

Molecular Evidence and the Evolution of Maize

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In this review, the contributions of isozyme and chloroplast DNA studies to questions surrounding the evolution of maize are summarized. These methods of analysis provide generally strong support for the hierarchical system of classification of Zea proposed by Illis and Doebley (1980). Molecular evidence is fully congruent with the theory that teosinte is ancestral to maize and suggests that Z. mays subsp. parviglumis was the ancestral teosinte taxon. Further, these data show that only those populations from the central region of the range of subsp. parviglumis resemble maize in both isozymic and chloroplast DNA constitution. Presuming no major changes in the distribution of subsp. parviglumis since the domestication of maize, these data would place the origin of maize in the Balsas River drainage southwest of Mexico City. Molecular systematic evidence provides no support for theories that maize was domesticated independently several times; however, this type of data can not disprove such theories. Analyses of isozyme and chloroplast DNA diversity in Zea provide evidence of limited gene flow between maize and teosinte, but are not consistent with models that postulate extensive genetic interchange between these taxa. Isozyme studies have added substantially to the understanding of evolutionary relationships among extant races of maize and suggest that there are a small number of major racial complexes in Meso- and North America which have often evolved in response to environmental constraints associated with altitude. Ultimately, molecular genetic studies may allow a resolution of the controversy surrounding the morphological evolution of the maize ear.

To elucidate the origin of maize (*Zea mays* L.), investigators have summoned the disciplines of botany, morphology, taxonomy, genetics, cytology, linguistics, anthropology, and archaeology. Several books and hundreds of journal articles have been written on the subject. The literature on maize evolution is so enormous and the points of view so diverse that a single paper can not reasonably attempt to summarize them. Moreover, the ancestry of maize has been the subject of so many general review articles over the past two decades that the need for still another seems questionable. For these reasons, the goal taken here is the much more limited one of reviewing the contributions made to the understanding of the origin of maize by the field of molecular systematics. This subject has yet to be fully treated in a review, and it offers a fresh look at many of the questions surrounding the origin and evolution of maize.

Because molecular systematic studies are not relevant to all questions surrounding the evolution of maize, this paper will focus on those aspects of the problem that are. The specific topics chosen for discussion are: (1) the taxonomy of the genus *Zea*, (2) identifying the wild ancestor of maize, (3) introgression between maize and teosinte, (4) the geographic origin of maize, (5) the origin of the maize ear, and (6) racial diversity in maize.

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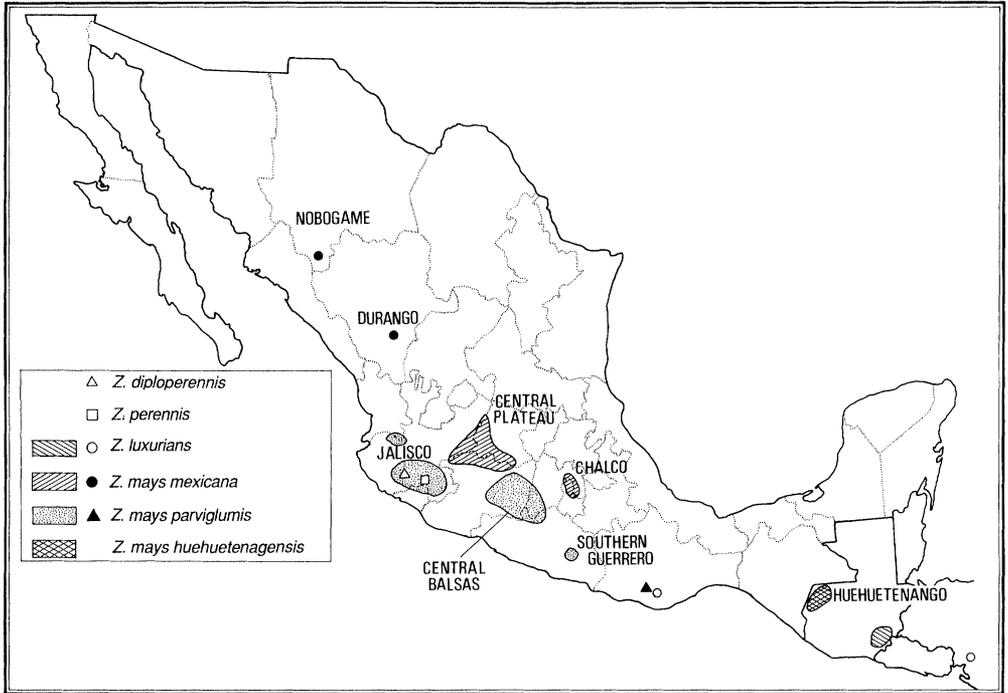


Fig. 1. Distribution map of teosinte in Mexico and Central America.

THE TAXONOMY OF *ZEa*

Zea L. is composed of a group of annual and perennial grasses native to Mexico and Central America (Fig. 1). The genus includes both the wild taxa known by the common name "teosinte" and the cultigen, maize. As an American crop, maize was unknown to Europeans until Columbus first encountered it on the island of Cuba. Knowledge of teosinte came to Europe much later, and it was not until 1832 that a German botanist, Schrader (1833), provided the annual form of teosinte with a scientific name, *Euchlaena mexicana* Schrader. In 1910, an American botanist, A. S. Hitchcock (1922), discovered a perennial form of teosinte, which he called *Euchlaena perennis* Hitchcock. These two grasses are so unlike maize in the appearance of their ears that their close relationship to maize was not recognized at first. But gradually, through the efforts of several botanists (Ascherson 1875; Beadle 1932; Collins 1921; Harshberger 1896), the fact that teosinte and maize are quite closely related was established. Kuntze (von Post and Kuntze 1904) and Reeves and Mangelsdorf (1942) gave formal recognition to this close relationship by transferring these species into the genus *Zea*, as *Z. mexicana* (Schrader) Kuntze and *Z. perennis* (Hitchcock) Reeves and Mangelsdorf.

Throughout this century, botanists continued to comb the hills of Latin America in search of teosinte and discovered numerous new populations (see Wilkes 1967; Iltis and Doebley 1984 for reviews). The search continues until this day (Guzmán 1982; Sánchez G. and Ordaz S. 1987), and many problems concerning the geography of teosinte have yet to be resolved (Iltis et al. 1986). As recently as 1978,

TABLE 1. THE TAXONOMY OF *ZEA* ACCORDING TO WILKES (1967) AND ILTIS AND DOEBLEY (1990).

Wilkes (1967)	Iltis and Doebley (1980); Doebley (1990)
Section <i>Euchlaena</i>	Section <i>Luxuriantes</i>
—	<i>Zea diploperennis</i> Iltis, Doebley & Guzmán
<i>Zea perennis</i> (Hitc.) Reeves & Mangelsdorf	<i>Zea perennis</i> (Hitc.) Reeves & Mangelsdorf
<i>Zea mexicana</i> (Schrader) Kuntze	
Race Guatemala	<i>Zea luxurians</i> (Durieu & Ascherson) Bird
	Section <i>Zea</i>
	<i>Zea mays</i> L.
Race Chalco	subsp. <i>mexicana</i> (Schrader) Iltis
Race Central Plateau	Race Chalco
Race Nobogame	Race Central Plateau
Race Balsas	Race Nobogame
Race Huehuetenago	subsp. <i>parviglumis</i> Iltis & Doebley
	subsp. <i>huehuetenangensis</i> (Iltis & Doebley)
	Doebley
Section <i>Zea</i>	
<i>Zea mays</i> L.	subsp. <i>mays</i>

a new species of perennial teosinte (*Z. diploperennis* Iltis, Doebley & Guzmán) was discovered (Guzmán 1978; Iltis et al. 1979), and there is every expectation that other discoveries await those willing to put in the long hard hours exploring the little known regions of Mexico and Central America.

Wilkes (1967) provided the first thorough monograph on the geography, taxonomy, and ecology of teosinte. Wilkes (1967) defined six geographical races of teosinte, but did not attempt to place these races in any formal hierarchy (Table 1). Wilkes' races each have their own characteristic morphological features, but while some of these are quite distinct from one another, others are only narrowly differentiated. The descriptions and illustrations of these races provided by Wilkes (1967) can be misleading because they are based in part on plants grown in Massachusetts. For example, Wilkes describes plants of his races Balsas and Guatemala as bearing numerous tillers, although these plants tiller rarely, if at all, in their native habitat. Wilkes (1967:64) noted the abnormal growth habit of teosinte grown at northern latitudes, but his observations have not always been appreciated.

Iltis and Doebley (1980) proposed a hierarchical system of classification for *Zea*, which reflected its presumed evolutionary relationships (Table 1). This system of classification was based on the morphological and ecological features of the taxa. As treated by Doebley and Iltis (1980), *Zea* is divided into two sections. Section *Luxuriantes* contains (1) *Z. diploperennis*, a diploid perennial teosinte with a very narrow distribution in the state of Jalisco, Mexico; (2) *Z. perennis*, a tetraploid perennial teosinte also with a very narrow distribution in Jalisco; and (3) *Z. luxurians*, a diploid annual teosinte found primarily in southeastern Guatemala (Fig. 1). Section *Zea* contains a single highly polymorphic diploid annual, *Z. mays*. Recently, Doebley (1990) recognized four subspecies within *Z. mays*: (1) subsp. *mexicana*, a large-spikeleted annual teosinte from the highlands of central and northern Mexico; (2) subsp. *parviglumis*, a small-spikeleted annual teosinte from the river valleys of southwestern Mexico; (3) subsp. *huehuetenan-*

gensis, similar to subsp. *parviglumis*, but more robust and later blooming, from western Guatemala; and (4) subsp. *mays*, maize or Indian corn, which probably had its origin in southern or central Mexico (Fig. 1). The sections and species recognized by Iltis and Doebley (1980) are distinguished by subtle morphological characteristics, but ones that are quite consistent and vary very little no matter what the conditions of growth (Doebley 1983a). However, the subspecies of teosinte, like some of Wilkes' races, are differentiated by traits which can vary widely depending upon the conditions of growth. For this reason, the subspecies can not always be readily identified. For example, Sánchez G. and Ordaz S. (1987) have identified the teosinte from Degollado, eastern Jalisco as subsp. *parviglumis* (i.e., race Balsas) when in fact it is subsp. *mexicana* (see Doebley 1983a; Doebley et al. 1984).

The Mexican annual teosintes, *Z. mays* subsp. *mexicana* and subsp. *parviglumis*, are those most similar to maize, and thus are of primary interest in a discussion of the origin of maize. The division of Mexican annual teosinte into subsp. *mexicana* and subsp. *parviglumis* (Iltis and Doebley, 1980) is based both on morphological and eco-geographic evidence. The former subspecies occurs from 1800 to 2500 meters altitude on the plains and valleys of central and northern Mexico. Rainfall in this region ranges from about 50 to 100 cm per year, and mean annual temperature ranges from about 15° to 20°C (Doebley 1984). Subspecies *parviglumis* occurs from about 400 to 1700 meters altitude on the upper slopes of the river valleys of more southern and western Mexico, where rainfall ranges from 125 to 200 cm per year and the mean annual temperature is about 20° to 25°C (Doebley 1984). These taxa have their own distinct morphological features, and each could be further subdivided into several races (Doebley 1983a). Thus, Wilkes (1967) recognized races Chalco, Central Plateau, and Nobogame, which are forms of subsp. *mexicana* differentiated along a cline from central to northern Mexico (Fig. 1). Populations of subspecies *parviglumis* have three natural geographic divisions as well: (1) southern Guerrero, (2) central Balsas, and (3) Jalisco (Fig. 1). These populations easily encompass as much variation as the three races of subsp. *mexicana*, and probably should not be treated as members of the single race Balsas (cf. Iltis and Doebley 1980; Sanchez G. and Ordaz S. 1987).

Molecular systematic evidence offers an opportunity to evaluate the taxonomic classification of teosinte and maize. Doebley et al. (1984, 1987a) analyzed isozyme variation in maize and teosinte for 13 enzyme systems encoded by 21 loci (see also Smith et al. 1984, 1985). This work included 56 populations of teosinte, representing the entire geographic range of the wild taxa of *Zea*, and 99 populations of maize from Mexico and Guatemala. Genetic control of the isozyme loci in *Zea* has been thoroughly analyzed (Goodman and Stuber 1983a; Stuber and Goodman 1983). Figure 2 is a graph of the first two components taken from a principal component analysis of isozyme data (Doebley et al. 1984). Figure 3 is an average linkage cluster analysis of the isozyme data (Doebley et al. 1984). These analyses show that *Zea* can be divided into two principal groups corresponding to the sections *Zea* and *Luxuriantes*. The one taxon that does not fall easily into either section based on isozymes is subsp. *huehuetenangensis* (cf. Fig. 2, 3). Within section *Luxuriantes*, the isozyme data show that populations of the same species cluster near one another (Fig. 2). Within section *Zea*, subsps. *mexicana* and *par-*

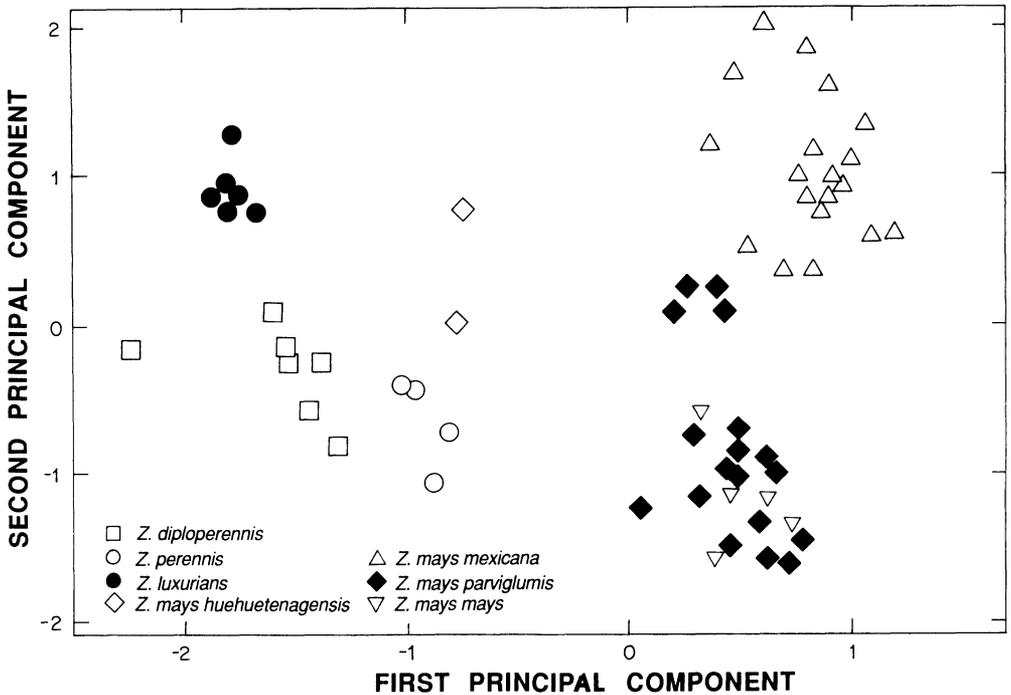


Fig. 2. Graph of the first two components from a principal component analysis based on isozymic variation in *Zea* (Doebley et al. 1984).

viglumis are well differentiated for isozymes with no overlap of their populations (Fig. 2). These two subspecies are also well differentiated ecologically (Doebley 1984). Subspecies *mays* (or maize) shows complete overlap with subsp. *parviglumis* in the principal component analysis (Fig. 2).

Chloroplast (cp) DNA restriction site analysis shows a pattern of relationships among the *species* that is fully consistent with that revealed by the isozyme analysis (Doebley et al. 1987b; Timothy et al. 1979). A Wagner parsimony phylogenetic tree (Fig. 4) based on the cpDNA data: (1) splits the genus into two sections with precisely the same constitutions as the isozyme data, (2) allies *Zea luxurians* with *Z. perennis* and *Z. diploperennis*, (3) shows *Zea perennis* and *Z. diploperennis* to be very similar, here distinguished by only a single restriction site mutation, and (4) demonstrates that *Zea mays* subsps. *mays*, *parviglumis*, *huehuetenagensis*, and *mexicana* are all closely allied. The major discrepancy between cpDNA data and previous isozyme and morphological studies is the failure of cpDNA analysis to resolve *Z. mays* subsps. *mexicana* and *parviglumis*. This is not surprising as cpDNA analysis is not generally useful below the species level. Curiously, the small amount of cpDNA heterogeneity in *Z. mays* (sensu lato) is not distributed along taxonomic lines. This suggests that either (1) the pattern of evolution among *Z. mays* subspecies is reticulate or (2) the subspecies have retained cpDNA polymorphisms present in their common ancestor (see Doebley 1990). Another curious result is that cpDNA data show subsp. *huehuetenagensis* to be identical to the Mexican annual teosintes (subsp. *mexicana* and *parviglumis*), which does not agree with the isozyme results. This teosinte shows different affinities depending on the traits one analyzes (Doebley et al. 1984).

Average Linkage Cluster Analysis

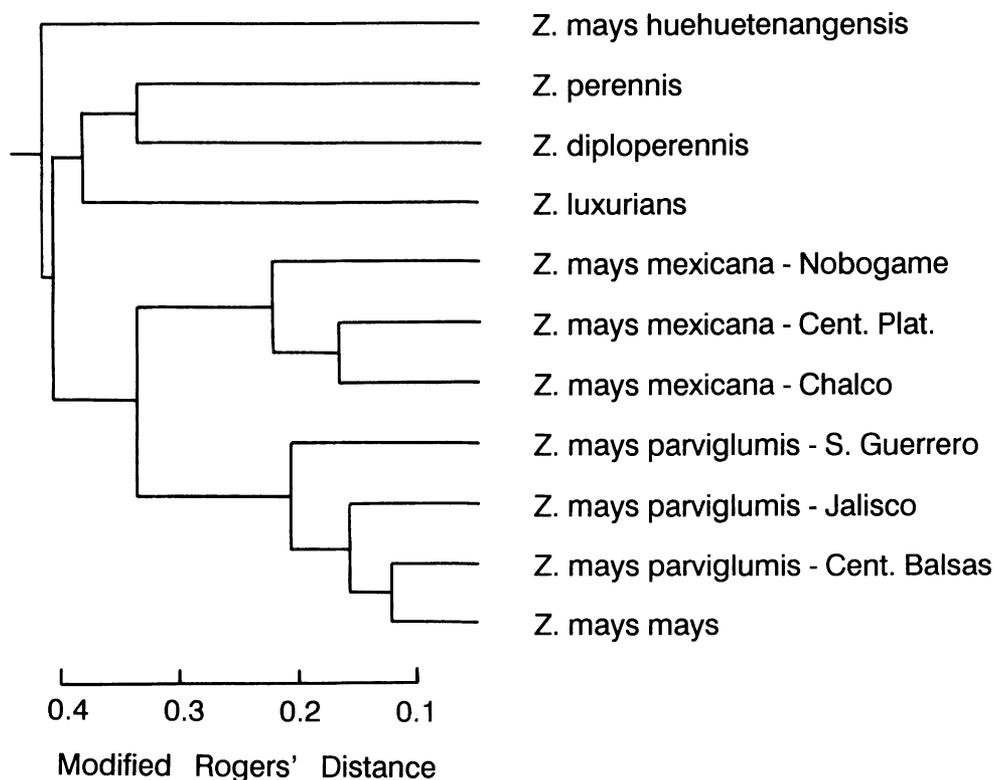


Fig. 3. Average linkage cluster analysis based on isozymic variation in *Zea* (Doebley et al. 1984).

THE ANCESTRY OF MAIZE

During the 19th century, the origin and evolution of Indian corn became a topic of great interest among botanists. The most perplexing fact that these scientists had to contend with was that maize, unlike the Middle Eastern cereals—wheat, barley, and rye, apparently lacked an associated wild form that could be considered its ancestor. This situation provided ample room for speculation, but little hope for resolution of the ancestry of maize. However, the focus of the debate changed with the discovery of teosinte and the subsequent demonstration that some types of teosinte and maize formed fully fertile hybrids (Harshberger 1896; Schrader 1833). This led many authors to incorporate teosinte into their theories on the origin of maize (Ascherson 1880; Collins 1921; Harshberger 1896; Montgomery 1913). By 1939, there was ample information for Beadle (1939) to make a strong argument that teosinte was the direct ancestor of maize. For Beadle, the compelling facts surrounding the origin of maize were the complete freedom with which maize and teosinte could be crossed and the complete fertility of their hybrids. This suggested to him that they were conspecific and only recently diverged.

While the “teosinte theory” was being formulated by Beadle, other scientists were developing very different views of the origin of maize (Montgomery 1906; Randolph 1959; Saint-Hilaire 1829; Weatherwax 1935). The theories of each of

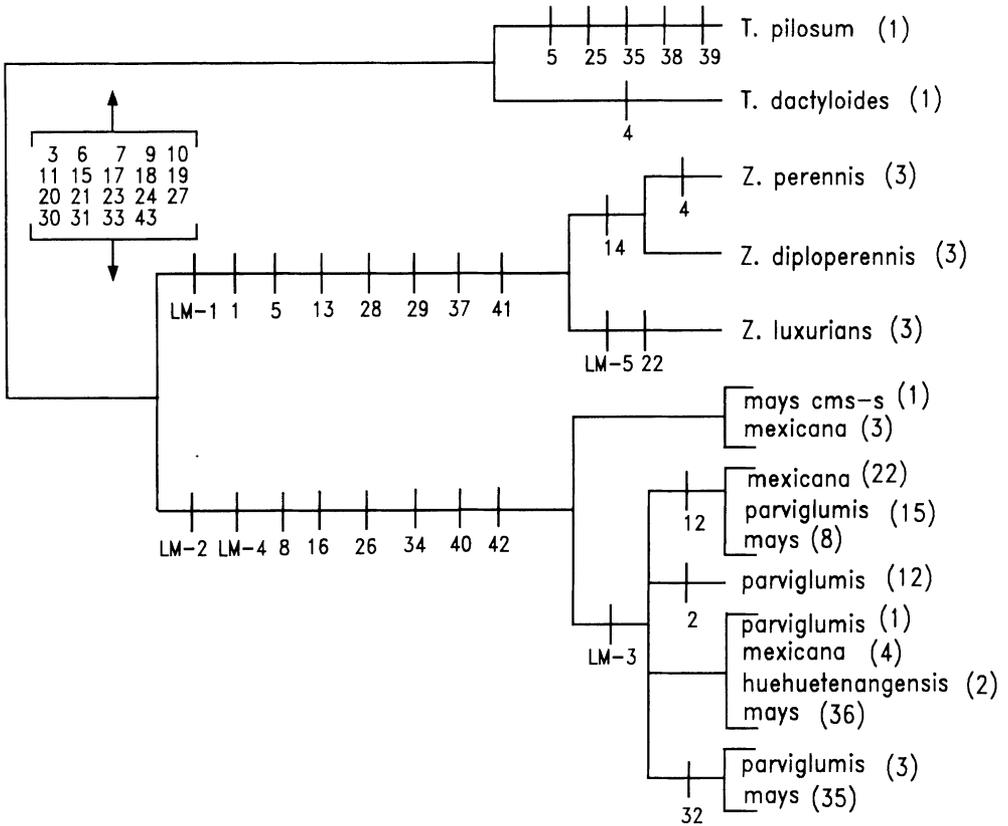


Fig. 4. Wagner parsimony phylogenetic tree for the genus *Zea* based on chloroplast DNA data (Doebley et al. 1987b; unpublished). Two species of *Tripsacum* were used as outgroups to root the tree. Identification numbers for specific mutations appear along the branches. Numbers in parentheses at the ends of branches are the number of populations in which that cpDNA type was found.

these authors excluded teosinte from any central role in the origin of maize and derived maize from a hypothetical "wild maize." Mangelsdorf (Mangelsdorf and Reeves 1939; Mangelsdorf 1974) was the primary promoter of this view. This author heavily weighted the enormous difference in the morphology between the ears of maize and teosinte, and concluded that the former could not have been linearly derived from the latter in so short a time as was available for the domestication of maize (less than 10,000 years).

Both the "teosinte" and the "hypothetical wild maize" theories have had their supporters over the last 50 years. There has also been a diversity of opinion within each of these two camps. Many of the older ideas, which did not stand the test of time, no longer have any supporters. Most people working in the field and familiar with the facts support the teosinte theory (Beadle 1972, 1980; Benz 1987; de Wet and Harlan 1972; Doebley 1983b; Galinat 1983; Iltis 1983; Kato 1984; McClintock et al. 1981); however, Mangelsdorf (1974, 1986) never swayed in his belief that teosinte is not the ancestor of maize.

Molecular evidence offers an opportunity to test these two hypotheses. If teosinte is the ancestor of maize, then the particular type of teosinte ancestral to maize

should be very similar to maize in its molecular features and the other types of teosinte should show varying degrees of dissimilarity. This expectation arises because, under the “teosinte” theory, human selection would have affected primarily those loci that determine the differences between the maize and teosinte ears. The other genes, such as those governing isozymes, would have remained largely unchanged. The molecular evidence meets this expectation, and thus it is fully concordant with the “teosinte” theory. Figure 2 shows that populations of maize and subsp. *parviglumis* could not be distinguished by their isozyme constitutions. Similarly, Fig. 3 shows that subsp. *parviglumis* is much more similar to maize than it is like the other teosintes. These analyses suggest that subsp. *parviglumis* and maize share a more recent common ancestor with one another than they do with the other teosintes. The fact that teosinte is wild and maize is fully domesticated forces one to conclude that their common ancestor was also a teosinte.

The close association between maize and subsp. *parviglumis* could be attributed to introgression, rather than recent derivation of maize from this teosinte; however, subsp. *parviglumis* grows mostly in wild places away from corn fields, such as prairies, rocky cliffs and roadsides. Thus, hybrids between this teosinte and maize are rare. Consequently, subsp. *parviglumis* has not been considered to be much affected by introgression from maize (Wilkes 1967, 1977), and the argument that maize resembles subsp. *parviglumis* because of introgression seems unlikely.

The degree of isozymic similarity between maize and teosinte can be compared to that between other crops and their wild relatives. From isozyme data, one can calculate genetic identities, I (Nei 1972). I is generally between 0.90 and 1.00 for populations of the same species and lower for separate species (Crawford 1983). Because crops and their wild relatives are members of the same biological species, I between them should be greater than 0.90. This is true for most crops (Doebley 1989). It is also true for maize and subsp. *parviglumis* ($I = 0.92$). Thus, maize shows no greater isozymic divergence from its presumed wild ancestor than do other crops from theirs.

The specific association between maize and subsp. *parviglumis* and the clear distinction between maize and subsp. *mexicana* (Fig. 2) deserve additional comment. Subspecies *mexicana* has been characterized as weedy, “maizoid” teosinte because of its general similarity to maize in its vegetative habit (Wilkes 1967). Iltis and Doebley (1980) argued, as is now known, incorrectly that this subspecies was ancestral to maize. Subspecies *parviglumis*, on the other hand, has been characterized as “pure wild” teosinte with a highly tillered, grassy growth form (Wilkes 1967, 1977). While these characterizations are not entirely correct (see section on taxonomy), subsp. *mexicana* does appear more maize-like (robust) in growth form. Thus, one is left with the paradoxical result that “maizoid” teosinte is isozymically less like maize, and “pure, wild” teosinte is isozymically most like maize. This result may indicate how convergence for vegetative characters, which change rapidly under selection, can mislead attempts to elucidate phylogenetic relationships (Doebley 1984).

The “hypothetical wild maize” theory suggests that maize and teosinte arose on entirely separate lineages. Thus, it would require that the various teosintes should be more similar to one another isozymically than any of them is to maize. This hypothesis is clearly refuted by the isozymic and cpDNA data (Fig. 2, 3, 4).

Mangelsdorf (1983, 1986) has placed a twist on the "hypothetical wild maize" theory by suggesting that originally there existed only one type of teosinte (*Z. diploperennis*) and wild maize. He speculates that, after maize was domesticated, maize and *Z. diploperennis* hybridized and that the other types of teosinte are the hybrid derivatives of this cross. Many difficulties with this hypothesis have been previously discussed (Doebley 1983a), and additional difficulties arise from the molecular evidence. Because cpDNA is maternally inherited in *Zea* and does not undergo recombination, diversity in this genome can not have arisen as a result of hybridization. Under this latest twist to the "hypothetical wild maize" hypothesis, there should be only two chloroplast genome types, the maize and *Z. diploperennis* types. As Fig. 4 shows, this is not the case. Further, the cpDNA data (maternal/non-recombinational) are nicely correlated with the isozyme data (biparental), suggesting that the isozyme differences among teosintes are also the products of gradual evolutionary divergence among populations and not of a recent hybridization event. In summary, the various versions of the "hypothetical wild maize" theory are not supported by the molecular systematic evidence. Rather, this evidence clearly supports the "teosinte" theory and suggests that maize is a domesticated form of the Mexican annual teosinte, *Z. mays* subsp. *parviglumis*. If this is correct, then maize must have undergone a very rapid morphological divergence from its teosinte ancestor.

THE GEOGRAPHIC ORIGIN OF MAIZE

It is clear that maize is of New World origin, and it appears an inescapable conclusion that maize is a cultivated form of teosinte. For these reasons, maize was probably domesticated within or near the geographic range of teosinte. The molecular evidence indicates that subsp. *parviglumis* is the teosinte most similar to maize, so one might also look for the cradle of maize domestication within or near its range. Because this subspecies contains much isozyme variation, one can examine the data more critically to determine if a finer relationship can be drawn between maize and a particular geographical subgroup to subsp. *parviglumis*. If such a relationship exists, it could be used to guide future archaeological searches for prehistoric maize remains.

Figure 5 displays the first two components from a principal component analysis of isozyme data. This analysis included all the Mexican annual teosinte populations (subsp. *mexicana* and subsp. *parviglumis*) that have been studied and 94 collections of maize from throughout Mexico (Doebley et al. 1987a). As in Fig. 2, only subsp. *parviglumis* shows any overlap with maize. Further, only a few of the subsp. *parviglumis* populations actually overlap with maize on this figure. These populations are all from the central portion of the Balsas River drainage in northern Guerrero, eastern Michoacán and western Mexico (Fig. 1). Collections of subsp. *parviglumis* from Jalisco and southern Guerrero are separated from maize in Fig. 5. Thus, isozyme evidence points to the central portion of the range of subsp. *parviglumis* as containing the teosinte populations which are biochemically most similar to maize. This does not necessitate that maize was domesticated there, but merely suggests that teosinte from this region is most likely to have been ancestral to maize.

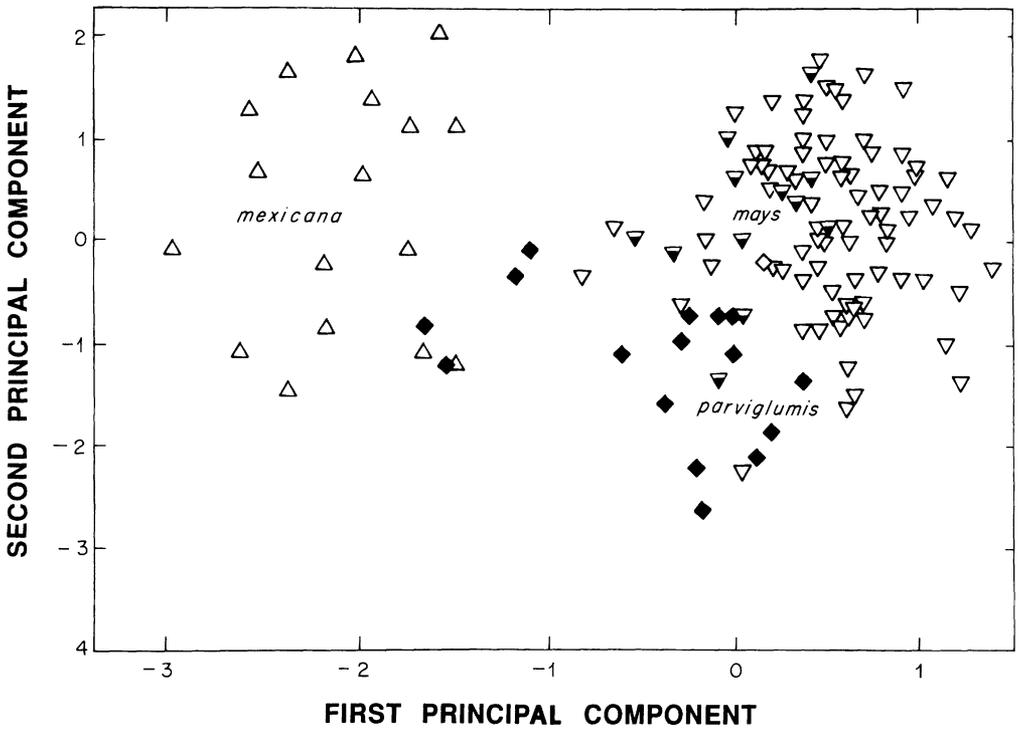


Fig. 5. Graph of the first two components from a principal component analysis of isozymic variation in Mexican annual teosinte and maize, including *Zea mays* subsp. *mexicana* (open triangles), subsp. *parviglumis* (solid diamonds) and subsp. *mays* (inverted triangles) (Doebley et al. 1987a). The half-darkened inverted triangles indicate maize accessions which possess the subsp. *mexicana* alleles, *Enp1-14* and/or *Glul-8*.

THE DOMESTICATION OF MAIZE

The molecular evidence can also help determine "how many times was maize domesticated?" Various authors have proposed that maize has undergone multiple independent domestications (Bird 1980; Kato 1984; Mangelsdorf 1974; McClintock 1959; Randolph 1959). Mangelsdorf and Galinat (1964) suggested that two or more types of maize were domesticated in Mexico, and various authors have contended that the distinct racial complexes in maize represent the products of separate domestication events. However, such racial groups may result from other processes including (1) the introgression of teosinte germplasm into some maize groups or (2) simple evolutionary divergence from the earliest domesticated maize. The multiple domestication hypotheses should not be embraced until these other explanations can be excluded.

The molecular evidence offers no support for the multiple domestications of maize. As shown in Fig. 5, maize from all regions of Mexico forms a single group, and this group has its closest relationship to subsp. *parviglumis*. Thus, the isozyme data lend no support to the hypothesis that some forms of maize were domesticated from subsp. *mexicana* or any of the teosintes of section *Luxuriantes*. If maize were domesticated several times, then subsp. *parviglumis* was the ancestral teo-

sinte in each case. I know of no good reasons for arguing that maize was domesticated from subsp. *parviglumis* independently several times. In fact, because any transformation of teosinte into maize must have involved a series of improbable mutations (Galinat 1983; Iltis 1983, 1987), it seems more probable to hypothesize that this transformation occurred only once.

INTROGRESSION BETWEEN MAIZE AND TEOSINTE

Introgression is of special interest to students of cultigens and their wild relatives. Because these plants generally lack barriers to hybridization and often grow sympatrically, the opportunities for gene flow between them seem abundant. Further, the impact on the co-evolution of crop-weed complexes is potentially enormous. However, there are problems in documenting the occurrence of introgression. Whenever sympatric populations of crops and their wild relatives show a similar trait, there will be several possible explanations: (1) retention of an ancestral trait, (2) convergent or parallel evolution, and (3) introgression. Perhaps even more difficult is establishing the direction of introgression; does gene flow go from crop into wild species, the reverse, or in both directions? Molecular evidence has considerable power in addressing these questions, although definitive answers are not always possible. For example, a crop and its wild relatives may be so similar genetically that there are no detectable genetic variants that typify one or the other. For this reason, introgression may be best studied between crops and their more distant wild relatives where the probability of finding taxon-specific genetic markers is increased.

Reciprocal introgression between Mexican annual teosinte and maize has been the subject of numerous papers since the beginning of this century (see Doebley 1984 for a review). Based on field observations alone, several authors have proposed extensive reciprocal introgression between Mexican annual teosinte and maize (Collins 1921; Wilkes 1970, 1977). These authors have generally given little or no consideration to alternate hypotheses such as convergence or retention of ancestral traits. Nevertheless, the supposition that teosintes are substantially affected by introgression from maize has been frequently cited in review articles (Barrett 1983; Heiser 1973; Ladizinsky 1985). Some have argued against extensive introgression between maize and Mexican annual teosinte on the basis of cytology (Kato 1976, 1984) and field observations (Doebley 1984).

Doebley et al. (1987a) examined isozymic evidence for introgression between maize and Mexican annual teosinte. Their data show that maize and subsp. *parviglumis* are nearly identical in isozyme allele constitution, and thus isozymes were not useful in the study of introgression between them. However, subsp. *mexicana* possessed alleles distinct from those of maize at several loci. An examination of the distribution of these diagnostic alleles revealed that, where maize is sympatric with subsp. *mexicana*, some of these distinct alleles (*Enp1-14* and *Glul-8*) are also found in the cultigen, although at much lower frequencies than in subsp. *mexicana* (Doebley et al. 1987a). Doebley et al. (1987a) concluded that this distribution provides evidence for introgression from the wild form into the cultigen. This evidence for introgression in *Zea* is similar to that found for tomato and one of its wild relatives (Rick et al. 1974).

Employing isozyme evidence, Doebley et al. (1987a) identified several races of

maize that contain isozyme alleles that have apparently been transferred to maize from subsp. *mexicana* by introgression. These races include Apachito, Arrocillo Amarillo, Azul, Celaya, Chalqueño, Cónico, Cónico Norteño, Gordo, and Harinoso de Ocho Occidentales, all of which contain either allele *Enp1-14*, or *Glu1-8*, or both. The accessions of these races show a closer relationship to subsp. *mexicana* than is typical of Mexican maize in general (Fig. 5). These races are all of the higher elevations of central and northern Mexico. If maize originated in the lower elevations of the Balsas River valley as suggested above, introgression from subsp. *mexicana* may have been an important factor in the adaptation of maize to higher elevations of central Mexico.

Doebley et al. (1984) reported some isozymic evidence for introgression from maize into two of its most distant wild relatives, *Z. luxurians* and *Z. diploperennis*. Several plants of the former species possessed allele *Glu1-7*, which is otherwise unknown in this species, although it is a common allele in maize. More convincing evidence exists for introgression from maize into *Z. diploperennis* (Doebley et al. 1984). One plant of this wild species was found to possess two alleles (*Enp1-8* and *Pgd1-3.8*) that are otherwise unknown in this species, but common in maize. The *Enp1* and *Pgd1* loci are tightly linked (3 map units apart) on chromosome 6, suggesting that the segment of this chromosome that carries these two loci has been transformed from maize into one *Z. diploperennis* plant.

The above examples support the occurrence of low levels of introgression between maize and teosinte. Some authors (see Doebley 1984) have suggested much more pervasive introgression between maize and Race Chalco of subsp. *mexicana*. This race is the most weedy of the teosintes and "appears" most like maize morphologically. For this reason, Chalco teosinte has usually been called "maizoid." The morphological similarity between maize and Chalco teosinte in the Valley of Mexico is said to have arisen through hybridization of some "pure" teosinte and maize. Thus, the weedy Chalco teosinte is envisioned as the hybrid derivative of a wild form and a crop. Wilkes (1967:124-125) has suggested that Chalco teosinte may be an introgressive form of Balsas teosinte (*Z. mays* subsp. *parviglumis*). Galinat (1973) has suggested that gene flow between maize and teosinte is facilitated because the genes that control the distinctive features of their ears are locked up in a small number of gene blocks. Thus, the remainder of the genome is free to undergo "a constant gene flow." This, if true, should lead to the homogenization of isozyme allele frequencies in sympatric maize and Chalco teosintes, unless the isozyme loci are tightly linked to the *hypothesized* blocks of morphological genes. Even if some linkage exists, it is unlikely that all 21 isozyme loci that have been studied (Doebley et al. 1984) should be linked to one of the hypothetical blocks of controlling genes. The 21 loci are known to reside on seven separate chromosomes.

Doebley et al. (1984, 1987a) examined isozyme constitutions of weedy Chalco teosinte and maize collected from the same fields in the Valley of Mexico, and of more wild forms of annual teosinte from other regions of Mexico. The results do not support the model for the origin of Chalco teosinte discussed above. Rather than showing a continuum from wild (subsp. *parviglumis*) to weedy (Chalco) to cultivated types, the data revealed that the weedy Chalco teosinte is isozymically far less similar to maize than the more wild subsp. *parviglumis*. Furthermore, maize and Chalco teosinte collected in the same fields maintained distinct isozyme

constitutions. These data essentially disprove the hypothesis that sympatric maize and Chalco teosinte populations undergo a constant gene exchange and maintain their distinct morphologies only by inheritance of a few blocks of genes controlling morphology. Similarly, they disprove the idea that Chalco is a Balsas teosinte (subsp. *parviglumis*) contaminated with maize genes. Rather, the isozyme data suggest that Chalco teosinte is a distinct taxon that has adapted to life as a weed in maize fields. There is no evidence that introgression from maize played a role in this adaptation. However, as discussed above, there is some evidence of limited gene flow from subsp. *mexicana* (including Chalco teosinte) into maize. These data agree with the cytological and field studies of Kato (1976, 1984) and Doebley (1984), which have provided evidence that introgression from maize is not a major factor in the evolution of the weedy Chalco teosinte.

Chloroplast DNA data offer another and much different means of assessing introgression between maize and teosinte. A feature of the chloroplast genome is that it has little effect on the phenotype of the plants. Thus, a plant with a maize chloroplast genome but a teosinte nuclear genome will look exactly like a teosinte. Chloroplast genomes could move freely between maize and teosinte by introgression without adulterating the adaptive complex of genes in the nuclear genome. Introgression of the chloroplast genome would require several generations of backcrossing to the male parent after the initial hybridization to restore the complete nuclear genome of the male parent.

The available chloroplast data provide some evidence for the introgression of the chloroplast genome between maize and teosinte. First, a type of male sterile maize called (*cms-s*) has a cpDNA type (type A; Table 2) not found in normal maize but present in subsp. *mexicana* teosinte. The occurrence of this cpDNA type in maize appears to represent the introgression of this cpDNA type from this teosinte into maize (Doebley and Sisco 1989). Second, Table 2 shows that maize and the Mexican annual teosintes share a number of the same cpDNA types. This situation could result from the introgression of these cpDNA types between the taxa. However, such gene flow could not be completely promiscuous as cpDNA type D is restricted to subsp. *parviglumis* and type E is not found in subsp. *mexicana* despite being common in maize. Further, none of the over 30 analyzed plants of *Z. luxurians*, *Z. diploperennis*, or *Z. perennis* contained any of the maize cpDNA types.

In summary, the molecular evidence provide evidence for limited bidirectional gene flow between maize and teosinte. This evidence comes both from isozyme loci in the nuclear genome and distinct cpDNA genotypes of the chloroplast. Specifically, these data indicate low levels of gene flow from subsp. *mexicana* into maize and from maize into *Z. diploperennis* and perhaps *Z. luxurians*. The molecular data do not support models for the evolution of the weedy Chalco type of subsp. *mexicana* that invoke extensive gene flow between this teosinte and maize.

ORIGIN OF THE MAIZE EAR

No review article on the evolution of maize could be complete without some comment on the greatest mystery surrounding the evolution of maize, the origin of the maize ear. However, because this topic is beyond the scope of molecular

TABLE 2. DISTRIBUTION OF CHLOROPLAST DNA GENOTYPES AMONG MEXICAN ANNUAL TEOSINTES AND MAIZE. THE NUMBERS INDICATE THE NUMBER OF POPULATIONS IN WHICH EACH OF THE FIVE cpDNA GENOTYPES WAS FOUND. DATA TAKEN FROM DOEBLEY ET AL. (1987B; UNPUBLISHED).

Taxon	cpDNA Genotypes*					Total
	A	B	C	D	E	
subsp. <i>mexicana</i>						
Nobogame	—	—	2	—	—	2
Central Plateau	3	2	11	—	—	16
Chalco	—	2	9	—	—	11
Total	3	4	22	—	—	29
subsp. <i>parviglumis</i>						
Jalisco	—	—	2	5	—	7
Southern Guerrero	—	—	4	—	—	4
Central Balsas	—	1	9	7	3	20
Total	—	1	15	12	3	31
subsp. <i>mays</i>						
USA	1	4	—	—	7	12
Mexico	—	16	—	—	6	22
Guatemala	—	6	—	—	1	7
South America	—	10	8	—	21	39
Total	1	36	8	—	35	80

* Using the teosintes of Section *Luxuriantes* as an outgroup, cpDNA type A would be judged most primitive. Type B is the next derived form, distinguished by a deletion mutation (LM-3 of Doebley et al. 1987b). Types C, D and E are the most advanced, each possessing LM-3 plus additional restriction site loss/gains. Type C has an unique *Eco* RI site; Type D has an unique *Cfo* I site; Type E has an unique *Eco* RI site.

systematics, discussion of it will be brief here. Readers desiring a full discussion of the origin of the maize ear are referred to Galinat (1983, 1985) and Iltis (1983, 1987).

At present, there are two views of how the maize ear could have arisen assuming that teosinte is the ancestor of maize. The older theory, presented in greatest detail by Galinat (1983, 1985), provides that the maize pistillate inflorescence (or ear) originated from the pistillate inflorescence of teosinte through a series of single gene mutations. According to Galinat (1983, 1985): the gene *Tr* controls two-ranked (teosinte) versus four-ranked (maize) ears; *Pd* controls single (teosinte) versus paired (maize) spikelets; *Ab* controls the presence (teosinte) versus absence (maize) of abscission layers in the ear; and *Tu* codes for soft outer glumes and a soft rachis. In addition to these few major genes, Galinat (1985) suggested that numerous modifier genes were involved in stabilizing the expression of the former major genes.

Iltis (1983, 1987) has a very different view of the evolution of the maize ear. Briefly, he proposed that the central spike of the teosinte tassel, which normally terminates the lateral branch was transformed into the maize ear by sexual transmutation (cf. Montgomery 1913). Thus, the principal event in the evolution of maize was a switch in sexuality from staminate to pistillate at the tips of lateral branches. Such sexual reversals are commonly induced by environmental effects in teosinte, and Iltis (1983) suggested that human selection at first was directed at genetic factors which allowed the stable expression of the sexually transmuted tassels. This theory is consistent with the existence of three of the genes studied

by Galinat (1983, 1985), but would require some reinterpretation of the genetic evidence for *Pd* because the tassel of teosinte already has paired spikelets, and thus under Iltis' theory this gene would not be required.

The determination of which, if either, of these two theories best explains the origin of the maize ear may soon occur. The first insights are coming from the study of floral development of the maize and teosinte inflorescences (Sundberg 1987; Sundberg and Orr 1986). Curiously, these data suggest that neither a teosinte pistillate nor staminate inflorescence but rather a sexually mixed inflorescence gave rise to the maize ear (Sundberg 1987). However, caution is necessary at this juncture, as these developmental studies were performed on *Z. diploperennis* and may not be applicable to the origin of the maize ear. Further, these studies were performed on plants grown in greenhouses, and such plants usually have abnormal inflorescences. The developmental studies must ultimately be correlated with genetic studies to arrive at a full understanding of the problem. These developmental and genetic studies may not answer all the questions, but they promise to reveal much more about the origin of the maize ear than is known at present.

SYSTEMATICS OF MAIZE

The first attempts to classify maize types produced strictly artificial groupings not meant to reflect the evolutionary diversification of maize. For example, Sturtevant (1899) classified maize based on endosperm type into flints, flours, dents, pops, and sweets. Later classifications attempted to devise categories which reflected the ecology and evolution of maize. Anderson and Cutler's (1942) preliminary treatment of much of American maize recognized five races with eco-geographic and morphological circumscriptions. This work, while being carefully conceived and insightful, was never carried to completion. The first thorough and uniform treatment of maize from throughout Latin America was conducted under the auspices of the Rockefeller Foundation, the National Research Council of the USA and the national agricultural agencies of many Latin American countries. The result was a series of booklets describing the Latin American maize races (e.g., Wellhausen et al. 1952, 1957). This series has made a tremendous contribution to the understanding of the diversity of maize.

The Races of Maize Booklets have been the standard references for the classification of Latin American maize. Some of this research was conducted with a very strong theoretical bias that has to some degree limited its value. Mangelsdorf, who worked in collaboration with many of the authors of the Races of Maize Booklets, had a great deal of influence upon them. For example, Mangelsdorf (1974, 1983, 1986) has consistently given hybridization a large role in the evolution of maize, while he has downplayed other evolutionary processes such as adaptive radiation, drift, convergence, and selection. This influence is seen in the Races of Maize Booklets such that if three races form a morphological continuum the intermediate race is usually judged to be the hybrid of the other two. Alternate hypotheses (for example, the three races represent points on a cultural-ecological cline) are not discussed. Moreover, Wellhausen et al. (1952, 1957) classified races as primitive or advanced based on Mangelsdorf and Reeves' (1939) belief that the ancestor of maize was a now extinct pod-pop corn. The lack of discussion of other points of view on the origin of maize (e.g., Beadle 1939) was detrimental

to some of the Races of Maize Booklets. Drawing on the volumes of valuable raw data in the Races of Maize Booklets, Brown and Goodman (1977) attempted to summarize racial diversity in New World maize and, at the same time, leave out most of the more fanciful ideas associated with the origins of the races.

Molecular evidence offers a fresh look at the systematics of the races of maize, and provides any opportunity to test the many ideas presented by the authors of the Races of Maize Booklets. This evidence will probably come primarily from the isozyme surveys of Goodman and Stuber and their associates (Bretting et al. 1987, 1990; Doebley et al. 1983, 1985, 1986, 1988; Goodman and Stuber 1983b), although the study of mitochondrial and chloroplast genomes may play some role (Weissinger et al. 1983). While the isozyme work is still in progress and it is not yet possible to summarize it, the studies that have been published provide many new insights.

Goodman and Stuber (1983b) examined isozyme variation in Bolivian maize. Their analyses revealed a strong correlation between altitude and isozyme allele frequencies and showed that the morphologically diverse Andean races share a common isozyme constitution. This suggests a common heritage for the Andean races with subsequent diversification into different morphological types. Goodman and Stuber (1983b) also demonstrated that the low elevation Coroicos are isozymatically distinct from other low elevation Bolivian races but show some affinity to the Andean races.

Doebley et al. (1985) examined isozyme variation among the races of maize of Mexico. Their analyses revealed a strong correlation between altitude and isozyme allele frequencies, and circumscribed three weakly differentiated racial complexes: (1) the high elevation Mexican pyramidal races, (2) north and northwest Mexican races, and (3) southern and western Mexican low elevation dent and flour corns (Fig. 6). This isozymic division is nicely correlated with morphology (Benz 1986) and eco-geographic features, and suggests a pattern of independent racial diversification within different ecological zones. This isozymic division of Mexican maize contrasts sharply with Wellhausen et al.'s (1952) division of this maize into (1) ancient indigenous, (2) pre-Columbian exotic, (3) prehistoric Mestizos, and (4) modern incipient races. The isozyme data also fail to support the many hybridization hypotheses proposed by Wellhausen et al. (1952). For example, these authors felt there was "little reason to doubt that race Tuxpeño is basically the product of hybridization of races Olotillo and Tepecintle" (Wellhausen et al. 1952:153). An examination of Fig. 6 does not show Tuxpeño to be intermediate between the two presumed parental races; rather it demonstrates that Tuxpeño is quite distinct from both of them. Thus, the hybridization hypothesis is not supported and alternative hypotheses such as convergence must be considered to explain the morphological similarities between these races.

Doebley et al. (1983, 1986, 1988) examined isozymic variation in North American maize. These studies supported the division of eastern North American maize into two major groups—Northern Flints and Southern Dents (Brown and Anderson 1947, 1948). The isozyme data also support the hypotheses that the Southern Dents are largely derived from similar dent corns of southern Mexico (Brown and Anderson 1948) and that the Northern Flints were derived from the maize of northwestern Mexico (Galinat and Campbell 1967; Galinat and Gunnerson 1963). Doebley et al. (1988) provided clear evidence that the Midwestern Dents

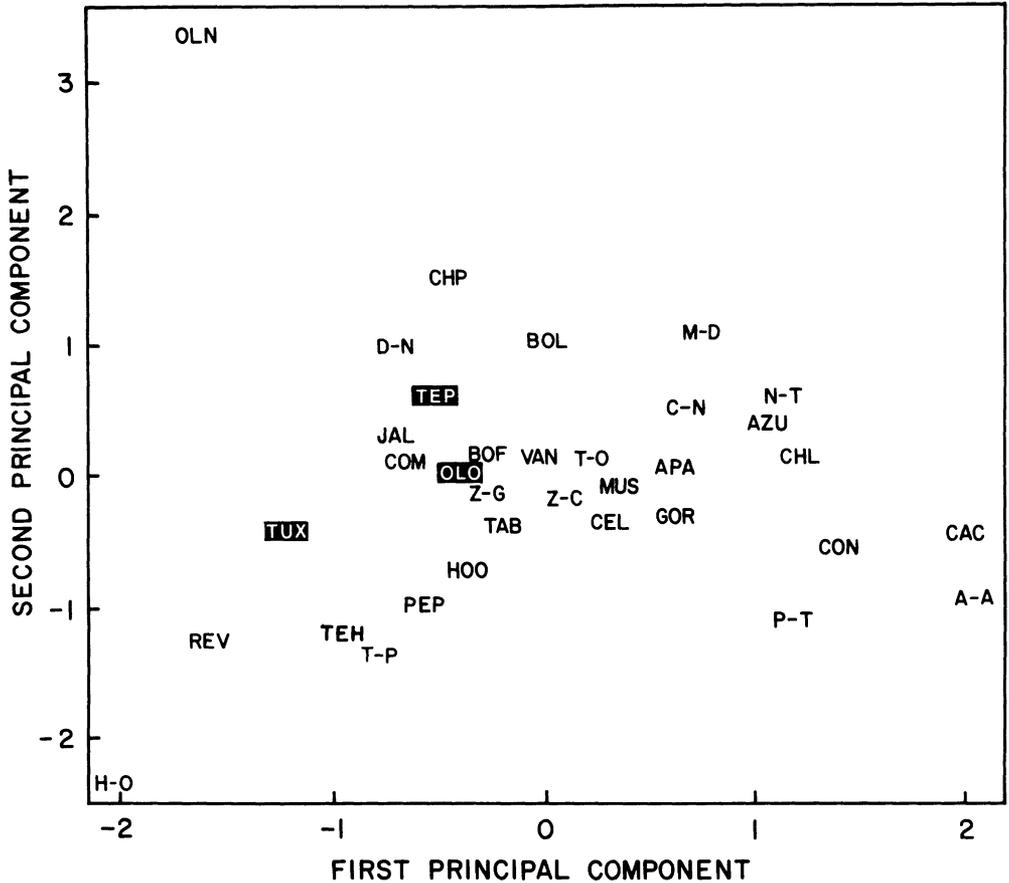


Fig. 6. Graph of the first two components from a principal component analysis of isozymic variation in the races of maize of Mexico (Doebley et al. 1985). Racial designations are: Apachito (APA), Arrocillo Amarillo (A-A), Azul (AZU), Bofo (BOF), Bolita (BOL), Cacahuacintle (CAC), Celaya (CEL), Chalqueño (CHL), Chapalote (CHP), Comiteco (COM), Cónico (CON), Cónico Norteño (C-N), Dulcillo del Noroeste (D-N), Gordo (GOR), Harinoso de Ocho (H-O), Harinoso de Ocho Occidentales (HOO), Jala (JAL), Maíz Dulce (M-D), Mushito (MUS), Nal-Tel (N-T), Olotillo (OLO), Olotón (OLN), Palomero Toluqueño (P-T), Pepitilla (PEP), Reventador (REV), Tablilla de Ocho (T-O), Tabloncillo (TAB), Tabloncillo Perla (T-P), Tehua (TEH), Tepecintle (TEP), Tuxpeño (TUX), Vandeño (VAN), Zapalote Chico (Z-C), and Zapalote Grande (Z-G). The three highlighted races were hypothesized to represent a hybrid race and its two parents (see text).

of the USA arose as the hybrid derivatives of Southern Dent-Northern Flint crosses as hypothesized earlier by Wallace and Brown (1956). Moreover, these data indicated that present-day Midwestern Dents have substantially more Southern Dent than Northern Flint germplasm in them. Isozyme analysis of the maize of the southwestern USA (Doebley et al. 1983) demonstrates a correlation between the cultural-linguistic identity of the Indian tribes and the corn that they grow.

Bretting et al. (1990) examined the isozymes of Guatemalan maize and compared their results to the classification of Guatemalan maize proposed by Wellhausen et al. (1957). The isozyme data segregated Guatemalan maize into two distinct complexes, one from high and the other from low elevations. The isozyme data also demonstrated that Guatemalan forms of race Nal-Tel from the highlands

are more closely related to other highland races than to lowland forms of Nal-Tel. Thus, these Nal-Tel types should not be considered members of the same race, but rather apparently represent populations with a similar ear morphology as the result of convergent evolution. The highland complex shows some isozymic similarity to the highland races of Mexico, suggesting the exchange of maize between these two regions. The isozyme data also failed to support the proposed hybrid origin of several Guatemalan races as hypothesized by Wellhausen et al. (1957).

Bretting et al. (1987) examined isozymic and karyological variation among the indigenous maize of the West Indies and compared this evidence to a very complicated scenario for the evolution of West Indian maize involving hybridization and introgression (McClintock et al. 1981). They found that the isozyme and karyological evidence would be equally consistent with several other scenarios and that the available evidence is "insufficient for proposing a detailed evolutionary history for these maize [races]" (Bretting et al. 1987:1608). The isozymic evidence shows that West Indian maize constitutes a group that is distinct from mainland maize, but has affinities to the maize from the Caribbean coast of South America and the Central American lowlands.

In summary, the isozyme evidence provides a powerful means of reassessing the systematic relationships among maize landraces. While the isozyme studies are not yet complete, many new insights have already emerged. Most notably, genetic variation in maize tends to be closely correlated with altitude, suggesting that the ecological parameters associated with altitude (e.g., length of growing season, temperature, and available moisture) placed severe restrictions on the diversification of maize and limited the degree of gene flow between varieties of maize adapted to different elevations. Because of these restrictions, maize apparently diverged into a number of morphologically distinct (for traits under human selection), though phylogenetically allied, types within these dissimilar habitats. In the few cases examined thus far, isozyme evidence has failed to support the hybrid origin hypothesized for several of the Mexican and Guatemalan races. The isozyme analyses offer little support for the view that hybridization was the primary force in the evolution of maize races (Wellhausen et al. 1952, 1957). Isozyme evidence has been useful in tracing the paths of migration of maize from northern Mexico to the northeastern USA, from southern Mexico to the southern USA, from the Caribbean coast of South America into the West Indies, and between the highlands of Mexico and Guatemala. In the near future, these types of studies will be performed on maize races from throughout the Americas. Nevertheless, it is likely that no matter how sophisticated our means of analysis, the accumulated molecular evidence will probably be insufficient to provide anything more than a very general reconstruction of the origins of the races of maize.

CONCLUSION

Molecular systematic studies have significantly advanced our understanding of the origin and evolution of maize. These investigations have helped clarify the taxonomy of *Zea*, and thus elucidate the relationship between maize and its wild relatives, the teosintes. In this regard, the molecular evidence provides strong support for the theory that maize is a domesticated form of teosinte, and further

suggests that *Z. mays* subsp. *parviglumis* was the direct ancestor of maize. This, if true, would place the origin of maize in the Balsas River valley of southern Mexico, presuming the distribution of this taxon has not changed significantly since the time of the domestication of maize. The available molecular evidence provides no support for the theory that maize was domesticated several times independently. This is not surprising when one considers that the conversion of teosinte into maize is so improbable that it is difficult to imagine that it happened several times. When used to examine the systematic relationships among the races of maize, molecular studies offer many new insights. In particular, these analyses suggest that maize in the Americas diverged along eco-geographic lines and that hybridization may not have been as predominant an evolutionary force as previously thought. Finally, molecular studies should be effective in improving our understanding of one of the greatest mysteries surrounding the evolution of maize, the origin of the maize ear itself.

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