Origin, Domestication, and History

Corn, Strange and Marvelous: But Is a Definitive Origin Known?

Garrison Wilkes
Department of Biology
University of Massachusetts—Boston
Boston, Massachusetts

> This corne is a marvellous strange plante nothing resembling any other kinde of grayne; for it bringeth foorth his seede cleane contrarie from the place where as the flowers growe, which is agaynst the nature and kindes of all other plantes, which bring foorth their fruite there, where as they have borne their flowers . . . at the highest of the stalkes grow idle and barren eares, which bring foorth nothing but the flowers blossomes.
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> *Henry Lyte,* Nieve Herbal, *or* Historie of Plantes, *1578. The first English description of corn. [being translation of the* Cruydeboeck *(1566) of Dodonaeus or Rembert Dodoens of the Low Countries]*

INTRODUCTION

Corn is indeed a strange and marvelous grass. Strange because by human selection the plant can no longer sow its own seeds and is therefore dependent on human care for survival, and marvelous not only because of its stately stature but also because of its importance as a food plant. There is also a mystery to corn, because it is one of the most studied plants on this planet, yet we cannot account with certainty for its complete origin. The one aspect that all students of this plant agree on is that corn is the plant of the Americas; it is native to the New World, and corn, more than any other plant, feeds the Americas. At the time of Columbus, corn was cultivated from Gaspé in Canada to Chile in South America, mostly on forested land that could be cleared by slash-and-burn agriculture followed by several years of fallow.

The U.S. Corn Belt monoculture that replaced the tall grassland of the midcentral United States is a recently developed (ca. 150 years) corn-producing region with its own landrace, Corn Belt dent. Corn is this country's single largest harvest and a $25 billion farm product. The United States produces 40% of the world's corn harvest, and it takes 25 corn plants per person per day to support the American way of life. This plant is found in more than the cornflakes on the breakfast table. Corn oil is in the margarine, corn syrup sweeteners in the marmalade, corn syrup solids in the instant nondairy coffee creamer, and corn was fed to the cows that made the milk, the chickens that laid the eggs, and the pigs that produced the bacon. This is the way the entire day would go—corn is in a candy bar, a beer or bourbon whiskey, a hamburger, industrial chemicals, ethanol in gasoline, plastics, penicillin (the fungus that produces penicillin is grown on a corn-steeped solution), and in the paper sizing of a glossy magazine. Considering the importance of corn to the American way of life, it is remarkable that so few appreciate and understand the uniqueness of this plant (Wallace and Brown, 1956; 1988).

Like wheat and rice, corn is a grass. It is unique among the grasses because its male flowers (tassel) are separated on the plant from the female flowers (the familiar ear of corn). This fact baffled Henry Lyte (1578) because he recognized only the tassels as flowers (Figure 1.1.1). The only grass with a similar pattern is teosinte, the closest relative of corn and in all its taxa a wild plant (i.e., not domesticated). The various taxa of teosinte are native to the western escarpment of Mexico and Guatemala. This fact alone would argue strongly for this region to be the location of origin for corn. Both teosinte and corn belong to the genus *Zea* ($2n = 20, 40$; $x = 10$, Table 1.1.1).

FIGURE 1.1.1. Corn in *Nieve Herbal* or *Historie of Plantes,* 1578. This is the first illustration of corn in an English book (1578), being a translation of the herbal *De fruigum historia* (1566) by Rembert Dodoens (in Latin, Dodonzeus). The corn appears to be a 10-row flint and is said to mature in 6 months. Bread made from the seed "nouritheth but little, and is evill of digestion, nothing comparable to the bread made of wheat."

The closest relatives of the genus *Zea* are the nearly 20 species in the genus *Tripsacum* ($2n = 36, 54, 72; x = 9$), all of which are native to the Americas. Their center of species diversity is again Mexico. The flowers of *Tripsacum* are borne distinctly, but unlike *Zea*, in the same inflorescence, the male flowers toward the tip of the spike and the female basally (Dewald et al., 1987; Cámara-Hernandez, 1992).

Hybrids between corn and *Tripsacum* can be made; there is gene exchange, but the F_1 generations are marginally fertile at best. Hybrids between the various taxa of teosinte and corn are easily made, the chromosome pairing is good to excellent

TABLE 1.1.1. Nomenclature for Teosinte

	Formal Species and Subspecies	Evolutionary Groupings in *Zea*
Annual races of *Zea mexicana* (Schrader) Kuntze (following the idea of race as used in the race of maize; Wilkes, 1967)		
Section: Euchlaena (Schrader) Kuntze in *Von Post and Kuntze Lexicon*, 599 (1904)		**Euchlaena**
Nobogame	*Zea mays* subsp. *mexicana* (Schrader) Iltis	*Zea mexicana* (Schrader) Kuntze Race Nobogame
Central Plateau	*Zea mays* subsp. *mexicana* (Schrader) Iltis	*Zea mexicana* (Schrader) Kuntze Race Central Plateau
Chalco	*Zea mays* subsp. *mexicana* (Schrader) Iltis	*Zea mexicana* (Schrader) Kuntze Race Chalco
Balsas	*Zea mays* subsp. *parviglumis* Iltis and Doebly	*Zea mexicana* (Schrader) Kuntze Race Balsas
Huehuetenango	*Zea mays* subsp. *huehuetenangsis* Doebly	*Zea mexicana* (Schrader) Kuntze Race Huehuetenango
Section: Luxuriantes (Durieu) *Bull Soc. Acclimat.* **19**:581 (1872)		**Luxuriantes**
Guatemala	*Zea luxurians* (Durieu and Ascherson) Bird	*Zea luxurians* (Durieu and Ascherson) Bird
Perennial tetraploid	*Zea perennis* (Hitchcock) Reeves and Mangelsdorf	*Zea perennis* (Hitchcock) Reeves & Mangelsdorf
Diploid perennial	*Zea diploperennis* Iltis, Doebley and Guzman	*Zea diploperennis* Iltis, Doebley & Guzman
Maize		
Section: Mays Linnaeus Sp. Pl. 971. 1753 Gen. Pl. ed. 5. 419. 1754		**Mays**
Zea mays	*Zea mays* L. subsp. *mays* Iltis and Doebley	*Zea mays* L.

Source: Based on Wilkes (1967), Iltis (1972), Bird (1978), Doebley (1980, 1990), Doebley and Iltis (1980), Iltis and Doebley (1980), Sánchez and Ordaz (1987).

(Ting, 1969; Hsu, 1988), and the F_1 and subsequent generations are fully fertile in all forms except the taxa in the section Luxuriantes. The *Tripsacum* × teosinte cross is problematic since most researchers have not been successful with this combination, although a tri-taxa hybrid was made as early as 1932 (Tantravahi, 1968). Clearly, *Tripsacum* shares common genetic architecture with *Zea* but is a more distant relative. Recently, the importance of *Tripsacum* to the evolution of corn has been established from studies of the progeny of a *Tripsacum* × teosinte cross (Eubanks, 2001a,b,c).

CLASSES OF EVIDENCE

The study of the origin of any crop plant is interdisciplinary because the evolution of the plant under domestication and the development of the society of the cultivator, with the increasingly assured food supply, is a very anastimozing or braided process. This was recognized by a Swiss botanist, Alphonse de Candolle, who outlined in his *Origin of Cultivated Plants* (1886) primary lines of evidence: (1) general reflections (geography), (2) botany, (3) archeology, (4) cultural history, (5) linguistics, and (6) combining the various lines of evidence (consilience). Today we could add (7) cytology and genetics, (8) biochemistry and molecular biology, and (9) genomics as necessary evidence to locate the origin of any cultivated plant, especially those that no longer have an obviously identifiable wild form.

Geographical Evidence

Corn and Its Relatives

Using climatic data where corn is most productive, Harshberger (1893), reporting originally in feet and inches, came to the conclusion that corn originated in Mexico and, more specifically, that it had once been a wild plant in central Mexico at elevations above 4500 ft (1372 m) in a semiarid region with rains during the growing season (summer) of approximately 15 in. (38 cm). These conclusions of Harshberger are remarkable because, unknown to him, they exactly circumscribe those areas of Mexico where the close relatives of maize are found and also the sites from which our archaeological evidence of "wild" and early corn have come.

Today, the naturally occurring teosinte populations and the landrace diversity of corn are to be found on the Central Plateau and western escarpment of Mexico–Guatemala in a seasonally dry, subtropical zone between 500 and 2200 m with summer rains. The vegetation is deciduous thorn scrub to oak woodland and inclusive of still existing subtropical humid mountane forest in Jalisco, Michoacan, and Oaxaca. The growing season, June to November, begins with the summer rains. The habitat preferences of *Tripsacum* spp. are less restrictive and often more xeric. There is strong evidence that the annual form of teosinte was maintained in several of the pre-Conquest botanical gardens of the Aztec (Nuttal, 1925; Maldonado, 1941; Langman, 1956) and its ability to hybridize with maize was known (Wilkes, 1966).

The most abundant and geographically dispersed teosintes are the diploid annual forms found growing wild in a number of distinct populations. These plants are so similar to corn in outward appearance (stalk, leaves, and terminal tassel) that the casual observer might mistake them for corn (Figure 1.1.2). The most reliable

FIGURE 1.1.2.   Teosinte at Amecameca 2420 m MSL of the population called Chalco within the field as a maize mimetic weed. The corn belongs to the race Chalgueño and has the tops above the ear removed for livestock forage use. This teosinte population hybridizes easily with corn and expresses many corn traits, such as salmon silks, intense sun red, hairy sheaths, and a well-developed central spike in the tassel (note also the limited number of secondary branching of tassel laterals) not found in other teosinte populations. Chalco teosinte just might have been introduced to the Valle de Mexico by the Aztec Botanical Garden at Xochimilco about five centuries ago.

character separating the two is the pistillate fruit (a polystictious ear in corn) with naked seed and a distictious (two-ranked) spike of teosinte with seed enclosed in a hard protective rachis segment (rachids). The seeds of teosinte are dispersed as rachis segments (called *fruit cases*) from the brittle, disarticulating spike and fall to the ground at maturity. This ability to disperse seed, an ability that corn does not possess, distinguishes teosinte as a wild plant. Another trait separating teosinte and corn is the small number of seeds in each teosinte spike (5 to 11) and the large number of spikes in a fruiting cluster, a fascicle (Figure 1.1.3). These clusters are borne on lateral branches, so that robust teosinte plants look more like a candelabra than like a single-stalked (culm) corn plant. In teosinte, each lateral branch is terminated by a male tassel (Doebley, 1983; Benz and Iltis, 1992). Teosinte can flower over an extended period of 4 to 5 weeks, whereas the lone tassel of corn is a brief 1 week to 10 days and sometimes not well timed with the female silks. The total seed output of an exceedingly robust teosinte plant can be 2000 seeds in 250 spikes, but the usual is 500 to 800 seeds in 100

FIGURE 1.1.3.   Cluster (fascicle) of teosinte spikes at a single node. To derive corn from teosinte, this fascicle needs to be transformed into a polistichous ear. At maturity the rachis tissue will be hard (indurated) and enclose a single seed in each rachis segment, which develops an abscission zone and disperses the seed. Note the two-ranked nature of the seed along the spike. This is Chalco teosinte, which has the largest rachis segment of all teosintes. The entire specimen is 185 cm across.

spikes. The seed output of robust teosinte plants is very comparable to or exceeds that of corn. The weight and size of the individual corn seed is much greater than those of teosinte (Bálint, 1957).

The natural distribution of all teosinte taxa falls within some of the best agricultural land in Mexico and Guatemala and fits very well within the cultural area of ancient Mexican and Mayan civilizations referred to by anthropologists as *Mesoamerica*. Quite clearly, these are the people who nurtured a wild plant across the threshold of domestication to become what we call corn or maize. The time frame appears to be about 6000 years ago. Archaeological evidence from Tehuacan, Puebla, and sites in the neighboring state of Oaxaca in southern Mexico indicate small cobs, dated at 6000 B.P., which are clearly cornlike in all respects. The origin of corn must be older because these cobs are not wild corn, as once thought.

Between 1920 and 1930, N. I. Vavilov, working from the Institute of Plant Industry in Leningrad, made over 2800 collections for corn alone in the New World (Kuleshov, 1929; Bukasov, 1930; Vavilov, 1931). Based on this collection, Mexico was recognized as the single center of greatest diversity. In the late 1940–1950s, the Rockefeller Foundation/National Research Council of the U.S. Academy of Sciences collected corn in the Americas and published a series of bulletins by country for the "Races of Maize." This series established an overview of the landraces of corn throughout the Americas (Anderson and Cutler, 1942; Cutler, 1946; Wellhausen et al., 1952, 1957; Hatheway, 1957; Roberts et al., 1957; Brown, 1960; Ramirez et al., 1960; Grobman et al., 1961; Timothy et al., 1961, 1963; Grant et al., 1963; Hernández-Xolocotzi and Flores, 1971; Paterniani and Goodman, 1977; Anon, 1984; Goodman, 1988; Goodman and Brown, 1988). Of the approximately 300 named races, half were to be found in Mexico–Guatemala and in the Andean zone of South America (Peru).

Clearly, Mexico and Peru stand out as centers from which the racial diversity of corn has spread. Of the 49 races found in Mexico, seven have counterparts in Guatemala, six in Colombia, five in Peru, and two in Brazil. Yet 30 of the 49, more than half are endemic to Mexico. The inclusion of Guatemala adds 12 more races. For Peru, much the same pattern of endemism exists, with 30 of its 48 races occurring only within its borders. Yet only Mexico is a center of diversity for corn and its wild relatives (Sánchez and Goodman, 1992; Sánchez et al., 2000).

Like other Vavilov centers, Mexico is characterized by mountainous regions along the Tropic (in this case, Cancer), long populated by agricultural people but isolated by steep terrain, arid regions, or other natural barriers. This same reasoning was expressed by Wellhausen et al. in *The Races of Maize in Mexico* (1952) to account for the racial diversity found in Mexico: (1) the preservation of primitive races, (2) the influx of exotic races from countries to the south of Mexico, (3) hybridization with teosinte, and (4) the geography of Mexico with its varied habitats and isolating factors conductive to rapid evolution.

Now, essentially the same conditions prevail in Peru, but for Vavilov the fact that teosinte was native to Mexico and not found in Peru favored Mexico as the site of the origin. Vavilov considered teosinte to be the progenitor of corn and attached considerable significance to the fact that teosinte was fully fertile with corn and that the naturally occurring hybrids between the two showed no sterility when backcrossed to either parent. George Beadle (1932, 1939, 1972, 1980) held very similar views. Mangelsdorf (1974) favored Mexico as the site of origin (earlier, in the 1930s, he thought it to be in South America) but could not rule out multiple origins elsewhere. The discovery of a perennial diploid teosinte in Jalisco, Mexico, in 1979 (Iltis et al., 1979) tipped the balance for him in favor of Mexico (Cámara-Hernández and Mangelsdorf, 1981; Mangelsdorf et al., 1981). But the progenitor question remains: Is teosinte the progenitor (Beadle, 1980) or is a wild corn the progenitor (Mangelsdorf, 1986)?

In 1974, Mangelsdorf, a life-long student of corn and one of the forces behind the monographs of the races, proposed six lineages for corn from the following landraces: Palomero Toluqueño (Mexico), Chullipi (Peru), Confite Morocho (Peru), Kulli (Peru), Chapalote/Nal-Tel (Mexico), and Pira Naranja (Colombia). Mangelsdorf also states that "carried to a logical conclusion, it postulates at least six different races of wild corn from which all present day races have descended." Since the founders of these lineages are dispersed, geographically it implies more than one domestication event.

These lineages were the extension of the parentage charts found in the "Races of Maize" monographs and reflect landrace clusters more than lineages of origin for corn. But Randolph (1976) clearly suggested "that more than one species of wild maize was involved in the origin." Similar views have been expressed by Kato-Yamakake (1984) and Sánchez (1994). This is in stark contrast to the monophyletic origin of corn from central Balsas teosinte (Doebley, 1990) or the diphyletic hybridization of two teosintes to form the corn rachis and cupule (Galinat, 2001).

Following different lines of evidence, Kato-Yamakake (chromosome knob patterns) and Sánchez (numerical taxonomic methods across environments) came to similar polygenetic patterns for corn in Mexico. The chromosome knob positions are known to be conservative from the evolutionary point of view and so are good evidence of past events (McClintock, 1978; McClintock et al., 1981). Even in populations where corn and teosinte hybridize, the distinct knob positions are maintained and not swamped (Kato-Yamakake, 1975, 1996). This fact alone was enough reason for Randolph (1976) to favor continued use of *Euchlaena* for teosinte and not merge it with *Zea*. Kato recognized five distinct patterns or migrations in corn knob position/frequencies. These could be considered either evolutionary pathways or possibly five multiple origins for corn.

The first is the Pacific coast migration out of Oaxaca–Chiapas from Zapalote Chico/Grande types to Nal Tel, Reventador, Tabloncillo, and Chapalote. Sánchez (1994) recognizes them as low-elevation types. Generally, this cluster is characterized by a plant height of 2 to 2.5 m, 16 to 20 leaves per plant, 70 to 80 days to flowering, wide kernels (10 to 12 mm), ears with 8 to 12 rows, usually long ears, and 12 to 18 tassel branches, which are often lax or dropping.

The second migration is from central Mexico and involves high-elevation Palomero Tolqueño, Arrocillo Amarillo, Cónico, and Chalqueño. Sánchez (1994) recognized these highland races as being primarily of the Cónico group. This cluster possesses conically or pyramidal-shaped ears borne high on the stalk, high row number (14 to 20), kernels 4 to 8 mm, erect central tassel spike, few tassel branches, weak root system, and drooping wide leaves that are strongly pubescent, especially at the sheath, and well pigmented by anthocyanin. The northern extension of this uniquely Mexican type of corn are the distinctive races of the Sierra de Chihuahua. These races are earlier, shorter, and possess more slender ears that are tapered at the base. This highland group is very different from the lowland group described above, so different that there is reason to consider a polyphyletic origin for maize.

The third, Pepitilla, migration was northward from Morelos–Guerrero up the Pacific coast. Sánchez found the Pepitilla landrace difficult to place taxonomically, and in many ways it is a stand-alone race. Hernández-Xolocotzi (personal communication) thought this race to be the key to understanding corn in Mexico.

The east coast migration path originated in Oaxaca–Chiapas: plants 95 to 115 days to flowering, very tall (3 to 4 m), many tassel branches (20 to 46), long ears, and broad kernels in 12 to 18 rows. This migration northward transverses the isthmus to Veracruz and extends northward up the Gulf coast. The race Tuxpeño is typical of this pattern. The Tuxpeño cluster is characterized by tall plants (2.5 to 3+ m), 85 to 105 days to flowering, 20 to 25 leaves per plants, many tassel branches (20 to 35), ears 12 to 18 cm, row number 12 to 16, usually deeply dented, and soft to medium-hard endosperm.

The last migration path is from the highlands of Guatemala, and this went both northward to Mexico and southward to South America. These are races with small

knobs or knobless positions such as Serrano and Salpor that can be found in South America. Kato considered this unique pattern to be explained best by domestication from "teosinte populations that were already cytogenetically well diversified." For him "maize had a multicenter origin in both space and probably also in time." These Guatemalan highland races are distinct from the highly pigmented, poor root system, medium to broadleaved, solitary central spike (no or few laterals) tasseled corn races with weak roots and pyramidal ears of the Mexican Central Plateau (2000+ m). The other three regions of domestication were midelevation (1250 ± 500 m) radiating from Oaxaca (Zapalote Chico and Zapalote Grande), Guerrero (Pepitilla and Maíz Ancho), and a two-pronged migration from the isthmus up the Gulf coast (Tuxpeño) or the Pacific coast (Tabloncillo).

Writing in 1989 (but finally published in a 1999 book chapter), Benz elucidated a dispersal pattern for maize that confirms both Kato and Sánchez. His dispersal center is the Balsas region of Guerrero, with a long slender-eared corn up the northwest coast in landraces Tabloncillo, Reventador, and Chapalote, a southward radiation of Olotillo types toward Chiapas, and Pepitilla remaining in central Guerrero. Pepitilla is a unique race, generally recognized as being a very old landrace and not immediately related to anything except Ancho and shoepeg, the southern U.S. dent corn. Hernández-Xolocotzi (1993 and personal communications) considered Pepitilla formative in the origin of corn at a time when Nal-Tel and Chapalote were favored as the most probable progenations of modern corn (Wellhausen et al., 1952). Pepitilla is morphologically one of the most distinctive of the midelevation (700 to 1400 m) races, a distribution centered in Guerrero, and a signature multibranched tassel and long shoepeg kernels. Morphologically, the nearly opposite extreme is the highland race (above 2000 m), Cónico, with its single massive central spike tassel, very limited number of laterals, and a conical ear with enlarged base (big butt). Pepitilla, the long, slender, grained race and the broadly grained races of western Mexico (Tabloncillo–Reventador), the drought-avoiding Nal-Tels, Zapalotes, and Bolitas, and the highland races seem to account for the ancestral stocks for the races of corn in Mexico. All but the highland forms have a dispersal coastally north and south from the broad area of the Balsas. There is more agreement than differences in the proposals of Kato (1984), Sánchez (1994), and Benz (1999).

The multiple origin of maize is dismissed by almost everyone, but in so doing we may be overlooking key evidence by making the story for the origin of corn too direct and simplistic. Surely the racial diversity of corn in Mexico and Guatemala holds clues to the origin. Certainly, the various taxa of teosinte point to the section Luxuriantes—*Zea luxurians* and *Z. diploperennis*—as being the least maizelike, in being the least fertile in crosses with maize, and being the only teosintes to be crossed successfully with *Tripsacum* in trigeneric hybrids (Mangelsdorf and Reeves, 1939) or intergeneric hybrids (Eubanks, 2001a,b,c). The five regions proposed by Kato ("present-day maize had a multicenter origin, i.e., different primordial maize germ plasms were domesticated and developed in several centers and by diverse peoples in different times") are all regions where teosinte now exists or was known to exist in the past based on the archaeological record. As an antidote to this paragraph, Doebley (1990) states: "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 corn is so improbable that it is difficult to imagine that it happened several times." Now, if corn originated from plants different from

teosinte as we now know the taxa, it could possibly have had multidomestication or geographically isolated domestications from "altered" teosintes, which were formed "predomestication" by natural selection. The key here is not to look at present-day teosinte populations and work backward to the origin of corn but to imagine an ancestral teosinte for both corn and teosinte as we know them today (Galinat, 2001).

Pre-Conquest Mexican Agriculture

Maize did not evolve in isolation in Mexico. Other crops of worldwide significance are the common bean, lima bean, squash, chili, potato, avocado, cacao or chocolate, papaya, guava, sapodilla, annonas, cotton, sisal, chayote, sunflower, and vanilla. These crops are the product of 8000 years of accumulated mutational events evolved by recombination and inbreeding in geographic isolation into more productive genetic systems selected under domestication by the indigenous people in the varied habitats of Mexico (Bye, 1993).

In the process of domestication, cultivated plants, which were once wild, have quite literally crossed a threshold from being required to seed themselves in the natural vegetation to dependence on human care in one way or another. Their survival is keyed to the human preparation of the ground, to decreased competition with other plants (i.e., weeds), the sowing of the seed in the proper season, the protection of the plants during growth, and finally, the collection of fruits, seeds, and other edible parts for human use. These aspects of cultivation have a profound influence on the genetic selection for traits valued by the cultivator. These events took place for corn and most of our other major food crops before there was a written record (prehistory), meaning that the origin is inferred from the sum total of many lines of evidence that indicate indirectly the domestication sequence and events. Only a very few crop plants have an origin documented by a written record; sugar beets and rubber are two such plants.

Part of the inference is the culture of the cultivator. The indigenous agriculture of Mexico was based on hoe cultivation. There were no large mammal domesticates such as horses or oxen. Therefore, sowing was not done in ploughed fields by broadcasting as is done with wheat, but by hilling up small mounds and with a fire-hardened pointed stick making several holes and filling each with seed. Into each hole there were placed multiple seeds of maize, beans, and squash, and the whole mound was smothered over. The corn grew tall and upright, the bean twined around the maize stalk, and the squash, with its large leaves, formed a ground cover, decreasing the competition from weeds (Cook, 1921). This is the classic milpa system. Tomatoes and chillies also were planted individually, and each plant was tended as a single plant. This resulted in plant-by-plant selection, not bulk or mass selection, since individual plants were observed in both their vegetative and reproductive phases. The modern-day Mexicans do not refer to their fields as a place of cultivation; rather, they refer to their corn or tomatoes. The land or the crop is not the sole focal point of the minds' eye—it is the individual plant. This fact alone can account for the tremendous difference between the wild form and the domesticated crop (Heiser, 1979; Pickersgill, 1981, 1983; Zeven, 1999, 2000).

The mind's eye has influenced the subconscious artificial selection that has taken place. The indigenous cultivator is not disturbed by the kitchen garden–like diversity of many crops all growing in the same place. This is not viewed as disorganization, because the individual plant catches the eye more than the totality of the field. This

individual selection has resulted in a portfolio of plants characterized by gigas fruits allometrically out of proportion to the rest of the plant and intense color: the red of tomatoes and the blue of corn kernels, or the largeness of squash fruits. Not only is there an intensity of color, there is a diversity of color in almost every crop: corn, beans, chili, and potato. In corn there are about 50 different kernel patterns and colors; in beans, more than double that number; in potatoes, there are purple, yellow, golden, or red in addition to the familiar white; and in many of these variants the taste also varies. The usual Mexican market has from 15 to 30 different types of chilies, from fiery hot to rich flavor, smoky to bright, all tasting distinctly different; several kinds of tomatoes, each used in a distinct way in the kitchen; and at least five types of corn: dent or flint, soft flour, large-seeded flour for soups, and pop, all used in different ways.

Often, Mexican farmers have two or more types of corn growing in the same field and yet are able to keep them genetically distinct, quite a feat for an open (wind)-pollinated crop. These are well established and recognized varieties, and I'm not sure we can say with confidence that early cultivators could select out promising mutants from teosinte without some sort of geographic isolation from the much larger and genetically swamping teosinte population—but perhaps they did. Teosinte is no longer the dominant *Zea* of Mexico, but it was in preagriculture times. If wild corn did exist, it could not have existed sympatric with teosinte and thus must have been geographically isolated. Probably such isolation at elevations above teosinte would have occurred at 1850 to 2000 m (Wilkes, 1986).

The isolating mechanisms that prevent or limit genetic exchange between teosinte and corn in naturally occurring populations are primarily spatial and seasonal. The largest teosinte populations are located in sparsely settled areas and are isolated by both distance from the nearest cornfield and by flowering time, typically being about 10 days later than corn. On the Central Plateau and Valley of Mexico, teosinte occurs either along the margin or in the field proper and is only partially seasonally isolated, flowering after corn. *Z. luxurians,* of southern Guatemala, is the most seasonally isolated teosinte, being several weeks later than the local maize.

Hybrids of teosinte and corn do occur at all localities where teosinte is found but are most frequent in the cornfields of the Central Plateau, Chalco, Nobogame, and Huehuetenango, where teosinte occurs either as a weed in the fields or as dense populations along the margin of the fields (Wilkes, 1967, 1977, 1985, 1988) (Figure 1.1.4). Over the years the cornfields at Huehuetenango have been displaced by barbed wire and cattle, dense hillsides of 100,000 teosinte plants have disappeared, and hybrids with corn are now rare. In the Balsas around Teloloapan, barbed wire and cattle also have displaced hillsides of teosinte. The population is not a carpet of millions of teosinte plants as it was in the early 1960s but is now a patchy quilt of cattle or teosinte. Interestingly, hybrids with corn are now more abundant. The Balsas is still the largest teosinte population, but even its breeding dynamics is changing with the ecology of land use intensification. In the last 40 years I have watched many local populations disappear, such as Cuitzeo (1982) on the Central Plateau or Los Reyes (1999) of Chalco, but what is more frightening is the contraction of the entire population of *Z. luxurians* to the point where extinction is probably a decade or two away. The populations of Nobogame, Oaxaca, Huehuetenango, and Guatemala are not holding their own and are much diminished from the benchmark of 1967 and therefore threatened [Table 1.1.2 and map (Figure 1.1.5)]. Without some sort of habitat protection in the next decade (Altieri and Merrick, 1987) (Benz, 1988) teosinte as I knew it in the 1960s will

FIGURE 1.1.4.   Corn × teosinte hybrid in a Chalco 2250 m MSL field, Valle de Mexico. Note the eight-rowed, four-ranked polishichous ear and the paired spiklets (both corn traits), but the yoking of opposite ranks has an abscission zone and this hybrid can disperse seed (a teosinte trait). The lower glumes enclose only about a third of the grain; if they enclosed the entire grain, perhaps this would approximate an ancient teosinte that gave rise to corn. The only trouble with this theory is that the morphology can be created only by hybridizing with corn.

be gone and only small, isolated, relict stands will represent what was once millions of plants. Without a change in the way that plants are viewed (Duvick, 1995; Fowler, 2002), I'm not sure that there will be a habitat left for teosinte 50 years from now.

Land use is changing the abundance of teosinte, and NAFTA is changing the corn grain markets and thus the subsistence corn farmers and the landraces they cultivate. Mexican cornfields are among the most complex assemblages of corn germplasm in the New World. Corn in Mexico is extremely variable; it not only varies from region to

TABLE 1.1.2. Annual Teosinte Populations in Mexico and Guatemala

Population[a]	Status[b]	Common Name	Location	Extent	Habitat
Nobogame or Nabogame	Rare	*Maicillo*	Tarahumare valley in the Sierra Madre of the state of Chihuahua about 16 km northeast of Guadalupe y Clavo.	No more than 30 km² on the valley floor.	Along margins of maize fields and in willow thickets bordering streams.
Durango	Rare	*Maicillo*	Valley of Guadiana 10 km outside Durango in the state of Durango.	No more than 20 km².	Limited to wasteland along irrigation canals.
Central Plateau	Indeterminate	*Maiz de coyote*	Isolated populations throughout the entire Central Plateau in the states of Jalisco, Michoacan, and Guanajuato. Largest continuous population is in region north of Lake Cuitzeo.	Once a continuous population covering thousands of square kilometers but now occurs in scattered, isolated pockets rarely larger than 10 km².	Occurs in cultivated fields and along field margins or stone walls and in areas protected from grazing.
Chalco	Indeterminate	*Accece or acece* (unwanted or disagreeable)	Valley of Mexico from Amecameca to Xochimilco, Chalco, and Los Reyes. Isolated populations around Texcoco.	Main populated centered in a 300-km² area around Chalco.	Found almost exclusively in maize fields as a "mimic" of the maize but also as a weed along roadsides.

Location	Status	Common name	Distribution	Size of population	Habitat
Balsas	Stable	*Maiz de huiscatote* (roadrunner = corre-camino) *maiz de pajaro* (bird) atzitzintle	Hills surrounding Rio de las Balsas Basin. Population distributed discontinuously, with one located south of Chilpancingo in the state of Guerrero and the other on the northern rim of the basin.	Population south of Chilpancingo covers hundreds of square kilometers, while the other extends over thousands of square kilometers in the states of Guerrero, Michoacan, and Estado de Mexico.	Sometimes observed in maize fields but generally in dense stands on hillsides, especially along gullies or other areas where there is rain runoff.
Oaxaca	Rare	*Cocoxle* (ground dove or roadrunner)	San Francisco de Honduras, 5 km from San Pedro Juchatengo in the Sierra Madre de Sur of Oaxaca.	No larger than 20 km², although there may be isolated outlying pockets.	Grows on hillsides and in maize fields surrounding the town.
Huehuetenango	Endangered	*Milpa de rayo* (where lightning strikes the fields) *salic*	Hills and valleys of the Departamento de Huehuetenango around the Guatemalan town of San Antonio Huista, near the Mexican frontier.	Probably not larger than 300 km².	Found along trails, in fields, and on hillsides of deserted *milpas* (maize fields).
Guatemala	Endangered	*Milpa silvestre* (wild corn) *teocintle*	Distributed discontinuously in southeastern Guatemala across the hills and valleys of Jutiapa, Jalapa, and Chiquimula.	Was once distributed continuously, covering 500 or more km², but is now fragmented, the largest population covering no more than 1 km².	Occurs at small, isolated sites along the margins of fields or in other areas protected from grazing.

[a]Size of populations: Balsas > Central Plateau > Chalco > Nobogame > Durango > Oaxaca. The populations of Huehuetenango and Guatemala are too fragmented to rate on size.
[b]Rare, occurring at a single location.
Source: Wilkes (1967, 1988), Sánchez and Corral (1996), Sánchez et al. (1998).

FIGURE 1.1.5.   Current status of teosinte populations in Mexico and Guatemala.

region by elevation and rainfall, but there is a marked tolerance of Mexican cultivators for a range of variation within a single field and also the presence of "unproductive" teosinte and other weeds, plus the intercropping of beans and squash. The folk knowledge that a field with greater diversity is "stronger or has greater potential" has important information to contribute to our understanding of the evolution of corn (Hernández-Xolocotzi, 1993). Only now are we learning how extensive is the role of seed exchange between farmers (Bellon and Reeves, 2002; Lovette et al., 1997; Perales et al., 2003a,b; Smale et al., 1998; Soleri and Cleveland, 2001), yet many locally grown landraces of corn, such as Chapalote and Pepitillia, are now threatened. I mention this here because both of these landraces had a unique role in the origin of corn. They are both becoming so rare that gene banks might soon be the only seed source (Taba 1997a,b). The current abundance of teosinte in Mexico is a shadow of its distribution in the 1960s, and maybe, like corn landraces, the only source in a few decades will be a gene bank.

Actually, most researchers think that the question regarding the origin of corn is: Did it evolve from wild corn or from teosinte, whereas, in fact, the central issue is whether the origin was sympatric with teosinte or allopathic. To view the origin as sympatric with teosinte is too optimistic regarding the selection powers of early agriculturist, and to claim an allopathic origin does not distinguish between a "new and novel teosinte" or "wild corn" as the prototype progenitor. Since corn is 90% teosinte and teosinte is 90% corn, the key evidence will have to come from the archaeological

record. One fact is clear; modern corn is an artifact of indigenous Mesoamerican agriculture and it is unique among all the grasses.

Corn in the Pre-Conquest Diet

Beyond our dependence on plants, especially cereals, for their high-calorie yield to meet the energy requirements of an expanding human population, there is a second aspect of our symbiotic relationship, which is well illustrated in the Mexican diet of corn, beans, squash, avocado, and tomatoes. There is, in any agricultural system where the cultivators eat and depend on what they grow, a natural selection for a balanced nutritional intake (Wilkes, 1977). Classically, over the millennia, if the nutrition was balanced, the cultivator was healthy and had the energy and wisdom to tend the crop and increase its yield. This natural selection promoted the cultivation of complementary protein plants, such as corn (deficient in lysine and methionine) and beans (deficient in cystine) in Mexico; of wheat (deficient in lysine and tryptophan) and curded milk in the Near East, and of cooking methods that increased the amount of digestible protein (steamed potatoes) or added an essential mineral to the diet (acid foods cooked slowly in soft iron pots). A good example of the latter is the soaking of corn grains in lime before processing into tortillas. The Mexicans were without a milk animal, their only domesticated animal being the turkey, and thus their diet was potentially calcium-deficient. The soaking of corn grains in lime to soften the pericarp added calcium to the diet and achieved the adequate nutritional balance found in diets that included milk, soybean curds, or stir-fry vegetables. The lime also increases the availability of the B vitamin niacin.

Although corn is the most important food plant of Mexico, it is not a complete nutrient package. Even with the addition of beans and squash, only the calories, proteins, and vitamins A and B needed by the population were met. Yet by the simple addition of tomatoes, chillies (vitamin C and fruity acids), and avocados (fatty acids and protein), the indigenous Mexican diet sustained one of the healthiest, most densely settled populations in the world at the time of the Spanish conquest in 1521 (Kempton, 1926; Whiting, 1944).

Just as corn is not a perfect nutritional package but is dependent on a number of other food plants to form a balanced regional diet, its evolution by indigenous cultivators did not take place in isolation but rather in conjunction with a number of other crops, especially beans and squash. Corn as a cereal in the diet did not evolve first. There is good evidence that *Setaria* were used widely before corn. There is good archaeological evidence that a number of basic crops in the diet were domesticated or in the process of domestication before corn entered the sequence as a productive food plant. Corn has been a major food source only for the recent half of indigenous agriculture in Mexico (i.e., 3500+ years). It was not the first, and it only comparatively recently became the major dominant carbohydrate source. Yet in this time frame people have developed uses for all parts of the corn plant, not just the grain (masa or dough for tortillas, tamales, and tostadas, but also ground meal for atole, pinole, and pozole), the stalk for fencing and fuel, the cobs for cooking fires, the smut as a fungal delicacy, and leaves or husk as wrapping for tamales. No other cereal has as many endosperm types (i.e., flour, pop, sweet, waxy, flint), each with distinctive taste and cooking qualities. These are all probably artifacts of human selection and not found

in the wild. The only exception is the popcorn trait, which could have characterized the small hard seed of the wild form. Teosinte seed will pop if removed from the rachis tissue and carefully heated (personal observation).

Archaeological Evidence

The oldest and most complete archaeological sequence for corn is from the arid hillside caves of the Tehuacan valley in southern Puebla near the border with Oaxaca (Mangelsdorf et al., 1967a,b; MacNeish and Eubanks, 2000). The Tehuacan sequence spans the evolution of corn for nearly 6000 years to recent times in combining the overlapping profiles of a half-dozen caves spread across the valley (Mangelsdorf et al., 1967b). The earliest cobs (5000 B.C., now corrected to 4700 ^{14}C years B.P., or 5500 calendar years) are characterized by a uniformity of size and a bisexual condition, with the pistillate spikelets below and the staminate spikelets at the tip of the ear (tassel tip). We do not know if these ears were borne terminally or at a lateral position, but such bisexual ears are seen when the ear is terminal on a tiller or when the nodes of the ear shank have elongated, pushing the ear beyond the ear husk. Most of the cobs are fragments; the only one that is entire is about 2.5 cm long and has about 50 seeds arranged in eight rows (Figure 1.1.6). The kernels were subtended by long, relatively soft glumes. Because soft glumes are not associated with teosinte, these earliest archaeological specimens are, to quote Bill Brown (1978), the "nasty problem" for the teosinte origin theory. There were no attached grains and they appear to have dispersed from the fragile rachilla. At the time these characteristics were all thought to be those of a wild corn (Mangelsdorf and Galinat, 1964). Later, Galinat (1971) and Beadle (1972) considered these as semidomesticates from teosinte, and more recently, some of these cobs have been called the teosinte proto-ancestor of corn (Iltis, 1972). These cobs are not teosinte; they are corn. If considered wild corn, this is based on attitude and not on any evidence associated with the specimens. The oldest specimen from Bat Cave, New Mexico is very similar to the oldest Tehuacan cobs.

The corncobs found at Guila Naquitz Cave, about 5 km from the town of Mitla, Oaxaca [1926 m mean sea level (MSL)] are older, 5420 ^{14}C B.P. or about 6250 calendar years (Benz, 2001; Piperno, 2001; Piperno and Flannery, 2001; Smith, 2001). These cobs have an indurated rachis and morphology indicating corn × teosinte hybridization or teosinte ancestry in the recent past. Archaeological seed of teosinte was recovered at Guila Naquitz but at a more recent time frame, after corncobs are present at earlier levels. The habitat of the Valley of Oaxaca is fit for teosinte, and there is no reason to question the teosinte rachis segments or the corn-introgressed "teosinte" rachis segments dated between 3000 and 2000 B.P. At Guila Naquitz, *Cucurbita pepo* cultivation predates corn by about 2000 years. So corn was not the first domesticate. Corn at Guila Naquitz is older than Tehuacan but shows induration of the rachis tissue, a trait not present until later in the sequence at Tehuacan. These are our two earliest corncob sites; one is indurated (corn from teosinte) and the other is not indurated (corn from corn). Obviously, we need more archaeological sites in the highlands of Puebla and Edo de Mexico and the slopes around 1250 to 1500 m MSL of the Rio Balsas, Guerrero to resolve the issue from an archaeological standpoint. Recently, even older corn pollen has been reported from the humid tropical lowlands of eastern Mexico (Gulf coast of Tabasco), which opens an entirely new dimension—perhaps the

FIGURE 1.1.6.   Oldest entire corncob specimen (5000 B.P.) from the Coxcatlán phase, San Marcos Cave, Tehuacán, Puebla, Mexico. Mangelsdorf considers this wild corn; Galinat and Beadle, semidomesticated corn. What is clear is that this small cob, which once held about 50 small seeds subtended by long, soft glumes and slender fragile rachises (possibility might have shed the seed), exhibits no traits associated with teosinte. This specimen does not fit the corn origin from teosinte model. The introgression of teosinte-induced morphologies in corncobs appears about two millenniums later.

origin is not in the highlands (Pope et al., 2001), but I tend to favor a midelevation and/or highland origin because corn has so many highland traits in its genome.

The concept that teosinte is fully fertile with corn is not a recent discovery. It is reported in the literature by Harshberger (1899) and Watson (1891) for teosinte from the Central Plateau, by Lumholtz (1902) for Nobogame in southern Chihuahua, by Lopez y Para (1908) for Chalco, Valley of Mexico, by Kempton and Popenoe (1937) for Huehuetenango in northern Guatemala, and by Melhus and Chamberlain (1953) for Jutiapa/Jalapa in southern Guatemala. In fact, teosinte is known to hybridize with corn throughout its entire range (Wilkes, 1967).

Later, cobs at Tehuacan are all larger (was this better agronomy?) and more varied in morphology, but except for scale, virtually identical with the earliest (soft glumes enclosing the seed and delicate rachis on an eight-rowed cob). Then about 3000 years ago (or said another way, halfway through the profile) there are explosive changes in the cob. The lower glume changes from soft to indurated, and the rachis elongates and becomes indurated (i.e., stiff). Hybridizing corn with teosinte can induce all of
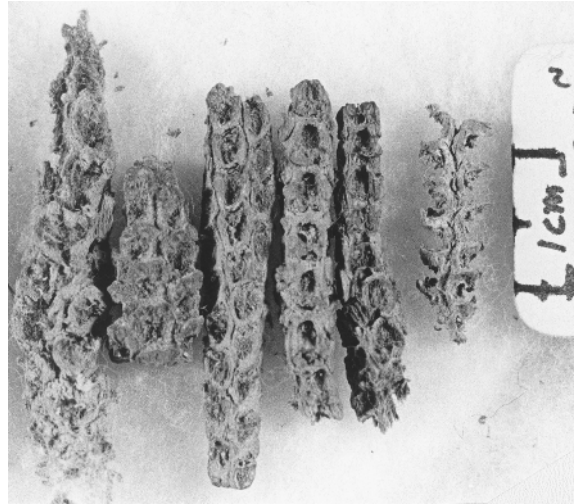
FIGURE 1.1.7.   Palo Blanco phase Coxcatlán, Cave Tehuacán, Puebla, with corn specimens from 2500 B.P. Note the specimen next to the tab, which is a distichous spike with single spikelets which are teosinte characteristics. At Tehuacán, teosinte characteristics do not appear early in the archaeological sequence but appear halfway through the record.

these changes (Figure 1.1.7). Unfortunately, teosinte has not been recovered from the Tehuacan excavations. In Mitla, Oaxaca at 2500 B.P. we do have teosinte and corn introgressed teosinte, as indicated by the seed expanding and pushing the glume away from the enclosing rachis segment. At Romero's Cave in western Tamaulipas (3000 B.P.), we have teosinte and maize × teosinte hybrids (Mangelsdorf et al., 1967a). These dates for the Oaxacan (south of Tehuacan) and Tamaulipas (northeastern Mexico) sites are comparable with the period at Tehuacan when corn, after two millennia of static change, suddenly exhibits an unmistakable change in morphology that is identical to that induced by controlled introgression from teosinte. The most extreme cobs exhibit characteristics of corn × teosinte F_1 hybrids, like those at Guila Naquitz, including distichious arrangement of the spikelets and free solitary cupules at the top of the cob. Other sites around Mexico indicate morphological characteristic associated with teosinte introgression and subsequent increased variability of cobs and evidence of heterotic effects in the lengthening of the cob at this time (3000 B.P.). Why this sudden change? Did corn cultivation extend into the distribution of teosinte? Did teosinte mutate and suddenly become fertile with corn, or did teosinte expand its territory so that it invaded abandoned milpas in the fallow period?

The evidence of teosinte introgression into corn in the archaeological record remains circumstantial at best because teosinte and hybrids have been recovered only at Romero's Cave and at Guila Naquitz, yet the dates fit Tehuacan, and since indurated cobs with hard, curved lower glumes and a stiff rachis tissue can be matched exactly by cobs of experimentally produced maize × teosinte hybrids, there is no reason to doubt that the origins of indurated glumes and rachis in the past were any different from those of the present day. Indeed, teosinte introgression is recognized in two-thirds of the races of maize growing in Mexico today (Wellhausen et al., 1952).

The key question is: Why the sudden appearance of teosinte-induced induration after three millennia of no evidence of teosinte in the corncobs at Tehuacan? Did we miss some key evidence in the sites we have excavated? One fact remains—corn became a major carbohydrate source in the diet only after the induration of the rachis tissue. Is this the domestication event? The archaeological sequence for maize spans 6000 years, but the yield take-off starts only 3000 years ago. Is it irrigation, site preparation, two races of (or hybridizing)? Did the ear move to a lateral position and develop husk protection, allowing for a massive ear? Did hybridization with teosinte make for a stiff stalk, no tillers, and preadapt corn for co-cultivation with beans and squash, which were already domesticated, to complete the triad of milpa agriculture? The answer to these questions are all stuck in prehistory and support the view that the final proof for the mystery will be solved by means of the archaeological record.

Botanical Evidence

The close relatives of corn are the genus *Tripsacum* of nearly 20 recognized taxa found in both North and South America (Tables 1.1.3 and 1.1.4) and the teosintes in the genus *Zea*. *Tripsacum* and *Zea* belong to the subtribe Tripsacinae of the Andropogonae tribe of the Poaceae family. The center of diversity for both is western Mexico from the states of Jalisco in the north to Chiapas in the south. All taxa of *Tripsacum* are perennial. Diploid ($2n = 36$) plants generally are sexual, while higher ploidy levels (triploids, tetraploids, and pentaploidy) generally are apomitic or colonize slopes vegetatively from strong fleshy rhizomes. Only one taxa, *T. zopilotense*, the small, narrow-leaved, xeric-adapated species from the Cañon del Zopilote in Guerrero, is lacking rhizomes.

At the present time only the broad evolutionary relationships in the genus *Tripsacum* are known (Randolph, 1970; Newell and de Wet, 1974; de Wet and Harlan, 1978; Brink and de Wet, 1983; Berthaud et al., 1997). It is hypothesized that the genus radiated out from the presumed center of origin and present center of diversity (Guerrero) on the western escarpment of Mexico (1000 to 1500 m), where the two morphological distinct Mexican diploids, *T. maizar* (big broad leaf, thick rhizome) (Figure 1.1.8) and *T. zopilotense,* are known to occur. These two divergent diploids moved both northward, into what is now the United States, and gave rise to *T. dactyloides,* $2n = 36, 72$, *T. lanceolatum,* $2n = 72$, and to the south, to give rise to South American forms of *T. dactyloides* and *T. austriale,* $2n = 36$. In South America, *Tripsacum* is associated with a woodland vegetation at moist midelevations. Also found in South America are three other taxa (probably more, once the genus is better known). One of them, possibly *T. andersonii,* was moved there from the Guatemalan region by humans because of its utility as a fodder.

In Mexico–Guatemala there are three clusters for *Tripsacum.* The northwestern group is characterized by the tetraploid *T. lanceolatum,* which reaches up to and across the Arizona border. The central group is characterized by multiple ploidy levels, and many taxa intermediates, such as between *T. pilosum* and *T. maizar* (Figure 1.1.9), on the hillsides outside Tequila, Jalisco. *T. bravum* was once thought to be limited to the Valle del Bravo but is now recognized as being widespread over the region, as is *T. dactyloides* var. *hispidium* and var. *mexicanum*. The southern group includes diploids *T. manisuroides* and *T. laxum,* diploid and triploids of the widespread

TABLE 1.1.3. Genus *Tripsacum* in Central and North America

	Distribution	Chromosomes	Remarks
Section: Tripsacum (characterized by absence of pedicel in male spikelet)			
T. bravum Gray	Central Mexico	$2n = 72$	
T. dactyloides (L.) L	Eastern half of U.S.: Mississippi valley to Massachusetts	$2n = 36, 54, 72$	Easily crossed experimentally with maize [Kansas clone ($2n = 36$) crossed experimentally with corn as early as 1931]
T. dactyloides var. hispidum (Hitchc) de Wet and Harlan	Sierra Madre Oriental, central Mexico	$2n = 36, 72$	
T. dactyloides var. mexicanum de Wet and Harlan	Central Mexico	$2n = 72$	
T. floridanum Porter ex Vasey	Florida–Cuba	$2n = 72$	
T. intermedium de Wet and Harlan	Southern Mexico	$2n = 72$	
T. jalapense de Wet and Brink	Southern Mexico	$2n = 72$	
T. latifolium Hitchc	Southern Mexico–Guatemala moist woodlands	$2n = 36, 54$	Robust, possible parent of Guatemala grass
T. manisuroides de Wet and Harlan	Southern Mexico	$2n = 36$	
T. zopilotense Hernandez–X and Randolph	Guerrero only	$2n = 36$	Very xeric environment limited to the Cañon del Zopilote, Guerrero; only member of genus without rhizomes
Section: Fasciculata (characterized by presence of a pedicel on a male spiklet of the pair)			
T. lanceolatum Ruprecht and Fournier	Northwestern Mexico, Sierra Madre–Arizona border, tetraploid	$2n = 72$	

T. laxum Nash	Veracruz to Guatemala	$2n = 36$	Hybridized with *T. maizar*–sterile triploids
T. maizar Hernandez-X and Randolph	Guerrero to Jalisco, western escarpment	$2n = 36, 54, 72$	In parentage of Guatemala grass; very robust, to 5 m
T. pilosum Scribner and Merrill	Western central Mexico	$2n = 36, 54, 72$	*T. maizar* × *T. pilosum* hybrid swarms Jalisco; tetraploid hybrids sterile but produce seed apomictically

Source: Based on Cutler and Anderson (1941), Randolph (1970), de Wet et al. (1971, 1976a,b, 1978, 1981, 1982, 1983), de Wet and Harlan (1978), Doebley (1980), Berthaud et al. (1997).

TABLE 1.1.4. Genus *Tripsacum* in South America

	Distribution	Chromosomes	Remarks
Section: Tripsacum			
T. andersonii Gray	Northern South America to Peru	$2n = 64; 3x = 54 + 10$	Known as "Guatemala grass"; robust plants possesses 10 teosinte chromosomes, sterile cultivated for forage. Also found in Guatemala as a forage but cultivated not wild or naturalized
T. australe var. *australe* Cutler and Anderson	South America	$2n = 36$	Widespread moist, open woodlands, as variable as *T. dactyloides* and distinguished by tomentose state
T. australe var. *hirsuttum* de Wet and Timothy	South America, Bolvia–Brazil	$2n = 72$	
T. cundinamarce de Wet and Timothy	Colombia	$2n = 36$	Robust glabrous
T. dactyloides (L.) L.	This species distribution extends from Massachusetts to Colombia–Venezuela	$2n = 36$	Diploids, triploids, and tetraploids
T. dactyloides var. *meridionale* de Wet and Timothy		$2n = 36$	Highly variable diploids, triploids and tetraploids
T. peruvanium de Wet and Timothy	Peru and Ecuador	$2n = 72, 90, 108$	Peru and Ecuador, gametophytic apomict

Source: Based on Cutler and Anderson (1941), Randolph (1970), de Wet et al. (1971, 1976a,b, 1978, 1981, 1982, 1983), de Wet and Harlan (1978), Doebley (1980), Berthaud et al. (1997).

FIGURE 1.1.8. *Tripsacum maizar,* the most cornlike in appearance, but clearly a *Tripsacum.* Photograph taken at the type locality Acahuizotla, Guerrero, 1100 m MSL, where teosinte is also to be found. *T. maizar* is diploid and not as zeric adapted as the tetraploid taxa. It also appears to be a stem stock from which the genus diversified.

T. latifolium, and the tetraploids *T. intermedium*, *T. jalapense*, and *T. maizar* (diploid and tetraploid).

In Chiapas on the slopes before Tuxtla Gutierrez between 750 and 1200 m it is possible to find *T. intermedium* ($4x = 72, 5x = 90$), *T. jalapense* ($4x = 72$), *T. laxum* ($2x = 36$), and *T. manisuroides* ($2x = 36$) (Berthaud et al., 1997). Within 30 km of the Chiapas border in Guatemala can be found *T. laxum* ($2x = 36$), *T. latifolium* ($2x = 36, 3x = 54$), and the Huehuetenango form of annual teosinte. Chiapas, Jalisco, and Guerrero are the richest zones of maize relative diversity. The luxuriant broadleaved *T. andersonii* is found in both Guatemala and South America, where it is fed to guinea pigs. It is thought to be a hybrid of *T. latifolium* (diploid) × *T. maizar* to produce a triploid *latilolium* ($3x = 54$) (Berthaud et al., 1997), which then crossed with a 20-chromosome teosinte (*Z. luxurians*) (Talbert et al., 1990). *T. andersonii* is the only example of a naturally occurring teosinte × *Tripsacum* hybrid. Repeated attempts to cross Mexican annual section Euchlaena-type teosintes have failed. The only other experimentally crossed teosinte with *Tripsacum* was with another section,

(*a*)

(*b*)

FIGURE 1.1.9.   (*a*) Isotype of *Tripsacum pilosium* from the Harvard University Herbaruim collected near Lake Chapala, Jalisco, Mexico, 1500 m MSL. (*b*) *Tripsacum pilosium* photographed in the same locality at the point when stamens are shedding pollen. The *Tripsacum* inflorescence bears male flowers above and female flowers below in the same inflorescence; not separated on the plant in a tassel and ear as found in teosinte and corn.

Luxuriantes, *T. diploperennis* (Eubanks, 2001a,b,c). These experiments need to be repeated by others because we need to better understand the genetic relations between *Tripsacum* and the most *Tripsacum*-like (tripsacoid) of all the teosintes, the Luxuriantes.

T. andersonii notwithstanding, *Tripsacum* spp. seem to be in the secondary gene pool of corn. In 1931, Mangelsdorf and Reeves first reported a corn × *Tripsacum dactyloides* (Kansas clone) cross, making it a successful intergeneric hybrid, at the time considered a breakthrough. They then crossed the hybrid with Florida teosinte, *Z. luxurians*, to produce a trigeneric hybrid. Teosinte is now recognized to be cogeneric with corn, and even in the trigeneric hybrid the teosinte chromosomes paired with the maize chromosomes and not the *Tripsacum* chromosomes, which underwent elimination. Experiments have established that exchanges can and do occur between corn and *Tripsacum* chromosomes (Galinat, 1977). Segments of *Tripsacum* chromosomes can be substituted for corresponding segments in corn, and over 50 homologous loci on the chromosomes of the two have been mapped (Galinat, 1973).

The accumulated information on corn–*Tripsacum* hybrids and their derivates indicate that the respective genetic architecture of corn ($2n = 20$) and *Tripsacum* ($2n = 36$ plus all levels of ploidy), although quite different, are more similar than their karyotypes would suggest. Many of the genes have a homologous *counterpart,* but the blocks of linked corn genes are spread over many *Tripsacum* chromosomes. Clearly, *Zea* and *Tripsacum* diverged early, probably in midsouthern western Mexico and long before the domestication of corn. Recently, an alternative view is that *Tripsacum* hybridized with teosinte and that this led to a soft glume, nonbrittle rachis that was quickly domesticated as maize (Eubanks, 2001a,b,c). The Eubanks cross changes everything. Was it this wide cross that kick-started the domestication of maize? The quick answer is "no," but in truth we don't know, so perhaps the thoughtful answer is "yes." Clearly, we need to do more research with this hypothesis in mind. To my mind the hottest experiments in corn evolution now are to cross *Tripsacum* taxa from Chiapas and Huehuetenango with section Luxuriantes teosintes, *Z. luxurians* and *dipolperennis,* and to recover backcross progeny to the *Zea* parents. *Tripsacum* might be the jump start that created the unstable genome (Lynch, 2002) that led to present-day corn under human selection. *T. andersonii,* with 10 teosinte chromosomes, is the other side of this evolutionary hybridization and an overlooked element in our understanding of how corn came about.

The *Tripsacum* spp. of northwestern Mexico are distinct from those of South America. Like some of the landraces of corn from the same region, the *Tripsacum* spp. of Chiapas and Guatemala, bear more than a limited relationship to their counterparts in South America. *Tripsacum* probably went to South America over the land bridge of Central America. Much later (postdomestication), corn did the same. The widespread presence in Mexico at the time of the Conquest of the South American crops—peanut, pineapple, cocoa, tomato, and non-Mexican chillies and squash—indicate effective exchange between the two regions. There is no evidence that annual teosinte ever invaded South America, although the most *Tripsacum*-like ("primitive") of the teosintes is found in southern Guatemala, Honduras (now extinct), and Nicaragua (Iltis and Benz, 2000). This annual teosinte (weakly perennial) has two growth forms: one along streams and water-saturated soils, and another in drier upland sites, such as along stone walls bordering cultivated fields or roads. The recently described new taxa from Nicaragua, *Zea nicaraguensis* (Iltis & Benz), appears to me to be the "wet

soil" form of *Z. luxurians*. I've withheld it from the teosinte table until there is more information. It is most certainly teosinte and does extend the geographic range farther into Central America.

Z. luxurians, in the older literature called Florida teosinte, is the most distinct of all the teosinte taxa, with its trapezoidal fruit case and complete absence of a central spike in the tassel. This is the only diploid teosinte that exhibits limited sterility in crosses with corn and the only annual teosinte that has been hybridized with *Tripsacum* successfully in the trigeneric crosses of Mangelsdorf and Reeves (1939). Its chromosomes are characterized by terminal knobs, not internal knobs, and therefore the similarities to those of *Tripsacum*. It should be separated from the rest of the seed-reproducing annual teosintes, and I made a judgment I now regret in not making it a separate species in 1967. For the next decade, Hugh Iltis urged me to make the formal taxonomic change before it was done for me (Bird, 1978). Unfortunately, the conservation status of the wild populations in Guatemala is now very much in danger of leading to extinction within the next decade. Only in two localities (one wet and one dry) are large panmitric populations (nonbottleneck) to be found. The population localities are now about 10% of what they were in 1963. Fewer milpa cornfields and more cattle grazing have changed the land vegetation pattern. *Tripsacum* also is less abundant in the oak woodland vegetation that remains in the departments of Juitapa, Jalapa, and Chiquimula.

The other most significant teosinte, the diploid perennial of Jalisco, Mexico, *Zea diploperennis* (Kato and Sánchez, 2002) has the protection of a bioreserve: the Sierra de Manatlán (Benz, 1988). I feel it is our last opportunity to do something to protect *Z. luxurians* in the departments of Jutiapa and Jalapa in Guatemala. A set-aside would be difficult for small landowners, but there are wealthy landowners with vast holdings and lots of barbed wire for which a conservation arrangement would be no hardship. The only thing lacking is bold and creative leadership on the issue (Oldfield and Alcorn, 1987).

Consilience: What Has to Happen

The grass family has a floral pattern of protective outer glumes and paired spikelets, each with two florets which has been long recognized (Hooker, 1878; Hackel, 1890; Arber, 1934; Bonnett, 1948, Kiesselbach, 1949; Hitchcock, 1950). Those differences in floral pattern that do develop are from units in the pattern that fail to develop. Scanning electron micrographs (SEMs) show beautifully the ennation of these structures and arrested development (Sundberg and Orr, 1986, 1990, 1996; Le Roux and Kellogg, 1999; Orr et al., 2001, 2002). Examples of this suppression are the even row number in corn, where grain is borne by paired spikelets with a single floret. The ancestral pattern was paired spikelets, each with two functional florets, as in the sweet corn Country Gentleman, which has such crowding that there are no visible rows. Since then there has been a progressive suppression of parts in the pistillate flower, with the lower floret of the spikelet tending to disappear or to be represented only by its lemma and palea in advance of the disappearance of the pedicellate member of the spikelet pair, as in teosinte and *Tripsacum*, with a single sessile spikelet with one floret enclosed in rachis tissue. Corn has paired pedicellate spikelets free of enclosing rachis tissue represented by the cupule, which now functions only in mechanical support. In the

staminate inflorescence of corn, teosinte, and *Tripsacum,* the pattern is ancestral; there are two florets in each spikelet (except in those *Tripsacum* spp. where the pedicellate spikelet is suppressed). In an evolutionary sense, both teosinte and *Tripsacum* are more specialized than corn in their fruit case–enclosed female flowers.

Basically, the framework to an understanding of the origin of corn was worked out 100 years ago. It was Kellerman (1895) who first pointed out the homology of the tassel central spike to the corn ear. She also clearly stated the origin of the ear system by a condensation of the internodes, resulting in the shortening of the lateral branches until the terminal ear was enclosed in protective leaves or husks. Kellerman made no mention of teosinte. Unaware of Kellerman's paper, Montgomery (1906) offered the same explanation for the origin of the corn ear but extended the theory to include teosinte by suggesting that corn and teosinte may have a common origin, and that in the process of evolution the cluster (fascicle) of pistillate spikes in teosinte were homologous to the lateral branches of a tassel-like female structure, while the corn ear developed from a female central spikelike structure. Thus the polystichous maize ear is the female counterpart form of the male polystichous central spike in the tassel, and the distichous spike of teosinte is the female counterpart of the distichous lateral branches of the male tassel. If a source were found for the hard indurated tissue enclosing the teosinte seed, the third distinguishing morphology will be accounted for to distinguish corn from teosinte. *Tripsacum* also has hard indurated rachis tissue enclosing the single seed and might be the source of the indurated fruit case. The indurated spathe enclosing the female spikelet of *Coix,* native to the Orient, is the next-closest counterpart.

The consensus on teosinte's role in the origin of corn can be seen in the three distinct hypotheses proposed to explain the same structure, the maize ear. Ascherson (1880) suggested the origin of corn from teosinte by fusion or nondivergence of teosinte spikes. This has been transposed to the pistillate inflorescence of two ranked lateral tassel branches (Beadle, 1980; Iltis, 1983; Doebley, 1990; Galinat, 1995). Harshberger (1899) proposed hybridization of two distinct forms of teosinte to form primitive corn, as has Galinat (2001). Mangelsdorf (1986) proposed that teosinte and half-tunicate (pod) wild corn hybridized, Eubanks (2001a,b,c) proposed that teosinte and *Tripsacum* hybridized and Randolph (1976), and Kato (1984) envisioned separate polyphyletic origins. Finally, Montgomery (1906) saw a common ancestor for maize and teosinte, but a separate evolutionary development along independent lines (Weatherwax, 1918, 1935, 1954, 1955; Arber, 1934; Randolph, 1976), more recently, others (Doebley, 1990; Iltis, 2000; Galinat, 2001) have favored teosinte as the wild ancestor, being transformed to maize by domestication.

The American Maydeae (now included in Andropogoneae), Weatherwax (1918) concluded, originated from a remote common ancestor, and the suppression of parts accounted for the differences of structure in the three. The theoretical progenitor was a herbaceous, rhizomatous perennial, with jointed leafy stems, bearing branches at practically every node (this is *Z. diploperennis,* not discovered until 1979), and having a loose panicle with perfect flowers—both male and female in a central spike. The brittle rachis, which distinguishes teosinte and *Tripsacum* from maize, came with the hardening of the outer glume of the spikelet and the walls of the cupule in which the spikelet is embedded. The disarticulation of teosinte is across a flat surface, while in *Tripsacum* this is a quite distinct stacking ball-and-socket arrangement between fruit cases (Galinat, 1970). These are evolutionarily more advanced traits than those

expressed in Mangelsdorf's hypothetical wild corn. In both 1935 and in 1954, Weatherwax continued to view the independent evolution of the three as stemming from a remote common ancestor, and Randolph (1976) continued to have very similar views. I find an exhaustive, detail-by-detail review of the differences between corn and teosinte (Randolph, 1976) to be very helpful because today, the arguments have become sound bites and too simplistic (Bennetzen et al., 2001), and the detailed architecture and life form of teosinte are not understood.

The sheer amount of information relevant to the origin of corn is overwhelming, and there has been a tendency to simplify this information in order to communicate with those not familiar with the twists and turns of discoveries, speculation, and constructs of generally recognized facts and opinions. A case in point is the well-developed isozymic and chloroplast DNA evidence that teosinte from the central Balsas region near Teloloapan, *Z. mays* subsp. *parviglumis* (Figure 1.1.10), indicates close affinity to corn in cluster analysis based on isozymes. This is quite interesting because central Balsas is the largest extant panmitric teosinte population and least

FIGURE 1.1.10.   Teosinte at 55 km, 850 m MSL, on Road 51, Teloloapan–Iguala Guerrero. Teosinte is an excellent colonizer of steep slopes and abandoned milpas. This is exactly the habitat from which the Balsas teosinte has come that molecular markers indicate is identical with corn. This is the most wild of all the teosintes and is thought by Doebley to be the ancestor of corn.

likely to have undergone an evolutionary bottleneck and is the most wildlike of all the teosintes. The evidence from 13 enzyme systems encoded by 21 loci indicates that isozymically, central Balsas teosinte is the most cornlike. That is evidence. The sound bite is that "*Z. mays* subsp. *parviglumis*" is the ancestor of corn (Bennetzen et al., 2001). Another way I could express this simplification is in the genes that separate corn and teosinte. In 1920, Collins and Kempton studied the mode of inheritance of 33 characters that differentiate corn and teosinte. They found only two (daylength and single vs. paired spikelets) that approximated the 3 : 1 ratio of single-gene inheitance. In 1947, Mangelsdorf found single vs. paired spikelets and distichous vs. polystichous ear to be controlled by genes on five different chromosomes. Add disarticulating rachis of teosinte on three different chromosomes and three traits and eight chromosomes are involved. In 1971, Galinat listed five essential traits: induration of the outer glume, development of the rachis abscission layer, single vs. paired pistillate spikelets, two-ranked vs. four-ranked ears, and sessile vs. pedicellate pistillate spikets. In 1974, Mangelsdorf reduced this list to four traits based on his studies and those of Galinat. Now I recognize that Galinat has been the master at *breeding dissections,* where lines are bred to use as parents to eliminate the "background noise" of polygenetic inheritance. The splendor and intelligence of his work, as shown in the compound tunicate gene (Mangelsdorf and Galinat, 1964) or the breeding backward synthesis of teosinte, has not been widely appreciated because there has been less concern for the quality of the evidence and more interest in the answer for the "origin of maize." In part, this is a statement about the impatience of our times and the sheer volume of the literature on the origin of corn that has been generated since I reviewed it last in 1967.

The challenge is to appreciate the wide variation and genetic integrity found in the Americas of 300 landraces of corn (Taba, 1997a), an "open" genetic system that tolerates wide crosses with wild relatives, and an encyclopedic detailed knowledge of the structural changes that distance corn from its relatives. The controversy develops because at present there is not enough archaeological evidence to document the origin of corn under domestication. Evolutionary genetic pathways (Galinat, 2001) and evolutionary taxonomic constructs (Iltis, 2000) require archaeological evidence to remove them from controversy. To say that "maize is a domesticated form of teosinte . . . is now broadly accepted among biologists familiar with the issues and data" (Bennetzen et al., 2001) isn't enough. Archaeological remains are unambiguous data, and unfortunately, we don't have enough sites and profiles to remove the controversy from what 16th/c Sir Francis Bacon called "wishful science." Bacon (Bacon, 1901) pointed out that good evidence is rooted in reality and develops over time, whereas wishful science is political and promoted by those with the "loudest whistle." The origin of corn under domestication is a complicated story at best and deserves more than a "reduced answer" to the exclusion of contrary evidence and a fragmenting mentality of cutting off debate by those who consider that the answer is already "established fact." Ideas emerge in surprising and unpredictable forms. Knowledge of the data is one aspect; to continue to have ideas yet keep a sense of doubt is to have wisdom, hopefully with openness to new discoveries and changing ideas. There have been over 50 papers in the last 100 years (Venkateswarlu, 1962; Mangelsdorf, 1983; Wilkes, 1986; Goodman, 1988), with a title of ancestry and/or origin and/or evolution of corn, and every last one of them is flawed in some aspect. Good science is rooted in reality, and reality for the wild corn has been a moving target. Any origin model presents imprecise, outmoded concepts that actually may limit our understanding of the exact

origin for corn if the origin model is taken too seriously. The trouble with origin models is their static nature when they are used more like a noun than like a verb.

HISTORICAL REVIEW OF THEORIES FOR THE ORIGIN OF CORN

The individual theories for the origin of corn run the gauntlet from a simple selection from teosinte (corn is domesticated teosinte) to complex, and in some cases bizarre, theories of hybrid origin between now extinct grasses (bizarre in the sense that they are basically untestable and take us nowhere in advancing of our knowledge but do offer psychic satisfaction because they somehow legitimize corn). These individual theories belong to one of three evolutionary patterns. The first pattern is direct evolution by domestication from a wild ancestor (teosinte, wild corn, or a third-party wild grass). In this theory the domesticated food plant is created through artificial selection by humans. The second pattern is a hybrid origin from two dissimilar parents which creates a plant that is essentially preadapted for domestication, and humans finish the process. The third has elements of both patterns: origin from a wild ancestor with repeated hybridization with other taxa in its polyphyletic origin or with its closest wild relative, teosinte, or a combination of wild corn, multiple origins, and teosinte or *Tripsacum* in any order.

Direct Evolution from Teosinte or Wild Corn

Teosinte has remained, since proposed as such by Ascherson (1875), the closest known relative of corn, but just what role teosinte has been suspected of playing in the origin has varied with the interpretation of the evidence. One fact has appeared repeatedly: Any theory on the origin of corn must also account for teosinte (Smith et al., 1981, 1982, 1984, 1985; Smith 1988).

Most theories on the origin of corn that are not based on the fertility of corn and teosinte begin by attempting to account for the wealth of variation in corn landraces, phenotypic plasticity, intolerance to inbreeding, geographic distribution of primitive landraces, isozyme patterns, genomics, chromosome knob patterns, or the origin of its most anomalous structure, the ear. The pistillate flower and subsequence fruit (caryopsis) on a polystichous structure, the ear, have been the part of the corn plant most changed by domestication; therefore, to account for the ear is to explain in part the origin of maize. Recognizing the close relationship of teosinte and corn, Ashcherson (1880) suggested the origin of corn from teosinte by the fusion of teosinte spikes. Subsequent studies have found no evidence of fusion in the corncob or rachis tissue. The ear is recognized generally as the counterpart of the central spike in the tassel, as suggested by Kellerman (1895), who pointed out the homology of these two floral structures. Montgomery (1906) extended these observations to the relatives of corn and indicated that corn and teosinte may have a common origin. In teosinte, the ears had developed from the homolog of lateral branches of the tassel and in corn from the central spike. In corn there is a single massive polystichous ear, and in teosinte there are distichous spikes borne in fascicles. The two plants have diverged along these parallel but distinctive evolutionary potentials from an Androponeae pattern. Somewhat similar views of a common ancestor but separate evolutionary

development have been held by Weatherwax (1918, 1954) of a perennial ancestor for corn and by Randolph (1955), of an annual ancestor.

The most complete enunciation of the tassel to teosinte spike to the polystichous ear of corn are the papers of Hugh Iltis. His sequence of papers: "The Maize Mystique: A Reappraisal of the Origin of Corn" (orthodox teosinte hypothesis, 1971); to: "From Teosinte to Maize: The Catastrophic Sexual Transmutation" (catastrophic sexual transmutation theory, 1983); to: "Homeotic Sexual Translocation and the Origin of Maize (*Zea mays*, Poaceae): A New Look at an Old Problem" (sexual translocation theory, 2000); creates a time line for a theoretical study of the changes that had to happen to transform teosinte to corn under domestication. The origin of the corn ear is based on the branching pattern of teosinte ear clusters (Cámara-Hernández and Gambino, 1990), sequentially maturing, sympodially branching, where each higher-order (younger) ear originates as a lateral branch of its lower-order, earlier-maturing predecessor, and secondarily on three or four key mutations that require human selection to fix [(cupule reduction, softening of the glumes, doubling of the female spikelets so that they are paired (which is a reverse mutation because the Andropogonoid ancestor was paired spikelets), and the outward projection of the grains [the horizontal rachilla of Galinat (2001)]. The outward projection of kernels was a favored mutation by humans because it made the grain accessible. Iltis (2000) has suggested that up until domestication, teosinte's most interesting attribute for humans was a sugary pith. This may seem farfetched, but is it? Singleton, working with Lancaster C-103, a high-sugar line, had made a similar observation. Ten percent of the calories for humans worldwide are refined sugars! Within each ear cluster, the earliest-maturing, hence nutrient-grabbing spike inhibited or suppressed all others. As fewer and larger ears evolved, and branch internode condensation moved male tassels into female hormonal zones, homeotic conversions translocated female morphology to terminal male positions: first replacing each of the secondary branch tassels, and ultimately, the primary branch tassel (male), with an ear (female). Now with the female structure in the apically dominant, hence most nutrient-demanding terminal position, gradually suppressing all subsidiary ears on the primary branch beneath it, mutations for polystichy (contingent on nutrient overload) were finally allowed to become expressed, and the multirowed maize ear evolved at first with an atauistic tail. [This may be seen in maize ears with a tassel tip on Oaxacan funerary urns (Eubanks, 1999). *Atauistic* means the reappearance of a characteristic after several generations of absence, usually caused by the chance recombination of genes (Figure 1.1.11).]

Hybrid Origin of Plant Preadapted for Domestication

The paragraph above represents very closely the abstract from Iltis (2000). It actually makes sense and describes rather well the condition in robust Chalco teosinte plants, where nutrient overload does favor the lead spike, especially the pistillate structure of plants with corn genes such as second or third backcrosses to teosinte. These plants have paired spikelets in a polystichous terminal structure and single spikelets in the lower distichous pistillate structures. These nutrient-overloaded "Chalco ears" cannot be used to explain the origin of corn because the only way to create them is to hybridize with corn and make the lead ear the homolog of the central tassel spike. What Hugh has shown through diagrams and drawings are essentially the steps necessary
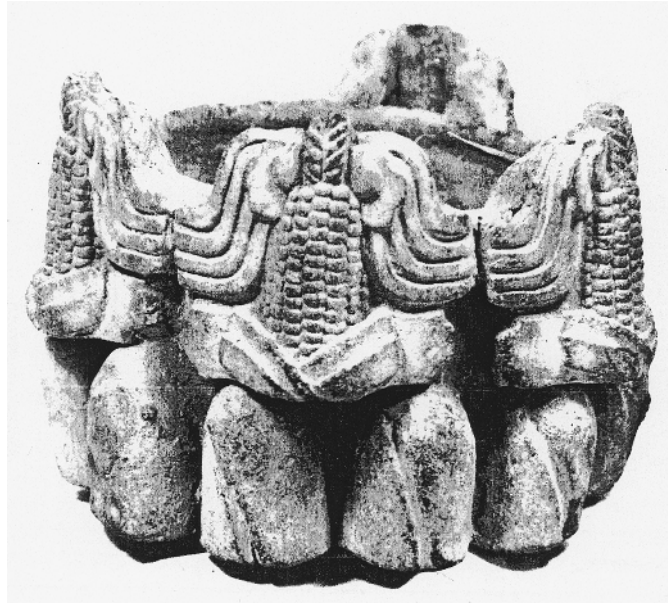
FIGURE 1.1.11.   Urn from Monté Albán, Oaxaca, with tassel-tipped maize, race Nal Tel/Pira. Collection of the Tulane University Middle America Research Institute. Pottery with a tassel tip is very common in the Oaxaca region, and I found a tassel-tipped Nal Tel potsherd on the ground at Mitla, Oaxaca while searching for teosinte in 1963. The widespread symbolism of the tassel tip in pottery from Oaxaca just might reflect a regional memory of primitive maize forms.

to transform teosinte into corn. Some of the details might have been different, but most students of corn will agree that the pattern is close to what actually happened. The real issue is: Was this artificial selection under human influence (domestication), or was it under natural selection by the influence of speciation forces that operate in natural systems. If humans created maize out of teosinte, then clearly, teosinte is the ancestor. If humans found a polystichous ear with distichous laterals farther down the shank, most of these changes occurred before domestication. If domestication starts with polystichous (eight rows) and soft glumes, the ancestor is the closest relative of teosinte, corn. The key issue is the point of domestication, and this can only be resolved in the archaeological record. Both Iltis (2000) and Galinat (2001) have told us exactly what to look for in terms of morphological changes found in the ear. Fortunately, cobs are found in relatively good preservation at archaeological sites and hold sufficiently complex morphology to tell us a lot about the domestication process.

The second most controversial element in any theory of the origin of corn is the fertility and ease of crossing corn and teosinte. For Beadle (1939, 1972) the fact that the two were so easily hybridized and show comparable linkage data was sufficient proof alone. For Galinat (1971, 1985), de Wet et al. (1971), Harlan and Grant (1971), and Iltis (1972), crossability was important and meant that teosinte was cospecific with corn, but on morphological grounds they considered teosinte clearly ancestral.

For them, the structures that differentiate the two (polystichous vs. distichous ear, paired vs. solitary spikelets, naked vs. covered grain) had taken place under domestication. Mangelsdorf and Reeves (1939) recognized the crossability of teosinte and corn but were able to eliminate teosinte as the ancestor by making it the product of maize × *Tripsacum* hybridization, a theory that Mangelsdorf abandoned in the early 1960s, and in his 1974 book, thought of teosinte as a mutant form of corn. Contrary to the "teosinte ancestor theory," corn was for Mangelsdorf (1974) the ancestor not only of cultivated corn but also of teosinte. With the discovery of *Z. diploperrennis* in 1979, he immediately took to the idea (which he called the *Wilkes hypothesis*) that corn crossed with the diploid perennial teosinte to produce the annual teosintes of Mexico to Central America (Mangelsdorf, 1986).

The complete text of his view of wild maize follows: "I now propose that serious consideration be given to the hypothesis that the remote ancestor of maize was an Andropogonaceous plant quite similar in its principal characteristics to our genetically reconstructed ancestral form of pod–popcorn except that it was perfect flowered. The change from the perfect flowered to the monoecious condition is not difficult to visualize. It has occurred in many genera of grasses. It was probably after maize had become monoecious that there occurred a series of mutations—from polystichous spike to a distichous one, from paired spikelets to solitary ones, from herbaceous glumes to indurated ones—all of which are in the direction of evolutionary specialization—that combine to differentiate teosinte from maize" (Mangelsdorf, 1974). Weatherwax (1918, 1954), with his common ancestor, would have added perennial with rhizomes to seed-producing annual as a necessary evolutionary change.

"Once maize and teosinte had diverged they remained spatially isolated until the domestication of maize and the subsequent spread of its culture brought them into sympatric relations and hybridization, accompanied by a flow of genes in both directions, became common" (Mangelsdorf, 1974). These two explanations: teosinte the ancestor and wild corn the ancestor, are both type 1 origins but diagrammatically opposed; yet the evolutionary events and morphological changes that would have taken place are identical. Galinat has emphasized disruptive selection; Beadle, selection under human guidance; Iltis, the taxonomic/evolutionary imperative; and Mangelsdorf, temporal and spatial isolation as the mechanisms that preserved the separate evolutionary histories of these two genetically compatible grasses.

Combination of Hybridization and Polyphyletic Origin

The hybrid origin hypotheses either accounts for teosinte as one of the parents in the hybrid origin of corn or that it itself is the product of a hybridization process. Having already suggested that corn originated from teosinte by human selection, Harshberger (1896) proposed the hypothesis that corn originated from the hybridization of teosinte and an "extirpated closely related grass to form a four-rowed ear." This extirpated closely related grass was very similar to a corn × teosinte hybrid (Figure 1.1.12). Four years later, Harshberger (1900) combined both hypotheses into a single hypothesis. This origin started with a partially ameliorated, four-rowed, paired-spikelets progenitor of maize, but still a species of teosinte that was selected out of teosinte. This ameliorated progenitor then crossed with wild teosinte to produce present-day Indian corn. He was just vague enough 100 years ago to meet
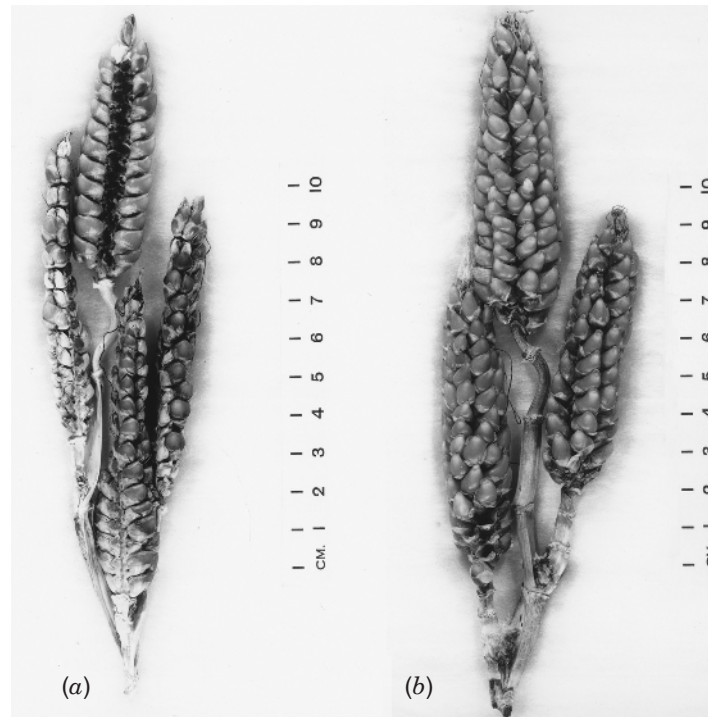
FIGURE 1.1.12.   F$_1$ corn × teosinte hybrids: (*a*) two-ranked, four-rowed condition typically found; (*b*) polistichous specimen that has a teosinte parent which is the backcross to teosinte ($\frac{1}{4}$ corn) following hybridization with corn. In the F$_1$ using "pure teosinte," the teosintoid distichous condition is expressed; when mazoid teosinte is used, the polistichous condition is expressed. Note how rows are dropped in the polistichus (*b*) and how the ear tapers in (*a*).

most of the criteria held essential to those that see teosinte as the progenitor of corn today.

Aware that corn × teosinte hybrids were to be found in Mexico, Collins (1912) advanced the concept that corn originated as a hybrid between teosinte and an unknown grass belonging to the tribe Andropogoneae. In 1918, he added supporting evidence to his previous theory that corn is of hybrid origin. First, corn is intolerant of inbreeding, a characteristic of hybrids, and is dependent on cross-fertilization for normal and vigorous development. He claimed that teosinte showed no such intolerance to inbreeding, but no evidence was presented. Second, the characters that separate corn from teosinte do not always show Mendelian ratios following hybridization, making the hypothesis that corn originated by mutation from teosinte highly improbable. Supporting the hybrid origin hypothesis, Collins (1918) further defined this Andropogonoid unknown grass as having naked or nearly naked edible seed borne on a rigid rachis. Collins's (1921) dilemma was founded on two assumptions: (1) that the prototype of corn was a relative or ancestor of teosinte, and (2) that the prototype of corn should be sought in a grass possessing the seed protection and soft glumes of a pod or tunicate corn. The dilemma is that only corn bridges the gap between the specialized floral divergence of teosinte and the perfect flowered Andropogoneae

unknown hypothetical grass. Collins concluded that a hybrid origin accounted best for the natural variability of maize and the "pronounced evidence of teosinte blood" in the corn of Mexico and Central America.

In her book on the origin of cultivated plants, Schiemann (1932) included a review of the literature on maize and drew very heavily from the papers of Collins in forming her interpretation for the origin of corn. She was an expert on European small grains, but the only cornfield she had ever seen was in Egypt on holiday. She was far more bold in print than Collins ever was by proposing a pedigree chart in which a perennial form of teosinte crossed with a sorghum species (Andropogoneae) to form the ancestor (*Z. antigua*) of corn. Perennial teosinte gave rise to annual teosinte (*Z. mexicana*), which in turn hybridized with *Z. antigua* to form present-day pop–podcorns. The popcorns then crossed with an ancient flour corn to produce the flint types, which in turn hybridized with modern flour types to produce the youngest and most productive type of corn dent. This proposed pedigree, although speculative, is significant because it was the most elaborate of the hybrid origin proposals and the first attempt to express diagrammatically levels of teosinte introgression into maize. This idea was fully exploited by pedigree charts in some of the "Races of Maize" bulletins two decades later.

In 1930, Collins reviewed the theories of domestication of corn and indicated where each fell short on evidence. The origin by gross mutation and human selection he objected to because crosses of corn × teosinte yielded a blended inheritance of polygenetic control and not the Mendelian units of mutation. Direct selection from teosinte he regarded as improbable since teosinte, with its hard fruit case, was a highly unpromising material from which to develop a food plant. Beadle (1939) has since shown that when heated, teosinte grains pop in much the same manner as the common popcorns and suggested that teosinte was once popped free of the enclosed fruit case, or better yet, popped as tassel seed where the glumes are not as protective. Subsequently, Beadle (1972) also has ground teosinte, fruit case and seed, to make small tortillas, and Flannery and Winter (Beadle, 1972) have shown that in about an hour of seed collecting in a naturally occurring wild stand at Mazatlán, Guerrero, teosinte could supply enough calories and protein to meet the daily needs of humans. Even with its small seed size, teosinte could have met the nutritional/labor-expended requirements of a hunting–gathering people.

The last theory of origin to be considered by Collins (1930) was the concept of independent evolution with the American Maydeae, now subtribe Tripsacinae of the Andropogoneae. Weatherwax (1918) proposed that corn, teosinte, and *Tripsacum* spp. had evolved as separate evolutionary lines from a common perfect-flowered perennial ancestor, and that suppression of floral parts accounted for the differences in the three. Weatherwax (1954) did not waiver from this view. Collins found the theory lacking by not accounting for the interfertility between corn and teosinte [George Beadle (personal communication) was obsessed by this fact while riding around Mexico for two weeks in 1969 as we visited teosinte populations], and therefore Collins (1930) favored his own theory for the origin of corn. Thus, the exact origin of corn remained to be discovered (Kempton, 1937), but one fact had become forcibly clear: "The many resemblances between corn and teosinte together with the fact that the two forms interbreed with perfect freedom make it certain that whatever the origin of corn, it must be intimately associated with teosinte or some near relative of that plant" (Collins, 1919).

The next major theory for the origin of corn accounted for teosinte by eliminating it as a possible ancestor. Following the hybridization of corn and *Tripsacum*, and then the trigeneric hybrid of (corn × *Tripsacum*) × teosinte, Mangelsdorf and Reeves (1939) concluded that "teosinte, far from being the progenitor of maize, is instead its progeny, or to be exact, the progeny of a hybrid between maize and *Tripsacum*. This conclusion obviously did not explain the origin of maize itself, but with teosinte eliminated (in our minds) as the ancestor of cultivated corn we were free to consider other possibilities explaining corn's origin, and the ideas that pop corn might have been the ancestral form appealed to us" (Mangelsdorf, 1974).

That wild corn was a pop–podcorn was the second postulate of the tripartite hypothesis of Mangelsdorf and Reeves (1939, 1959a,b). The third element was that modern corn is the product of introgression of primitive corn with teosinte and/or *Tripsacum*. This tripartite hypothesis [Mangelsdorf was always careful to call it a hypothesis rather than a theory (personal communication to us graduate students in the Botanical Museum 1960–1966) because it was an idea in search of evidence, whereas a theory already had a lot of facts to support it] was the basis of 25 years of research which was read widely by those interested in the origin of corn. In recent years it has been demonstrated that teosinte is not a hybrid of corn and *Tripsacum,* and there are questions now about the effectiveness of introgression following corn × teosinte hybridization from chromosome knob studies (McClintock et al., 1978; McClintock et al., 1981; Kato-Yamakake, 1984). The middle hypothesis is wrapped in controversy over the question of whether the ancestor was wild corn or ancestral teosinte, yet there appears to be more disagreement over what the ancestor is called than on the traits it possesses. The tripartite hypothesis is essentially historical at this time in corn studies.

Now that the hybrid origin of teosinte has been laid to rest, the most favored alternative is a revived interest in teosinte as the ancestral form (de Wet et al., 1971; Beadle, 1978; Doebley, 1990; Benz, 1999; Galinat, 2001; Iltis, 2001). The teosinte as ancestor theory has been the dominant view of the last 20 years. The only researchers declining to join have been Goodman (1965, 1976, 1988), Wilkes and Goodman (1995), and Eubanks (1995, 1997, 2001a,b,c). The latter has proposed the fresh idea of teosinte × *Tripsacum* hybridization and Galinat (2001) has seen merit in the work, but Doebley has not. The only other person to consider *Tripsacum* in the origin was Cutler (1954), and the only mention of it in the literature is Randolph (1976).

Forty Years of Controversy

It has been my privilege to be a part of this debate and watch firsthand since the 1960s. From the 1940s through the mid-1960s, the Botanical Museum of Harvard University was a center of graduate training in corn (E. Hernández-Xolocotzi, W. Hatheway, S. Sehgal, R. Tantravahi, R. Changti, A. Grobman, and myself) with P. C. Mangelsdorf and his research associate W. C. Galinat (Galinat, 1959, 1967, 1970, 1971, 1973, 1975, 1985, 1988, 1995). In the mid-1960s through the mid-1970s the center of graduate training moved to the University of Illinois (R. Gray, G. Price, and C. Dewald) with Professors Jack Harlan and Jan de Wet. Then the center shifted to University of Wisconsin (J. Doebley and B. Benz) with Professor Hugh Iltis, and North Carolina State (P. Bretting, R. Bird, J. Doebley, J. Sánchez, and J. S. C. Smith) with Professor Major

Goodman. The most famous group of maize graduate students was those of R. R. Emerson at Cornell (G. Beadle, B. McClintock, L. Randolph, G. Sprague, C. Burnham, and M. Rhoades) in the 1920s and 1930s. The rival group was at the Bussey Institution of Harvard (E. Anderson and P. C. Mangelsdorf) with Professor East. Part of the enticement of corn studies is all the truly good work that has been done and yet we still don't have the final answer.

The last part of this review I am doing as a personal narrative if there are events in which I was personally involved. In 1957, I took a course at Rancho Santa Ana Botanical Garden on the origin of crop plants with Lee Lenz, who had been a student of Edgar Anderson, and Anderson and Mangelsdorf had been roommates at the Bussey Institution studying under Professor East. Over Thanksgiving break during my junior year, I read *The Origin of Indian Corn and Its Relatives* (Mangelsdorf and Reeves, 1939) and thought: Why do we know so little about the natural distribution of teosinte? Then I read Randolph (1955): "In connection with this problem there have been too much speculation and too little field study of teosinte, *Tripsacum,* and corn in areas where all three species are sympatric." That did it! In 1967, my 1966 thesis on teosinte was published as a monograph, and in the fall of 1967 Beadle wrote to me asking why I had referred to his 1939 paper on teosinte as the ancestor of corn paper with the sentence: "The theories that teosinte is the primitive ancestor of maize, although they cannot be dismissed entirely, are on the whole crude attempts to explain the origin of maize." That did it for him! And after a hiatus of almost 40 years, George got back into corn research following his retirement as president of the University of Chicago. He had been actively involved in field studies of teosinte in Mexico for a decade, and he and Walt Galinat have probably scored more corn teosinte hybrids and their segregates than anyone I know. His renewed investigations started the renaissance of teosinte as the ancestor of corn (Doebley, 2001; Galinat, 2001).

Well, the Beadle (1939) paper was weak on evidence except for the crossibility of teosinte × corn and the fertility of the hybrids. But corn is unusual for a plant with so many races and such a widely separated distribution in the fact that it essentially has no alterations of the chromosomes, such as translocations and/or inversions, and no sterility. The biggest barrier is the short arm of chromosome 9, which shows no linkage data in teosinte × corn hybrids. Why is maize so openly fertile? Probably because of farmer selection for full ears. Corn is one of the few plants where the farmer can observe nonfunctioning ovules. Why is the short arm of teosinte chromosome 9 non-homologous with corn? Quite possibly because that is where the rachid disarticulating genes are located. The ability to disperse seed characterizes teosinte as a wild plant. Its husk cover actually gets in the way of this function. In *Tripsacum* the rachis segments are free to fall and they are not preyed upon because of their protective indurated rachis tissue and enclosing lower glume. Teosinte has the same protection, so why the multiple husk? Only when the plant is down on the ground and trampelled is the last of the teosinte seed freed of the husk. One of the signal traits between wild and cultivated in the grasses is nonbrittle rachis. This has not been resolved in *Zea* because teosinte is brittle and polystichous maize nonbrittle. This is a perfect trait for quantitative trait locus mapping. Mary Eubanks (1995, 2001a,b,c), in the progeny of the cross *Z. diploperennis* (brittle rachis) × *Tripsacum dactyloides* (brittle rachis), recovered a nonbrittle hybrid that was both polystichous and nonbrittle. Why haven't a half dozen of us repeated these crosses? I remember that everyone thought that Barbara McClintock had lost her marbles with the jumping genes and P. C. Mangelsdorf

grew out her seed and repeated the crosses, and I remember him walking out of the field in late August after taking a sneak look under the ear pollination bags saying: "Damn it, she is right, but how did she figure it out?" In September 1964, he and Marcus Rhoades knew she was right because they had repeated the experiments. Albert Longley (1924, 1937, 1941a,b, 1952) repeated all the teosinte pachytene smears and *Tripsacum* chromosomes counts of Reeves. He taught me how to prepare pachytene slides at Chapingo, Mexico in 1962 after I'd spent the day at Chalco counting corn × teosintes hybrids per 1000 plants in the field, and at the same time he told me stories about Collins and corn research in the 1930s.

Fritz Randolph thought the corn × *Tripsacum* hybrid (Mangelsdorf and Reeves, 1931) was a milestone in corn studies, but he didn't buy the idea that "trisacoid genes" came from *Tripsacum*. "An alternative interpretation is much less involved; namely that parallel mutation accounts for the occurrence of similar characteristics in corn, teosinte and *Tripsacum*." Obviously, these species must have many genes in common or they could not be hybridized. The concept of identical mutations occurring at the same loci in these species offers an entirely adequate and much simpler explanation of their phenotypical similarities than does that of the transfer through numerous hybrid generations of specific character from one species to another under natural conditions" (Randolph, 1955). To test Mangelsdorf's hypothesis of corn × *Tripsacum* hybridization in Guatemala and Mexico under natural conditions, Randolph tested over 100,000 maize ovules with *Tripsacum* pollen from seven taxa from 1946 to 1949 and obtained only two hybrids, both of which were still vegetative after four years. Randolph concluded that the crossability test with corn and *Tripsacum* did not support the Mangelsdorf and Reeves (1939) hypothesis for the hybrid origin of teosinte (Randolph 1955, 1959, 1976). Reeves came after him: "Randolph's experiments are not a critical test of any hypothesis and, in fact, are essentially meaningless." To which Randolph replied: "Perhaps the lack of appreciation of what constitutes a meaningful test explains the failure of the originators to undertake the experimental verification of the central feature of their tripartite hypothesis during the interval since it was proposed 15 years ago" (Randolph, 1955). The Mangelsdorf exchanges with E. Anderson in the 1940s, with P. Weatherwax in the 1950s, and G. Beadle in the 1970s make for high theater (Mangelsdorf and Reeves 1959a,b; Mangelsdorf 1973).

Mangelsdorf was read widely, especially by nonspecialists in corn, because he was clear. There were never more than three points—the tripartite hypothesis. Mangelsdorf wrote like a lawyer, and in rebutting a critique of his work he never took on the evidence but showed flaws in the logic of his critic (Mangelsdorf vs. Weatherwax dialogues) (Mangelsdorf and Reeves 1959a,b). If the logic is flawed, this somehow cast suspicion on the evidence. Finally, Mangelsdorf used really good illustrations, and his mentor E. M. East once told him (1920) that he liked to photograph endosperm mutants more than to be in the cornfield (he told the story about himself at a 4 o'clock popcorn and tea get-together with graduate students).

The tripartite hypothesis became monolithic because it was a 1, 2, 3 sequence and because the unfolding archaeological record (bat cave and Tehuacan) were a match for his progenitor but were equally a match for Weatherwax and Randolph. They were half-tunicate pod corn, small, and because they were small, they were presumed to be popcorn (although no seeds were found attached); probably Chapalote, and therefore a lot of the postulates in "Races of Maize" in Mexico published in 1952 were confirmed [see Benz (1994) for a critical review]. To the end, I think Mangelsdorf

thought that the oldest cobs at Tehuacan were wild corn. The truth is that they most probably are not. But more important is his retreat from the central tenants of the tripartite hypothesis. This came in three stages. The first and the weakest was complete knowledge of the extent of the teosinte populations. Teosinte was no longer a weed in corn fields (Weatherwax, 1955) but was wild, covered tens of thousands of acres, and had formed a number of geographically and morphologically distinct races (Wilkes, 1967). It took over a year to swallow these findings and come to terms with their implications. The second stage was the brilliant cross-mapping of maize and *Tripsacum,* where genes were in distinctly different linkage groups between corn and *Tripsacum* (Galinat, 1971). For example, *Tga* (teosinte glume architecture) chromosome 4 in maize × teosinte was not linked to the chromosome 4 *Su* gene in *Tripsacum.* The gl_3 locus on the long arm of maize/teosinte chromosome 4 was carried elsewhere on chromosome 13 in *Tripsacum.* Simply put, *Tripsacum* was not a parent of teosinte. The scanning electron microphotographs of pollen by Umesh Banerjee was the third blow (Banerjee and Banghoorn, 1970). The pollen exine pattern of teosinte was not intermediate between that of *Tripsacum* and corn. Teosinte could not possibly be a hybrid.

The tripartite was over (Goodman, 1965) and at exactly this point of time, Hugh Iltis, whom I had gotten to know when I taught at the University of Wisconsin during the summers of 1967, 1968, and 1970, and George Beadle revitalized the theory of teosinte as the progenitor of corn. The natural distribution of teosinte was well enough established by this time that it could not be considered an artifact of corn evolution. Now Langham (1940), Longley (1941a,b), and Miranda (1966) had preferred teosinte as the progenitor, but Iltis and Beadle clicked with the times and the idea was accepted widely. Add Galinat (1971) and the stage was set for the corn conference at Harvard's Botanical Museum in 1972. All the principals were there: Mangelsdorf (who had retired to North Carolina), George Beadle, Hugh Iltis, Walt Galinat, Elso Barghoorn, Umesh Banerjee, Ramana Tantravahi, Raju Changti, T. C. Ting, A. Grobman, Suri Sehgal, and I—and so was all the evidence: Belle Artes pollen cores and Tehuacan cob specimens before their return to Mexico. The ensuing debate ended with the *Scientific American* article "The Ancestry of Corn" (Beadle, 1980), the rebuttal (Mangelsdorf) letter in the April 1980 *Scientific American,* and the Mangelsdorf reply article "The Origin of Corn" (Mangelsdorf, 1986). Beadle states his case—teosinte as the progenitor of modern corn—and the idea is supported by new evidence from plant breeding, archaeology, and folklore. Mangelsdorf argues that corn had not one ancestor but two: It is derived from a cross between primitive corn and a perennial form of the wild grass teosinte, and this origin is supported by breeding experiments. Look what has happened in Mangelsdorf's last paper: teosinte as a half progenitor of maize (the opposite of Mangelsdorian ideas for 35 years), yet Beadle was wrong because he chose the wrong teosinte. The new hard data in support of the teosinte origin have come in the last 20 years from two of Hugh Iltis's former graduate students, John Doebley and Bruce Benz, and a third graduate of the University of Wisconsin from many decades earlier, Walt Galinat.

Paul Mangelsdorf proposes "wild maize" as the progenitor (pistillate paired spikelets and polystichous spike protected by husk), but it is extinct. George Beadle felt that the proposals cited above, being hypothetical, were untestable, and favored teosinte, saying that it clearly exists and shares a common ancestry. Teosinte is wild, corn is a cultigen, and since cultigens always come from wild plants, teosinte is the

progenitor. Beadle also favored mutation and selection as the source of gene changes between wild and crop plants. In the interpretation of Beadle's work, John Doebley seems to hold to a similar idea. Very early on, Mangelsdorf had been very successful with the results of wide crosses (corn × *Tripsacum*), and his view of the domestication process depended on the hybridization burst of quantum evolutionary energy. His view of the origin of many landraces as reflected in the ancestry charts in the "Races of Maize" in Mexico are a case in point. The very productive high-elevation (2000+ m MSL) race Chalqueño is charted as having parents of Cónico (another high-elevation landrace) and Tuxpeño [a very productive tropical low-elevation (>300 m MSL) landrace], which is now widely recognized as not being in the parentage. Simply said, Mangelsdorf favored wide crosses and introgressive hybridization to account for variation, and Beadle looked to mutation and selection for single traits.

To test his single-trait hypothesis, Beadle grew out an F_2 population of Chapalote × Chalco teosinte at El Batán, the headquarters field of CIMMYT, Texcoco, Mexico. In October 1970, Walt Galinat and George scored 15,464 plants for the traits that separate teosinte from maize. "Good maize-like and teosinte-like plants were recovered, each with a frequency of approximately one in 500" (Beadle, 1978). Two of the important differentiating traits, paired versus solitary fertile pistillate spikelets and four or more ranked pistillate spikelets can be separated as single discrete genetic units (Galinat, 1971). To test the mutation rate, George organized a mutation hunt in November 1971. About 18 people were involved and we split into two teams. George took a group to Chilpancingo, Guerrero and collected in the Palo Blanco area around Mazatlán (1200 to 800 m MSL), and I took eight people to Teloloapan, Guerrero (1250 m MSL) and collected at various sites between Acapetlahuaya and Rancho Nuevos along the Teloloapan–Arcelia road. We each had a plastic bottle with a small tube at the top and we put a single seed from every teosinte plant into the bottle. The rest of the seed we put into a bulk bag and continued on to another plant. We also had a tally counter and we counted the number of plants collected. On a good day we might come close to 5000 plants sampled, and Glen Price (Harlan et al., 1973) often exceeded this number. At the end of 5 days we had 178,661 single-plant collections (5 days × 8 collectors = 40 workdays) and we had 25 kg of bulk collection. The other team made similar collections at Mazaltán at a site where the hills were not as steep. George scored short of $\frac{1}{2}$ million rachis segments and found only a few mutant candidates ["soft-shelled teosinte" (Galinat, 1985)], and when grown out they appeared wild-type in every way. He found no open glumes or papery glumes. He did have paired glumes, but these reverted to solitary in the progeny test. After he was finished with the mutation hunt, the seeds were deposited at the U.S. Department of Agriculture Ames North Central Plant Introduction Station, where it was all bulked and the "individual plant–individual site" uniqueness of the collection was lost. There were funds left over from the $10,000 National Science Foundation grant, and in 1972, Marcus Winter, George Beadle and I, with the help of people living in Mazatlán, collected over 100 kg of teosinte seed in 2 days. This 1971–1972 period saw the most extensive human predation for teosinte on record or at least since the origin of corn (Figure 1.1.13). For the last 18 years, the vast valley behind Mazatlán where the collections were made has been planted to tomatoes, and teosinte has essentially disappeared. It is still found along the Teloloapan–Arcelia road, but there is more barbed wire and cattle than in 1971 and less teosinte. George was convinced that if we looked at enough teosinte, we would find a papery lower glume. We did not.

FIGURE 1.1.13.   George Beadle collecting teosinte seed in early November 1972 at Mazatlán, Guerrero, 1300 m MSL. In 3 days over 100 kg of seed was collected for long-term storage in the U.S. seed storage system. George considered this his most significant career achievement. This was a man who had been both a University president and a Nobel Prize winner.

The mutation hunt was undertaken with Balsas teosinte because it was the largest panmitic, truly wild teosinte population and the least likely to have undergone a genetic bottleneck effect. This is just the population outside Teloloapan, Guerrero, that Doebley (1990) has found to be indistinguishable from corn based on their isozymes. All other teosinte populations, including Mazatlán (also Balsas), can be distinguished via isoenzymes. The Teloloapan site was chosen because it is the most removed from cornfields of all the collection sites in Mexico. Introgression with corn was not a factor in the 1971 biology of this population. George would have taken great pride in the molecular confirmation that corn is a domesticated form of central Balsas teosinte. Interestingly, *Z. perennis* and *Z. diploperennis* have distinct isozyme and chloroplast DNA genotypes and could not have figured in the origin of annual teosinte, and this put to rest the Mangelsdorf (1986) hypothesis that annual teosintes are the result of corn × perennial teosinte hybridization. These same studies indicate that Balsas and the highland teosintes are distinguishable on isozymes, but not chloroplast DNA. "Finally the molecular evidence provides strong support for the theory that corn is a domesticated form of teosinte and further suggests that *Z. mays* var. *parviglumis* was the ancestor of maize. This, if true, would place the origin of maize in the Balsas river valley of southern Mexico, presuming the distribution of the taxon has not changed significantly since the time of domestication of maize" (Doebley, 1990). Miranda (1966) was the first to propose the Balsas as the site of origin for corn, and my reconstruction of the habitat and distribution of wild corn (Abstracts, XI International Botanical Congress, Seattle, 1969) around Huetamo, Michoacan or above Arcelia, Guerrero was the second. Miranda also favored the Balsas because of the wild bean (*P. vulgaris*) found in the region. I gave this same evidence at the September 11–12, 1969 Conference on the Origin of Maize at the University of Illinois (Iltis, 1971). I

had not been invited, but Hugh Iltis encouraged me to go. The Second Conference was at the Botanical Museum Harvard University in 1972 (Doebley, 2001). These two meetings were the last of the "classical" evidence, and since 1975, corn evolution has continued with studies of isozymes and molecular studies (Gepts, 1998). In this, Major Goodman has led the way in our understanding of landraces (Goodman and Brown, 1988) and John Doebley in the areas of molecular systematics and origin (Timothy et al., 1979; Dorweiler et al., 1993; Rong-Lin et al., 1999).

John Doebley's early contributions were in classical studies of corn, such as taxonomy and morphology, which is unique for a molecular biologist. His 1983 study of the teosinte and corn tassels is the most complete ever undertaken (Anderson, 1944; Doebley, 1983). He clearly and unequivocally eliminated the teosintes of the section Luxuriantes (these are the only teosintes known to cross with *Tripsacum*) as possible progenitors of corn, because of their diagnostic many-nerved, winged outer glumes and flattened male spikelets, which are unknown in corn. The Luxuriantes can be distinguished from all other section Euchlaena teosintes by the unique shape of the trapezoidal pistillate rachis segment, or fruit case, and their terminal chromosome knobs (Pasupuleti and Galinat, 1982). The seed proteins of *Z. luxurians* also are quite distinct from those of corn (Smith and Lester, 1980). The teosinte race from Huehuetenango (Figure 1.1.14), northern Guatemala, is based on the cytology of terminal knobs, the most primitive of the triangular-seeded teosintes (Longley, 1941b; Kato, 1975) and Doebley (1984) has shown it to be isoenzymatically divergent from the Mexican annual teosintes: those of the Balsas *Z. mays* var. *parviglumis* or Central Plateau *Z. mays* var. *mexicana*. Interestingly, Balsas teosinte is less cornlike in appearance and Central Plateau more cornlike (larger seed, thicker culm, broader leaf, fewer tassel branches, erect tassel, red hairy sheaths, large glumes in the tassel),

FIGURE 1.1.14.   Central Plaza, San Antonio Huista, 1300 m MSL, Huehuetenango, Guatemala. Forty years ago the hillsides above the town were covered with tens of thousands of teosinte plants. Since the town has been connected to the national road system, the hills have been fenced for cattle and teosinte has all but disappeared. This valley at 1100 m was the Mayan mythical site for the "birth of corn." The Huista Valley is home to teosinte, three *Tripsacum* species, and the corn race Olotón.

yet by isozyme analysis the small-seeded central Balsas is not distinguishable from corn (Doebley, 1990; Doebley et al., 1995).

The evidence implicates Balsas teosinte, but how does one go from teosinte morphology to the polystichous structure, which is the cultigen: corn. The "parsimonious interpretation of facts is to the distichous taxa, the teosintes, as the products of natural selection within the purely distichous Andropogoneae, and the anomalous polystichy of maize that is found only in the cultigen as the utilitarian artifact of domestication" (Doebley and Iltis, 1980). The descriptive theory developed by Iltis reviewed earlier lacks experimental verification. John Doebley has done the experimental breeding and gene expression studies of teosinte glume architecture (*Tga*) and teosinte branched (*Tb-1*), which are the genetic factors that controlled the development of polystichy and plant architecture. His studies give us an idea about primitive states and advanced morphologies, but they do not give us chronology as found in archaeology (Benz, 1999), racial clusters of variation as found in landraces (Goodman and Brown, 1988), or migration of corn landraces (Sánchez, 1994).

Evidence from Teosinte Branched: *Tb-1*

Teosinte branches at the nodes of the main culm, and each branch is terminated by a male tassel. Each node up the branch bears pistillate spikes and in some cases, secondary branches. Corn has one or two massive ears at a lateral position (the popcorns often have more) and no branching except basal tillers, which often have a terminal male tassel but seldom a pistillate ear. These differences have been studied using quantitative trait locus mapping with molecular markers (Doebley et al., 1995). *Teosinte branched 1* (*Tb-1*), on the long arm of chromosome 1, is a null or loss-of-function mutant that produces plants with long lateral branches tipped by tassels. Cloning the *Tb-1* gene by transposition tagging, Doebley et al. (1997) showed that it encodes a protein that represses the growth of axillary branching (Doebley and Wang, 1997). During development, *Tb-1* acts as a repressor of organ growth (meristems) in those organs in which its messenger RNA accumulates. The corn form of the repressor accumulates more *Tb-1* mRNA in lateral-branch primordial and has ear-tipped shorter branches and considerable husk cover. The teosinte allele accumulates less *Tb-1* mRNA and produces a branched structure but with less husk cover over the pistillate spikes. The action of *TG-1* confirms my observations during husking of literally hundreds of green teosinte plants in Mexico, many of which were F_1 hybrids or subsequent backcrosses to teosinte. Of all the races of teosinte, the race Chalco exhibits the least branching on overwise robust plants. Therefore, they must be *Tb-1* suppressed, yet show no signs of corn hybridization in the pistillate spikes (i.e., "true" to teosinte taxa). I always had trouble with these nonbranched teosinte plants because I thought in terms of a corn trait, not suppression of a teosinte trait. In the field this is compounded by phenotypic plasticity, where at least half the teosinte plants do not have the robustness (energy and/or water inputs) to branch with fewer than 100 seeds of total plant output. Truly robust branching at full expression occurs in perhaps 5% of the population under wild conditions in the Balsas, but John Doebley is right: The effect of this trait is profound and was central in the creation of maize. I wonder how many Zapotec tassel-tipped ears in our record in clay (Figure 1.1.11) are an expression of the non–*Tb-1* wild or lost phenotype.

What is probably a first for a gene involved in domestication has been a measurement of the number of years required to fix the trait by looking at nucleotide polymorphism (Wang et al., 1999). Since domestication should reduce polymorphism of the sequence of genes under human selection, we can establish a wild-to-domesticated path. In *Tb-1* the protein coding remained polymorphic, but the regulatory regions of *Tb-1* showed corn and Balsas teosintes to belong to a single clade. Using selection factors of between 0.04 and 0.08 and population sizes of 1000 plants, Doebley was able to demonstrate that the garden plots of Iltis (2000) or Galinat (1995) or the estimated field population size at Mazatlán Guerrero (Flannery and Ford estimated teosinte population density at Mazatlán in 1971 from 4-m^2 plots at 50,000 per hetacre $\times$ 2 ha $=$ 1 $\times$ 10^5 plants). Wang et al. (1999), using an arbitrary selection of 0.04 and 0.08 (1 $\times$ 10^3 and 1 $\times$ 10^5) for the two population sizes, established a time of from 315 to 1023 years for domestication. This time frame for domestication is quite reasonable and considerably longer than the off-the-cuff estimates for corn of 50 to 100 generations that have appeared in some of the proposals made in the last 20 years.

The teosinte branched study is a significant contribution to understanding the transformation of teosinte, the wild plant, to corn, the massive eared cultigen. It needs confirmation from the archaeological record. That critical vegetative parts have been found in the past gives hope that this is not an unreasonable expectation. In addition, we do not know how far along this repression factor had operated in unique teosintes prior to human selection. A "cold start" for the selection of a useful trait is to overromanticize the role of humans in its establishment. Humans are opportunist now and we must assume that they acted similarly in the past, so once something was obvious, they probably went for it, but it is, in my view, a false assumption that early farmers know what they were wanting and then proceeded accordingly. To be honest, the current process of farmer selection with maize is not well understood (Louvette et al., 1997; Smale et al., 1998; Soleri and Cleveland, 2001), so caution is in order for the past. All this aside, the single teosine branched trait explains a lot of the plant architecture.

Changes that may be attributed to the *Tb-1* locus in the transition teosinte to maize include (1) arresting the full elongation of the internodes, (2) arresting the growth of the leaf blades, (3) arresting the outgrowth of some auxiliary buds, (4) suppressing the outgrowth of secondary branches, (5) increasing the number of leaves (husk) formed on the branch, (6) changing the leaf (husk) phyllotaxy from single alternate to decussate, and (7) transforming the tassel (male inflorescence) at the tip of the lateral branch with an ear (female inflorescence) (Doebley and Wang, 1997). Obviously, once the ear is lateral and not out on the end of a long axis, the weight of the ear can increase dramatically. The weight of the seed in the tassel can increase only to a certain point before it will cause the plant to lodge by its sheer weight. Now we have to learn how much of *Tb-1* fixation is predomestication and how much is postdomestication through human selection.

Because of its influence on husk cover, *Tb-1* interacts with yoking of the pistillate rachis and the loss of abscission zones in the rachis. Loss of this wild-type trait even occurred in the *Z. diploperennis* $\times$ *Tripsacum* hybrid (Eubanks, 2001a,b,c). But rachis abscission is only one of the abscission zones for the dispersal of seed. There is a second abscission zone between the rachilla and the caryopsis—the familiar dark specks in corn chips. Is this a vestigal trait from an ancient Andropogonaeae? This abscission is in operation in teosinte, where it is obviously ineffective, because the

seed is inside the rachis segment and dispersal is effectively blocked. But if the teosinte grain was free of the rachis tissue and naked, such as in tassel seed, the abscission expression would have aided the effective dispersal of seed. Most corn kernels shell along the narrow rachilla. But even here there are differences in the two systems. The long-rachilla highland corns with broad kernels are different from the short-rachilla lowland corns. Many short-rachilla lowland forms have long, narrow kernels, which creates a longer kernel length/ratio and facilitates mechanical shelling. Pepitilla is an example of a long, narrow seed that will literally shatter if the ear is dropped to the floor. Many of the long-rachilla × short-rachilla landrace hybrids exhibit heterosis (Galinat, 1971, 2001). Was corn polyphyletic in origin? Is the rachilla a hint of vestige evidence?

Evidence from Teosinte Glume Architecture: *Tga-1*

The teosinte rachilla, its angle, and the lower glume and cupule are part of a major locus called *teosinte glume architecture* (*Tga*) on chromosome 4. This gene alters development of the teosinte cupulate fruit case so that the kernel is exposed on the ear at harvest (Sehgal, 1963). The lower glume of teosinte seals the opening of the rachis segment or rachid. In teosinte, with the corn allele *tga-1*, the glumes do not fully protect the kernel. When the teosinte allele *tga-1* is in corn, the glumes are pronounced and curved upward, as is the rachilla. In corn with the corn *tga-1* allele, the glume is horizontal to the cob long axis, as is the rachilla (Sehgal, 1963; Galinat, 2001). One of the mutants that Beadle hoped to discover on the mutation hunt of 1971 was the maize allele of *tga-1* in teosinte. This is exactly the morphology that we should be searching for in the archaeological record. What we have found at about 2000 B.P. is the teosinte *tga-1* in corn based on cob morphology (Figure 1.1.7). This gene is on the short arm of chromosome 4 between *sugary* (*Su-1*) and *brittle endosperm* 2 (*bt-2*) and very near the centromere. The corn allele (*Tga-1*) behaves as dominant over the teosinte allele (*tga-1*). Dominant alleles usually characterize wild populations (Harlan, 1992) and recessives characterize cultivated selections; however, *Tga-1* is such a keystone trait for access to the grain that there is a strong case for the evolution of dominance. The naked grain also is tied to polystichy and to loss of yoking and/or abscission in the rachis.

The idea of Walt Galinat is that of recombination after hybridization of a four-rowed spike resulting from four ranks of single spikelets borne in yokes back to back with a four-rowed spike resulting from two ranks of paired spikets (as seen in approximation with teosinte × corn F$_1$ hybrids). Both have four rows, but each is a morphologically and genetically distinct type of four rowing. Two different mutant types of four-rowed teosinte form by hybridization the double-recessive eight-rowed maize with four ranks of pair spikelets. All the earliest archaeological cobs are eight-rowed. Is the eight-rowed condition the domestication event, the four-rowed condition the domestication event, or is the bringing together of the two different four-rowed types by human migration the actual domestication? Was the point of domestication when human-driven selection started on naked seed (i.e., *Tga-1*)? Clearly, the morphology change of *Tga-1* made domestication possible. We are in a much better position now to interpret the archaeological record based on molecular studies of *Tb-1* and *Tga-1* than we were 30 years ago. John Doebley has established the sequence of gene change for the spectative descriptive morphology put forward by Hugh Iltis to account for the corn ear. We now need to look at archaeological materials from the Balsas Basin

and the region of midelevation between Guerrero and Oaxaca for answers to what actually happened.

A LOOK AT DOMESTICATION

We know that teosinte is the closest relative of corn; we also know that *Tga-1, Tb-1*, paired spikelets, and polystichy can explain the transition to corn; but we don't know if humans started domestication once or twice (or more), if they started "cold turkey," or if the mutant exposed grain was already present in the population. Molecular tools have helped tremendously, but if we become too arrogant about our discoveries, we may miss some key evidence. Our understanding of the origin of corn is not completed. Remember that Mangelsdorf looked at the earliest Tehuacan cobs with flexible rachis and papery glumes and said "wild corn—job's over." Early corn, yes, but the short answer proved to be the wrong conclusion.

Maybe it is appropriate to end with a long quote from a mimeographed report of Kent Flannery and Richard Ford from the 1971 Mazatlán mutation hunt, which I don't think was ever published (quoted directly except for brackets):

> Harvesting and processing teosinte is very labor-intensive. Unlike corn, with its kernels firmly attached to a cob, teosinte seeds are loose in their spikes. When they are ripe, a slight breeze or a disturbance caused by animals or a man walking through the stand results in a shower of falling seeds. If early man used the ripe seeds, he probably did so by collecting the intact fruiting bodies [fascicle of spikes enclosed by the sheath of the node] which are easily stripped from the main stalk or lateral branches. Our experiments suggest that 2–4 plants can be stripped in a minute, or 120 to 140 plants per hour. These would be brought in skin or fiber bags to a camp where the seeds could be threshed from the spikes by beating them with a stick, and collected on a hide. [A similar technique is used by Mexican Indians today to thresh beans.] Shattering and plant height would render a seed beater almost worthless. [Interestingly, that is exactly the technique we used in 1972 to collect 100 kg of seed—it is very effective.] According to Garrison Wilkes, some 25,000 seed [Balsas teosinte type] are needed for a kilogram, half of which is inedible roughage.
>
> Preparing teosinte for consumption is also very demanding. The seeds can be popped (and taste like popcorn), but the equipment for performing this operation—stone or pottery griddles, or features for heating sand—have not been found in pre-ceramic contexts so far. Otherwise, the very hard seedcoat requires a mortar and pestle for cracking; then the course meal could be cooked by means of hot stone boiling. George Beadle has conclusively demonstrated that teosinte flour can be made into "tortillas," but it is not known whether this technique was used in the pre-agriculture period. Appropriate stone mortars and pestles, however, go back to 7200 B.C.
>
> For storability, teosinte has no equal. Insects don't attack it, mice don't eat it and birds, when given a choice, select it last. Storage pits (with acorns, etc.) are abundant in Mexico's pre-ceramic archaeological sites (though none found so far can be shown to have been for teosinte).

How much easier life would be to grow corn! One informant we spoke to at Mazatlán Guerrero (near Chilpancingo) had the answer: "lazy bird corn" as teosinte is called in that village [the actual bird is the roadrunner = huiscatote] "just comes up and grows"; in a couple of years "it turns into corn." Hopefully (to avoid eternal embarrassment for archaeologists and geneticists) domestication is not that easy. But there are many reasons for appreciating why teosinte was the perfect candidate:

1. As a pioneer of disturbed habitats it produces large quantities of seed (at its densest, equally the 500 kilograms per hetacre of wild wheat in the Levant).
2. It is an annual.
3. It shows wide genotypic and phenotypic variability in seed size and color and plant growth.
4. It has a tremendous ability to withstand drought. . . . [I would change this to say it is a wild plant with high reproductive capacity under varied environmental conditions.]
5. It stores well.

It is becoming clear how chromologous the genetic changes were in the domestication of New World corn and Old World wheat and barley. In the Near East, wild ancestors of cereals also formed dense stands of plants possessing brittle (shattering) rachis and hulled grains. Naturally occurring deleterious mutations were selected by man and the tough rachis and naked grain of the domesticated cereals evolved. Teosinte may have undergone similar changes. In Beadle's view, a non-shattering rachis, paired spikes, two ranked cob, a soft hull [lower glume] and protective husk and day neutral maturity are the basic mutations needed to convert teosinte to maize.

The evolution of corn was a real labor-saving device for man. The labor input differential between teosinte and corn is enormous. Even the most primitive maize would have been easier to harvest, process and prepare than the most productive teosinte stand. Man was spared additional harvest time when teosinte/corn was moved from steep barranca sides to rich, alluvial bottomlands where production could be regulated and harvest time further reduced. A change in habitat opened the way for further productivity and eventually to agricultural support of the great Mesoamerican civilizations.

That was written 30 years ago and knowing what we do about the cupule (Galinat) teosinte branched (Doebley), polystichy (Galinat), teosinte glume architecture (Doebley), chromosome knob patterns (Kato), teosinte distribution (Sánchez), the corncob in archaeology (Benz), the racial diversity of corn (Goodman), and the SEM of development (Orr and Sunderland), the origin of corn is coming together. At this point we need the archaeological record to confirm what we think we know. The recently proposed destabilized corn genome based on hybridization with *Tripsacum* (Eubanks, 2001) needs to be confirmed with additional breeding experiments. Interestingly, the only *Tripsacum* that is known to carry teosinte chromosomes is found almost exactly on the spot (Paxil) that Mayan (Quiche, Cakchiquel) mythology claims to be the site for the origin of corn. More attention needs to be paid to this

Chiapas–Huehuetenango region. The other intriguing idea is that *Tripsacum* destabilized the teosinte genome to produce the four-ranked single-spiklet parent or four-rowed paired-spikelet (in two ranks) parent that figures for Walt Galinat (2001) in the origin of eight-rowed corn. If the row number is four, it is teosinte, and if eight, then corn. Eight-rowed corn is four-ranked, but with paired spikelets it yields eight rows. Even with heavy lower glume coverage this would be called corn, not teosinte, yet its two parents were both teosinte. In the origin of corn, this transition is, I think, the best definition for when corn is not teosinte.

Hybridization has formed a key role in the evolution of corn and the exploitation of yield has possibly created heterosis (Mangelsdorf, 1958). Corn appears to have had two or more ancestral forms in Mexico: a highland (above 1500 to 1750 m) type, characterized by an enlarged base to the ear (big butt), where the rank number increases and the rows are not clearly delineated, and a lowland type (below 1500 to 1750 m), which has eight clearly delineated rows and tapers at the base. The highland is pyramidal in outline, whereas the lowland is cigar-shaped, tapering at both ends. Hybridization between these two extremes yields heterosis. Were there two distinct origins for corn, or were there two distinct ancestors? We don't know, but what we do know is that teosinte is not a recent artifact of corn evolution but a major participant. We also know that the tripartite hypothesis does not explain the origin of corn, yet we cannot entirely rule out a role for *Tripsacum* in the origin. Clearly, teosinte and corn are fully interfertile: Hybrids and subsequent backcrosses in both directions occur in all the sites where teosinte and corn are sympatric; yet it is extremely difficult to document introgression of teosinte into corn using chromosome knob positions, molecular markers, or B chromosomes. Most of the critical traits separating corn and teosinte show association or linkage to chromosome 4, but abnormal pairing at pachytene is often associated with the long arms of chromosome 8 or 9. These are the silent arms for which we have the least number of genetic markers. B chromosomes are often found in populations where corn and teosinte hybridize. Do chromosome-heterochromatic B chromosomes or chromosome knobs represent silenced teosinte germplasm? A geographic center for these morphologies is southern Mexico: Does this tell us something? There are still many unanswered questions about the origin of corn. We know where—southern Mexico (Guernero–Oaxaca–Chipas); we know when—6000 to 5000 B.P.; but we don't know exactly how.

SUMMARY

The more vague the origin of corn (Weatherwax, 1918), the more timeless the ideas. The more specific the ideas, the more popular they are in the short run [the tripartite hypothesis of Mangelsdorf and Reeves (1939)], but ultimately, there are facts for which they cannot account. New evidence on the origin of corn has come like waves about every 20 years. Some ideas remain durable, whereas others are washed away.

Starting a century ago, the origin of corn based on discoveries in Mexico (Harshberger, 1900) with the *Tb-l* wild trait and *Tga-l* was a botanical dream (i.e., it fit so well and accounted for all corn traits) until it was discovered to be based on a corn × teosinte hybrid and not a truly wild taxon. The next 20 years saw an expansion of our knowledge of the distribution of teosinte and the inheritance of corn × teosinte hybrids. Weatherwax (1918) published the common-ancestry hypothesis

and Collins (1920) the hybridization hypothesis. Twenty years later, Mangelsdorf and Reeves (1939) publish the tripartite hypothesis, where teosinte is the hybrid and therefore excluded from being an ancestor. This hybrid origin hypothesis lead to the view that the natural populations of teosinte are an artifact, and therefore the chromosome knob work of Longley (1941a,b) was ignored. In 1942, Edgar Anderson and Hugh Cutler published their watershed paper on classifying corn landraces and a two-decade search began for primitive maize varieties and taxonomic studies of the wild relatives, teosinte and *Tripsacum.* By the mid-1960s, the last of the "Races of Maize" bulletins had been published, teosinte had been monographed (Wilkes, 1967), and the framework for understanding the genus *Tripsacum* had been established (Randolph, 1970; de Wet and Harlan, 1978). The years 1969 and 1972 saw the Origin of Maize Summit meetings, and the tripartite hypothesis replaced by teosinte as progenitor (Galinat, 1971; Beadle, 1972; Iltis, 1972). The maize summits do not seem like ancient history, but I guess they are (Doebley, 2001). Isozyme studies indicate that central Balsas teosinte is the closest form to the progenitor of corn (Doebley, 1990) in addition corn that has had a morphological catastrophic sexual transmutation (Iltis, 1983) and the two forms of teosinte hybridizing to form an eight rowed ear which formed the rapid transformation to maize (Galinat, 2001). There are truths in all these contributions, but there are still elements of mystery in what remains unresolved.

ACKNOWLEDGMENTS

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