic studies on the two cultivated species and the wild relatives in the genus *Echinochloa*. *Cytologia* 27: 296–305.
- Zhivotovsky, L.A. and M.W. Feldman (1995) Microsatellite variability and genetic distance. *Proc. Natl. Acad. Sci. USA* 92: 11549–11552.