HOMEOTIC SEXUAL TRANSLOCATIONS AND THE ORIGIN OF MAIZE (*ZEA MAYS*, POACEAE): A NEW LOOK AT AN OLD PROBLEM[1,2]

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Iltis, Hugh H. (*Botany Department, University of Wisconsin-Madison, Madison, WI 53706-1381*). HOMEOTIC SEXUAL TRANSLOCATIONS AND THE ORIGIN OF MAIZE (*ZEA MAYS*, POACEAE): A NEW LOOK AT AN OLD PROBLEM. *Economic Botany 54(1):7–42, 2000. In the Origin of Maize Controversy, the Orthodox Teosinte Hypothesis (OTH; Beadle 1939, 1972; Iltis 1971), five key mutations change 2-ranked (distichous) ears of teosinte (wild Zea) with a single row of grains per rank to 4- to many-ranked (polystichous) maize ears with a double row of grains per rank. BUT teosinte ears are lateral to the I° branch axes, maize ears, like their male homologues, the teosinte I° branch tassel spikes, terminal, an enigma long unrecognized, hence ignored. In the Catastrophic Sexual Transmutation Theory (CSTT; Iltis 1983b, 1987), now abandoned, the I° branch tassel (male) of teosinte (spikelets soft-glumed, paired, i.e., double-rowed per rank, as in maize ears), when brought under female hormonal control by branch condensation, becomes feminized into a maize proto-ear. BUT lateral ears should then have remained teosintoid (2-ranked, each rank with a single row of grains), yet are in fact double-rowed.*

Combining OTH and CSTT, the new Sexual Translocation Theory (STLT) is based on: first, the branching pattern of teosinte ear clusters (Cámara-H. & Gambino 1990), sequentially maturing, sympodially branching, typically Andropogonoid systems, called rhipidia (sing. rhipidium), where each higher order (younger) ear originates as a lateral branch of its lower order, earlier maturing predecessor; and second, on 3 or 4 key mutations [cupule reduction, softening of glumes, doubling of female spikelets], which, by projecting outward the grains, invited human domestication by making them accessible. Within each ear cluster, the earliest maturing, hence nutrient-monopolizing and largest ear would be selected, all younger ears, already nutrient-inhibited, suppressed. As fewer, 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 II° branch tassels, and ultimately the I° branch tassel (male), with an ear (female). With this, now female structure in the apically dominant, hence most nutrient-demanding terminal position gradually suppressing all subsidiary ears on the I° branch beneath it, mutations for polystichy (contingent on nutrient overload) were finally allowed to become expressed, and the multi-rowed maize ear (at first with an atavistic male tail) evolved. Favored by human selection, these increases in apical dominance by stepwise homeotic sexual conversions explain both archeological and morphological realities, but need to be harmonized with recent results of developmental genetics.

Current evidence suggests that teosinte was first tended for its green ears and sugary pith by hunter-gatherers as an occasional rainy-season food in small "garden" populations away from its homeland, and not for its abundant grain-containing, hard fruitcases, which easily mass-collected but useless as food, are as yet unknown from the archeological record. A rare grain-liberating teosinte mutation (probably expressed in only one "founder" plant, a mazoid "Eve"), which exposed the encased grain for easy harvest, was soon recognized as useful, collected and planted (or self-planted). Thus maize was started on its way to a unique horticultural domestication that is not comparable to that of the temperate Old World mass-selected agricultural grains.

En la controversia sobre el origen del maíz, la Hipótesis Ortodoxa del Teosinte (OTH; Beadle 1939, 1972; Iltis 1971) propuso que fueron cuatro o cinco las mutaciones claves que cambiaron las mazorcas del teosinte (el Zea silvestre) de doble fila (dísticas) con una sola hilera de granos por fila a una mazorca de cuatro a muchas filas (polística) con dos hileras de granos por fila. Pero las mazorcas del teosinte están en una posición lateral orientadas a la rama principal, en forma similar a las estructuras homólogas masculinas, la espiga terminal, un enigma que no se había reconocido y por lo tanto ignorado. En la Teoría Catastrófica de la Transmutación Sexual (CSTT, Iltis 1983b, 1987), actualmente abandonada, se propuso que la espiga masculina de la rama principal del teosinte (con las glumas suaves, en pares, o sea con dos hileras por

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fila, como la mazorca del maíz) cuando sucede el cambio a un control hormonal femenino, por condensación de la rama, se convierte en un órgano femenino, como un "prototipo" de mazorca de maíz. Sin embargo, las mazorcas laterales debieron haberse quedado como las del teosinte, es decir, en doble fila y cada fila con una hilera sencilla de granos, aunque en realidad tienen dos hileras. La nueva Teoría de la Translocación Sexual (STLT) combina el OTH y CSTT en base a ciertas características como son: primero el patrón de ramificación de los racimos de las mazorcas del teosinte (Cámara-H. & Gambino 1990) y el tiempo de maduración, en una secuencia simpodial, como es típico de un Sistema Andropogonoide (ripidio), donde la mazorca de un nivel superior (más jóven) se origina como la de una rama lateral de un nivel inferior y así su predecesor madura más tempranamente. Segundo, como resultado de las tres o cuatro mutaciones claves (reducción de la cúpula, ablandamiento de las glumas y duplicación de las espiguillas femeninas), los granos quedaron expuestos, invitando así a su domesticación por el ser humano por facilitarse los granos a ser cosechados. Dentro de cada racimo, la mazorca que maduraba más tempranamente, por consiguiente la que acaparaba los nutrientes y por consecuencia la de mayor tamaño sería seleccionada, mientras que, las otras no bien desarrolladas, por falta de nutrientes se verían suprimidas. En el transcurso de la evolución de las mazorcas más grandes, los internudos se vieron disminuidos en tamaño y con ésta reducción, las espigas masculinas se trasladaron hacia las zonas de hormonas femeninas. Mediante éstas conversiones homeóticas, se cambió la morfología femenina hacia los sitios masculinos terminales: primero, reemplazando cada uno de los racimos masculinos y posteriormente, el racimo masculino de la rama primaria. Ahora con la estructura femenina en una posición terminal o con dominancia apical y siendo la que necesitaba una mayor concentración de nutrientes, gradualmente inhibió el crecimiento de todas las mazorcas auxiliares inferiores. Las mutaciones polísticas (eventual sobrecargo de nutrientes) finalmente pudieron ser evidentes, evolucionando así en una mazorca con muchas hileras, aunque a menudo, con una espiga atávica. Con el tiempo, las mazorcas fueron mejoradas y seleccionadas por el hombre aumentando así la dominancia apical, originalmente promovida por las conversiones sexuales homeóticas, lo que explican la mayoría de las evidencias arqueológicas y morfológicas. Es necesario comparar tales evidencias con los resultados derivados de la genética de la ontogenia. Ahora se cree que los cazadores y recolectores en la temporada de lluvias, inicialmente utilizaban las mazorcas verdes y tiernas del teosinte, traídas de poblaciones o pequeños "jardines" de áreas alejadas a sus hogares. En realidad, ellos consumían sólo la médula dulce de la mazora y no los granos duros encapsulados, difíciles de comer y aunque éstos eran fáciles de cosechar, el registro aqueológico no demuestra que fueron utilizados. Es probable que haya ocurrido una mutación en el teosinte en la que se liberó el grano de la cápsula, hecho ocurrido en una sola planta "fundadora" (la "Eva" del maíz), la cual expuso el grano encapsulado haciéndolo fácil de cosechar, al que muy pronto se le reconoció como útil, se colectó y sembró (o sembró por si mismo). Es así como el maíz tuvo una domesticación única en la horticultura, la cual no se compara con la de los cereales seleccionados de cosechas masivas en el Viejo Mundo.

Key Words: *Zea mays*; maize; corn; teosinte; homeotic sexual translocation; horticultural origin; mazoid "Eve"; taxonomic history.

Of all the many plants domesticated by mankind, none has had as enigmatic and contentious an evolutionary origin as *Zea mays* L. ssp. *mays*, the plant that we call maize, or in America, simply corn or Indian corn. On the one hand, its now generally accepted ancestor, *Zea mays* L. ssp. *parviglumis* Iltis and Doebley (the Balsas teosinte of Wilkes, 1967), one of the several wild Mexican and Central American grasses called *teosinte*, is often so similar to maize in appearance, especially when growing unbranched in dense native stands or as a weed in maize fields, as to be indistinguishable—except for the ears. Cover the ears, and it sometimes takes a specialist to tell teosinte from maize. Maize is teosinte—domesticated. But compare a many-rowed, 1000-grained ear of maize to a 2-rowed, 5- to 12-grained ear of teosinte—and be perplexed! How could such a massive, useful monster be derived from such a tiny, fragile, inedible, useless mouse?

But morphological-evolutionary enigmas aside, we need to understand maize for purely economic reasons, for it is mankind's third most important food crop, worth annually over 75 bil-

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lion dollars world-wide. How maize evolved during the past 8000 years, and from what wild ancestor, is a fascinating story that can be approached in two interrelated ways, by the study of structure and function on the one hand, and by genetics on the other (Doebley and Wang 1997; Scheiner 1999).

Almost from its inception in 1900, Mendelian plant genetics adopted maize as its poster child, its *Drosophila,* and modern molecular and developmental genetics continues to yield today vast, almost magical, insights into evolution, phylogeny, and biogeography, with isozymic evidence (Doebley 1990b), DNA sequences and dissections of Quantitative Trait Loci (QTL's = ±genes) dramatically elucidating how genes alter development to change morphological structure (Doebley and Wang 1997; Peterson and Bianchi 1999). Now that sequencing the whole of the maize genome is only a matter of time and money, both genetics, systematics and morphology are about to enter a new and portentous age.

The study of *Zea* gross morphology on the other hand, and the steps needed to change the teosinte plant architecture into that of maize, has progressed much more haltingly. Carried out until recently mostly by systematists or comparative morphologists, and hardly ever by agronomists or geneticists, there has been slow progress in unravelling the peculiarities of either wild teosinte or cultivated maize. In fact, until a few decades ago, such studies were hampered by the lack of field work in Mexico and the consequent absence of teosinte in herbaria or greenhouses; by the inability of growing normal teosinte in the (for it) abnormally long days of northern latitudes; by the endless arguments whether teosinte itself is even an ancestor at all; and finally by the surprising general lack of interest to really study *Zea* morphology with energy and commitment.

In fact, with few exceptions (Cutler and Cutler 1948; Galinat 1956, 1959; Iltis 1971) no one had seriously studied the morphology of the maize ear in any depth, nor interpreted its structures and homologies in relation to teosinte (e.g., Kiesselbach 1949, 1980; Ritchie et al. 1986). Similarly, the taxonomic classification of the teosintes, the wild species of *Zea,* was not seriously approached until the 1960's (Wilkes 1967), and not rigorously established in a formal way until the 1980's (Doebley and Iltis 1980; Iltis and Doebley 1980).

The four main topics discussed in this paper are, first, the historical background of *Zea* systematics and its bearing on the origin of maize; second, the abnormal growth of teosinte in the long-day regimes of northern latitudes, and the unsuspected morphological difficulties that this caused for stay-at-home botanical explorers; third, the new Sexual Translocation Theory (STLT) to account for the increase in apical dominance, which lies at the heart of the evolution of the maize ear controversy; and fourth, a new, and radically different view of why teosinte was brought into the human household in the first place, and how its apparently useless grain, the resulting agricultural crop and the steps in its evolution are unlike that of any other cereal, a truly unique domestication resulting in a truly unique crop.

The ideas presented here are not meant to contradict the work of developmental genetics (Doebley, Stec and Hubbard 1997; Doebley and Wang 1997), but to supplement it by a closer look at *Zea* morphology, ecology and natural history, especially as these attributes interacted with the ancient people who did the selecting, and how the inherent Andropogonoid morphology of *Zea* allowed domestication to come about in the first place.

I. THE SYSTEMATICS OF THE GENUS *ZEA* AND THE LONG ROAD TO A VALID TAXONOMY

Although E. O. Wilson's (1996) quip that "a taxonomist is a systematist who is responsible for so many species that he has time only for their classification" has some merit, to arrive at a valid classification of even a very small genus such as *Zea* can be a difficult, long drawn-out process. Though taxonomy is generally thought of as old-fashioned, what with a formal history of three centuries or more, and until recently much unappreciated and as always underfunded, yet without a carefully constructed taxonomy, there is continual confusion, as the case of *Zea* amply demonstrates.

For over a century now, hundreds of authors have agonized over maize morphology and published their pet theories to account for the origin of its ear, as a veritable babel of titles and conflicting views amply demonstrates: "The primitive corn" (Kellerman 1895); "What is an ear of corn?" (Montgomery 1906); "The origin of maize" (Collins 1912); "The evolution of maize" (Weatherwax 1918); "The metamorphosis of *Euchlaena* into maize" (Collins 1925); "The phylogeny of *Zea mays*" (Weatherwax 1935); "Maize—our heritage from the Indian" (Kempton 1937); "Discusion sobre el origen y la evolucion del maíz" (Miranda 1966); "The evolutionary emergence of maize" (Galinat 1975); "The ancestry of corn" (Beadle 1980); "The maize mystique" (Iltis 1971); and many others (Iltis 1911; Wilkes 1967; Mangelsdorf 1974; Galinat 1985a,b; Iltis 1983b, 1987; Iltis and Doebley 1984; Doebley 1990b; Benz and Iltis 1990, 1992; Benz 1999; Goodman 1988; Doebley and Wang 1997; Cámara-H. and Gambino 1990).

Even though teosinte is vegetatively nearly indistinguishable from maize, and native farmers of the valley of Mexico to this day call it "madre de maíz", no botanist, at least not until the 1840's (Wilkes 1967:6), related teosinte to maize. For whatever reason, be it the enormous difference in their female inflorescence structures; be it the often highly local—though locally often abundant—geographic distribution; be it that herbarium specimens of green and flowering maize or teosinte easily mold, massive and fleshy as they are, or that a fully mature teosinte looks exactly like a tattered, dried-up plant of maize; teosinte specimens were simply not available for study. By 1900, field collected herbarium specimens numbered less than a dozen. In fact, the earliest surviving herbarium specimen of any *wild* teosinte was not collected until 1842, by the Danish botanist F. M. Liebmann, in coastal Oaxaca, Mexico (cf. Wilkes 1967:10), and then, amazingly, of the mostly Guatemalan *Zea luxurians* (Dur. & Asch.) Bird, a species very possibly not native to Mexico.

In the Twentieth Century, teosinte fared a little better. But after 1939 and the publication of Mangelsdorf and Reeves' (1939) book-length monograph, in which teosinte was officially declared to be a sporadic hybrid of a "hypothetical wild maize" with a species of the distantly related, cytogenetically all but incompatible genus *Tripsacum,* teosinte became an "unplant" not to be seriously studied. Mangelsdorf was by then at Harvard, and who was to question theories from Mount Olympus? Furthermore, the "father" of this wild theory, my sometime favorite but often irascible mentor at the Missouri Botanical Garden (and Mangelsdorf's former Harvard Graduate School roommate), the brilliant geneticist Edgar Anderson (1969), who liked to take credit for these taxonomically undisciplined ideas, wrote about the "blind alley labeled 'teosinte'," and suggested instead that maize evolved far away from teosinte, perhaps in the Amazon, or the high Andes, or Guatemala, or by "pre-Columbian transfer across the Pacific" from the "hills of upper Burma" (Anderson 1945). He apparently did not like to collect teosinte either. In fact, while Anderson (in litt.) mentions *seeing* teosinte around Jirosto near Purificacion, Jalisco, Mexico, where Michael Nee and I, in following up on this extremely interesting off-hand suggestion, did indeed locate in January 1979 extensive stands of Balsas Teosinte (*Zea mays* ssp. *parviglumis*), it is significant that there are no collections as far as I could determine in the Missouri Botanical Garden Herbarium of this or any other teosinte collected by Anderson, committed student of maize evolution though he was, and one who for fully 25 years devoted his great talents to the elusive origin of maize, of which he did collect, assiduously, its ears and tassels.

But the earlier history of teosinte is even more perplexing. There is a short reference to teosinte in Sahagun's *Historia General . . . de Nueva España,* written in the 1530's and another in Francisco Hernandez' *De Historia Novae Hispaniae Plantarum,* written between 1572 and 1577, but not published until 1790 (Madrid edition; cf. Wilkes 1967:3–6; Mangelsdorf 1974, Chapt. 3). But both these books refer only to its supposed medical uses. In the first, though reference is made to teosinte's similarity to maize, its weediness and self-seeding in maize fields, its only reported use is in the making of a medicinal drink, in which parched, carbonized teosinte fruitcases and wheat grains are ground up, and, together with "chia" (*Salvia hispanica* L., a blue-flowered sage containing essential oils, native of Mexico and still commonly grown there for tea) and "Chili" (*Capsicum*), made into "atole" to be drunk three times a day by those who "pass blood" (in the urine?). The second book gives identical instructions for the same condition, except that the milled material is made into biscuits (=tortillas?), then "drunk [sic!] three times a day" (was this miscopied from Sahagun?).

In short, except for these two published ref-

TABLE 1. THE TAXONOMY OF *ZEA* ACCORDING TO WILKES (1967), ILTIS AND DOEBLEY (1980) AND DOEBLEY (1990).

Wilkes (1967)	Iltis and Doebley (1980) and Doebley (1990)
Section *Euchlaena* (Schrader) Kuntze	Section *Luxuriantes* Doebley & Iltis
	Zea diploperennis Iltis, Doebley & Guzman
Zea perennis (Hitchc.) Reeves & Mangelsdorf	*Zea perennis* (Hitchc.) Reeves & Mangelsdorf
Zea mexicana (Schrader) Kuntze	
Race Guatemala	*Zea luxurians* (Durieu & Ascherson) Bird
	Section *Zea*
	Zea mays L.
	ssp. *mexicana* (Schrader) Iltis
Race Chalco	Race Chalco
Race Central Plateau	Race Central Plateau
Race Nobogame	Race Nobogame
Race Balsas	ssp. *parviglumis* Iltis & Doebley
Race Huehuetenango	ssp. *huehuetenangensis* (Iltis & Doebley) Doebley
Section *Zea*	
Zea mays L.	ssp. *mays*

erences, teosinte appears to have been ignored for over 300 years after Cortez's invasion of Mexico, even though it is common enough in and around Mexico City and Morelia, cows love to eat it, children like to chew it, hybrids with maize are common, and the fruitcases are beautiful.

It was not until 1832 that the first of the six taxa of teosinte now recognized (cf. Table 1) was scientifically named as *Euchlaena mexicana* by Heinrich Adolph Schrader, based on plants cultivated in the Botanical Garden of the University of Göttingen, Germany, from "seeds" collected in Mexico by D. Mühlenfordt, a German mining engineer, who sent them to his brother, a professor of Botany and Zoology in Hannover, who then passed them on to Schrader (Wilkes 1967:6). That famous botanist recognized this strange grass as a distinct new genus (alas, wrongly assigned by him to the bambusoid tribe *Olyrae*), described it first in a footnote to the extremely rare, four page *Index Seminum Horti Academici Gottingensis* for 1832, which he then republished a year later in the journal *Linnaea* (8:Litt. 25, 1833).

There are five surviving specimens of these plants: four herbarium sheets in the Trinius Collection now in the Komarov Herbarium, St. Petersburg, Russia, where I located them in 1975 after a two-days' search, all misfiled, unmarked and unidentified as to their type status; and one in the old Bernhardi Herbarium now in the Missouri Botanical Garden Herbarium, St. Louis, labeled only with the original name, *Euchlaena mexicana,* and nothing else [and therefore once slated to be discarded by the fastidious Robert E. Woodson, my former major professor (cf. Solomon 1998)]. These five are all slender, depauperate plants, with only a few empty, white fruitcases and lacking any hard, fertile ones, typical of teosinte stragglers growing on dry roadsides, cliffs, or in other abnormal, deprived environments such as greenhouses (cf. Iltis photo in Doebley 1990c:445), and almost unidentifiable as to subspecies [N.B.: Langman 1964:528 cites four publications by an Eduard Muehlenpford, a travel writer (?) with strong botanical interests (cacti), author of a two-volume description of Mexico (1844), who visited Oaxaca and Chiapas and other places from 1829 on. I have not been able to locate these references, which may well turn out to contain information on teosinte and its unknown type locality. No Mühlenford or Muehlenpford are listed in Taxonomic Literature Ed. 2. Does the initial D. cited by Schrader refer perhaps to a *Dr.* Mühlenfordt? Could the two be the same?].

Now, it is surely astonishing, considering how locally common teosinte is in southwestern Mexico, and how well known these often majestic plants are to the *campesinos,* that not a single herbarium specimen, nor any of the abundant, indestructible, admittedly useless but still very pretty teosinte "seeds," or the even lovelier F_1 hybrid ears, were ever collected before then, not by Sessé and Mociño and the grand Royal

Botanical Expedition sent out at the end of the 18th Century by Charles the III to Nuevo España (McVaugh 1998), as Mexico was then called, who worked off and on for some dozen years in and around teosinte territory; nor by Humboldt and Bonpland a few years later, who in 1803 collected not only near Chilpancingo (in March, when at best only beat-up, dried-out old plants are to be found)), but also in and around Mexico City and Morelia (in the fall, at the right time, and in a region where teosinte is abundant); nor by any botanist—not at least until the middle of the 19th Century (see Iltis and Doebley 1980:1001–1002).

The near total lack of teosinte specimens until recently in the world's herbaria is astonishing. Wilkes (1967) lists less than 30 collections (not counting duplicates) gathered in the wild in the five major U.S. herbaria, an average of only five each of the six taxa now recognized! The Mexican herbaria, at least until recently, had practically none! Wilkes, of course, accumulated a splendid series, and our own extensive collection of teosinte fills three standard herbarium cabinets at the University of Wisconsin Herbarium. No doubt, the forbiddingly large size of a well-grown teosinte, with stems sometimes 3 m tall and 4 cm thick, may have had something to do with this neglect. Maize, teosinte and the related genus *Tripsacum,* are all large, complex grasses, difficult to collect, hence woefully under-represented. "Making an accurate and complete record of a *Tripsacum* [or maize, or teosinte] plant on an ordinary herbarium sheet is like attempting to stable a camel in a dog kennel" (Cutler and Anderson 1941). The necessity to collect at the right time (late fall or early winter, at the tail end of the wet season); the lack of knowledge about the very existence of teosinte and thus what to look for; the great and perplexing similarity to maize, imperceptibly woven as these teosinte plants often are into the very fabric of a maize field; and finally the general aversion of taxonomists to collecting cultivated plants in general, and weeds in particular, and of the agronomists to the collecting of any herbarium material whatsoever (e.g., I. E. Melhus; cf. Iltis et al. 1986), all must have been factors in the neglect to collect teosinte, and the subsequent monumental ignorance about its morphology and behavior.

Finally, could it be that teosinte was once much rarer, what with less than 10 million people in Mexico then, and agriculturally-created "open" habitats, in which the often weedy teosintes thrive, much more restricted? [A cultigen mimic, *Cleome chapalaensis* Iltis, appears to have had an analogous fate (Iltis 1998); for an opposing view, see Sauer 1993.]

On the other hand, the solitary, giant ears of maize are so different from the clustered, slender teosinte ears in size, structure, and utility, that even though by the 1840's Guatemala teosinte (*Z. luxurians*) was cultivated in southern Europe as potential cattle fodder, it was not until 1849 that the Italian Brignolia described a teosinte as the new *Reana giovannini* and placed it in the tribe *Zeineae*(!), and the 1870's that the close relationship of *Euchlaena* (i.e., teosinte) to *Zea mays* was recognized by Ascherson (1875; cf. Iltis and Doebley 1984; Iltis 1993). In 1877, the French agronomist Vinson declared it to be wild maize, but in the 1890's, Liberty Hyde Bailey declared a commonly found maize × teosinte F_1 hybrid (X *Zea canina* S. Wats.) with perfectly intermediate ears to be the ancestor of maize. Harshberger (1893) initially agreed, but later (1907:399), after seeing teosinte and its hybrids growing in Guanajuato, Mexico, suggested (no doubt influenced by the then new science of Mendelian genetics) that "our maize is of hybrid origin, probably starting as a sport of teosinte, which then crossed itself with the normal ancestor producing our cultivated corn," surely a prescient conclusion! [We can thank Harshberger, a man of both monumental ego, diligence and ability, for coining the term *ethnobotany* (cf. Davis 1994), which we still use to this day.] In a long paper honoring Ascherson, Schumann (1904:157), too, came to the conclusion that maize should be considered a form of teosinte, the "teratological" inflorescence of which was "fixed" during its extended cultivation.

In the 1930's, the idea that teosinte is the wild ancestor of maize received enormous support from R. A. Emerson and his brilliant group of young geneticists at Cornell University (G. W. Beadle, B. McClintock, L. F. Randolph and M. M. Rhoades). What should have clinched this highly charged controversy was Emerson and Beadle's demonstration of the cytogenetic homology between teosinte and maize, both having 10 pairs of chromosomes, which in their hybrids paired normally and closely at meiosis with the same frequency of crossing over as in maize, and the ability of the two taxa to produce fully fertile F_1 hybrids (Galinat 1988:5). That should have settled many an argument, but the "New Systematics" was still in its infancy. In fact, as soon as Mangelsdorf and Reeves' (1939) Tripartite Hypothesis came out, Beadle (1939) immediately shot back that teosinte *was* the one and only true "wild maize" and not any intergeneric hybrid. But his view was not universally accepted, even among some geneticists, who were evidently more impressed by maize ear morphology than cytogenetic homology.

But while Reeves and Mangelsdorf (1942) did accept the teosintes as species of *Zea* [e.g., *Zea perennis* (Hitchc.) Reeves & Mangelsd.; *Zea mexicana* (Schrader) O. Ktz., a combination made by the maverick Otto Kuntze already in 1904], the confusion among taxonomists regarding the wild annual taxa lasted well into 1960's, when intensive, wide-ranging field work focusing on teosinte was carried out in Mexico and Guatemala by ethnobotanist Garrison Wilkes (1967, 1977, 1979, 1986), Mangelsdorf's energetic graduate student at Harvard. In his splendid monograph, he finally gave the world a picture that suggested a geographically-speciating, monophyletic clade, that is, a "good" taxonomic genus of two wild species, *Z. perennis* and *Z. mexicana,* with the latter divisible into six allopatric "races," each with its own morphology and ecology (Table 1). Although not abandoning Mangelsdorf's notions of hybridization with maize as a major contributor to teosinte diversification, Wilkes was careful to state that this evidently indicates *not* some recent intergeneric hybrid origin for "teosinte," but a rather lengthy evolutionary history.

Shortly thereafter, and following a suggestion by Darlington (1956), Iltis (1972) finally transferred the two wild, annual species of teosinte to *Zea mays* as subspecies, thus supporting his then current interpretation of the Orthodox Teosinte Hypothesis that the maize ear evolved directly from the teosinte ear (Iltis 1971), while *Euchlaena luxurians* was soon transferred, as a species, to *Zea* by Bird (1978).

Highly focused fieldwork in Mexico, first with Garrison Wilkes as members of George Beadle's "teosinte mutation hunt" of 1971, then alone in Mexico and Guatemala (Iltis, Kolterman and Benz 1986), and later with my student John Doebley, we at the University of Wisconsin were able to accumulate sufficient teosinte herbarium material to allow the study of *Zea* taxonomy in a formal, taxonomically rigorous way. Taking a detailed look at the comparative morphology of both maize and Wilkes' teosinte races, the resulting monograph (Doebley and Iltis 1980; Iltis and Doebley 1980; Doebley 1983, 1990a) was based in large part on a detailed morphological analysis of the tassel and especially its spikelets, both of these male structures deliberately chosen because they remained largely uninfluenced by human selection for larger ears and larger, more abundant grain. Previous to this, maize tassels were studied by Edgar Anderson and his associates, as were their male spikelets by his student, my friend and schoolmate Reino Alava (1952; Doebley 1983), but only of maize and not of its ancestor, what with teosinte having been all but excluded from serious consideration by some strong Mangelsdorfian mental block.

In our revision, we stated as a general ethnobotanical principle that "*. . . the uniqueness of the maize ear notwithstanding . . . the fundamental systematic classification of economic genera should never be based primarily on those morphological features deliberately selected for by man*" (Doebley and Iltis 1980), such as polystichy or gigantism of the maize ear, which, with the sole exception of maize, are attributes totally unknown among the one thousand species of the Andropogonoideae, the giant tribe to which *Zea* belongs.

Compared to Charles Gilly's preliminary taxonomy (1948; cf. Iltis and Doebley 1984; Iltis 1993) or Wilkes' (1967) racial classification (Table 1), the Section *Zea* was expanded to include not only maize, but also (though rearranged into three sister subspecies) those five of Wilkes' (1967) annual teosinte races of Mexico and Guatemala which *in their identical male spikelet morphology* and great interfertility with maize betrayed their close relationship to each other and to maize. The Section *Luxuriantes* was established to recognize the taxonomic affinities of both the two Mexican perennials from Jalisco (*Zea perennis, Zea diploperennis* Iltis, Doebley & Guzman, 1979) as well as the annual *Z. luxurians,* native to (Mexico?), Guatemala, Honduras (now extinct?), and Nicaragua (Iltis and Benz, unpublished), all these three taxa held together by their double-keeled glumes, a unique character of the male spikelet previously unrecognized in the genus.

The taxonomy then proposed has stood the test of time. Now, in addition, with new molecular techniques, the ancestral populations that gave rise to maize were soon identified as the central meta-population of Balsas Teosinte, *Zea mays* ssp. *parviglumis* (Doebley, Goodman and Stuber 1984; Smith, Goodman and Stuber 1984), a wonderful achievement previously only hinted at (McClintock, Kato and Blumenschein 1981; cf Iltis 1987:213).

II. TEOSINTE TILLERING IN TEMPERATE LATITUDES, A CAUSE OF UNEXPECTED CONFUSION

An accurate understanding of the natural history of living organisms, *how they live in their native habitat,* is crucial to make evolutionary sense of their biology. Thus, the widespread failure to know how teosinte grows in Mexico or Guatemala has lead to misleading illustrations and enormous conceptual difficulties, doubly so because field work, often frowned upon, has rarely been carried out with teosinte, and then, even now, mostly for the collection of germ plasm. Thus, the question of teosinte tillering has to be addressed.

Most large, open-grown annual teosinte plants *in Mexico or Guatemala* have a monopodial, distichous, "herring-bone" (Kempton 1937:pl. 17-2) or "candelabra" (Wilkes 1967) branching pattern, or, if crowded, develop several lateral branches but only near the top. All these primary branches end in tassels (A^1, Fig. 1). Tillers (suckers) are very rare in most populations, hardly ever more than one or two from the base of a plant, and in most ways reiterate the structure of the main stem, with a tassel at the apex of their culm and ear clusters at every but the top-most nodes, but *no lateral* (i.e., *primary*) *branches* in the axil of the leaves. In fact, tillering is so unusual in Balsas Teosinte that when, during our field work in Guerrero or Guatemala, we happened to come across out first tillered plant, I felt compelled to stop whatever we were doing, and photograph it from every angle. Indeed, "the growth habit of teosinte in naturally occurring populations [in Mexico and Guatemala] is uniformly the same. A single culm is the rule, and tillering is encountered in only a small fraction of the plants" (Wilkes 1967:7).

Previous to the 1970's, only a handful of people had ever studied any of the teosinte species in the field, only one person, Garrison Wilkes, had seen them all, and except for a single photograph (Kempton 1937:pl. 17) and a starkly diagrammatic but prescient drawing of the monopodial, candelabra-branched, hypothetical teosinte ancestor of maize by Montgomery (1906: 61, reproduced in Iltis 1983a:89), no other such illustrations, as far as I know, had ever been published.

Thus, scientists who only studied teosinte cultivated at ca 30° to 50° North latitude were often misled. Annual teosintes growing in such high latitudes, under long- (lengthening-) day regimes during the early part of their life cycle, produce tillers (=suckers) in profusion, with a dozen or more from the base of a single individual plant, with the main stem all but lost inside such a dense cluster of strong stems (see illustrations of plants grown in Boston in Wilkes 1967:111–118, reproduced in Mangelsdorf 1974:27–33). "Teosinte is a short-day plant and develops a highly tillered, almost perennial growth form under continuous long days" (Wilkes 1967:34) such as one finds in midsummer in Madison, Wisconsin (43°) or Boston, Massachusetts (42°). Moreover, under such crowded, self-shaded conditions, not only do the *tillers lack primary lateral branches,* but these shade out and thus suppress the development of all the primary lateral branches of the central (main) stem as well (Iltis 1983b:894, footnote 66).

We must now consider the fact that, during the evolutionary transition to maize, the tassel that terminates these branches in teosinte somehow became substituted by its homologue, the large, polystichous ear of maize. Thus, any theory that attempts to explain the origin of the maize ear is made incomprehensible by illustrations of abnormal ancestral teosintes that lack the critical tassel-tipped primary branches on the main stem. Such drawings have, in fact, made it very difficult for anyone to visualize teosinte's natural candelabra growth form as it develops in its native environment in Mexico, and hence to visualize the evolution of maize and its ear.

And yet, to this day, densely-tillered, branchless teosintes have haunted the scientific literature. J. D. Hooker's (1879) beautiful illustration (plate 6414 in Curtis' Botanical Magazine) of a *Euchlaena luxurians* [=*Zea luxurians*] with many (30–40?) densely crowded stems, grown presumably in London (51°N); an old (1898?) drawing of presumably the same species (here called *E. mexicana*) with an estimated 30 or more tillers, in A. S. Hitchcock's widely accessible *Manual of the Grasses of the United States* (1951:793) of plants probably grown in Europe; or J. P. Gay's photograph (1984:109, 125) of a teosinte grown in France (45°N)—all are misleading, for they show an incredible proliferation of tassel-tipped *tillers* (suckers), but no main stem whatsoever, with or without primary branches.

Similarly misleading are the widely copied pictures of teosinte in George Beadle's (1972:4; 1977:617; 1978; 1980:114) papers defending the Orthodox Teosinte Hypothesis. They show a plant with a *branchless* main stem, from the base of which radiate anywhere from four to eight tillers, that also *lack lateral branches.* Drawn apparently by a Field Museum of Natural History staff artist of one of the many hundred plants grown by Beadle at Chicago (42°N) of "Northern Teosinte" (a somewhat long-day tolerant segregate developed by Galinat from maize × Nobogame teosinte hybrids backcrossed to teosinte; cf. Wilkes 1970), it shows the kind of tillered growth form that one would expect at that latitude. Plants of this cultivar grown in Madison by James Coors (UW Agronomy) were similarly tillered. Unfortunately, this illustration, in one form or another, was later picked up by Galinat (1974, 1985a:250), as well as by picture editors needing an illustration of teosinte for a newspaper story, a scientific article or a book. It reappeared in S. J. Gould's (1984: 14; 1985) discussion of my now discarded Catastrophic Sexual Transmutation Theory (CSTT), in B. D. Smith's *The Emergence of Agriculture* (1995:153; though corrected in edition 2, 1998: 153!), and now in Balick and Cox's *Plants, People and Culture* (1997).

Credit for being the first to publish a life-like drawing of a teosinte with a candelabra-branching pattern (albeit stylized but basically accurate, even if, inexplicably, only half as tall as the Mexican *campesino* standing next to it) must apparently go to the artistically talented Walton Galinat (1974; 1977:13). Though the drawing is the first in a series of five illustrating the evolution of maize from teosinte, the legend does not explain the significance of the "candelabra" branching pattern or of its tassel-tipped branches.

Undoubtedly, Galinat's "candelabra" teosinte drawing was influenced by his participation in Beadle's 1971 "Teosinte Mutation Hunt" to Guerrero, Mexico, where both he and Beadle, as well as I, saw an abundance of such branched teosintes. Nevertheless, Beadle (1972), who was more interested in genetics than morphology, must have missed the significance of such branching, for he published the picture of his basally-tillered, Chicago-grown teosinte only a year later. Inexplicably, Galinat (1985a) then used either Beadle's tillered teosinte drawing or his own "candelabra" teosinte to illustrate his articles during the next few years, only eventually to combine both drawings into one diagram to show what, according to him, were the two separate pathways by which maize and its races evolved. In this bizarre new theory on the "Double Origin of Maize," Galinat (1992:214–221, Fig. 4; 1995:10–11) illustrates one of the ancestors by a redrawing of Beadle's tillered "basal branching type," this supposedly representing *Zea mays parviglumis,* Balsas teosinte, as (he claims) it is found "under good growing conditions" in its native habitat in the Basas River basin; and the other ancestor of maize by his own old drawing of the "lateral branching [i.e., candelabra] type," this supposedly representing *Z. m. mexicana,* the Chalco teosinte of the Valley of Mexico, the two evolutionary streams independently evolving into two types of maize, and these eventually, by combining millennia later, into our Corn Belt "dents."

This new twist on an already much too convoluted story is totally unsustainable and exceeds the limits of acceptable confusion on both genetic and morphological grounds: first, overwhelming evidence points to Balsas teosinte as *the* ancestor of maize, without *any* genetic input from Chalco Teosinte (Doebley 1990c); and second, candelabra-branched plants are the rule in *both* open-grown Balsas and Chalco teosinte, with excessive tillering, as shown in Beadle's (1972) and now Galinat's (1992) drawings, simply a response to long-day growing conditions not found in Mexico (Iltis 1987:204). There are perils in deeply held points of view (I ought to know!), for, as in the case of teosinte ear-cluster architecture, they blind you to even the most obvious morphological facts. And in teosinte, these have always been difficult to come by.

Tillering is common in some races of maize, such as the several "suckers" often seen in early sweet corn varieties, in the 8-rowed New England Flints (Galinat 1967:351; 1985a:270; 1995: 10–11) or in the 8-rowed flour corns indigenous to the Upper Missouri River area (Galinat 1995:

10–11), and may simply reflect relatively recent introduction of subtropical, low-latitude maize cultivars to higher latitudes.

It is of great interest that the earliest scientific illustration of a maize plant, the oft-reproduced woodcut of *Turcicum frumentum,* or *Türckisch korn,* in Leonhart Fuchs's *De Historia Stirpium* of 1542 (Meyer, Trueblood and Heller 1999; Finan 1948) and in its abridged German translation, the *New Kreuterbuch* of 1543, shows a robust plant with three tillers (suckers) at its base, a central main stem bearing four ears, two of the tillers bearing one ear each, and one, none. Faithfully drawn from nature by Fuchs's artist, Albrecht Meyer, to show its eight rows of grains (but not a thickened central spike in the tassels), the tillering in this splendid illustration also reflects the teosintoid response of maize to the long-day growing regime of Germany, to which this strange crop, "*newly brought to us from Asia, Turkey, and Greece,*" and "*now popular, almost common, and grown in many gardens*" (Fuchs 1543), had yet to become adapted.

III. THE ORIGIN OF MAIZE BY SEXUAL TRANSLOCATION

Among recent investigators of the origin of maize there is general agreement that, on genetic grounds, the small-eared, few-grained, distichous Balsas Teosinte (*Zea mays* ssp. *parviglumis*) is the direct ancestor of maize, that the multi-grained, multi-ranked (polystichous) ears of maize are anthropogenic, the result of human selection, and that there is no such an entity as a polystichous "wild maize." Still, one has to choose from several theories how teosinte could have been transformed into maize.

1. The *Orthodox Teosinte Hypothesis* (OTH) states that *maize is directly derived from teosinte* [Harshberger 1907; Beadle 1939, 1972, 1977, 1980 (please note the totally confusing illustration on p. 116! To correct, delete top row and add Chalco teosinte to bottom row; the intermediate ear that belongs in the middle can be copied from Beadle 1939: Fig. 1B. A correct version was printed in the German edition: *Spektrum der Wissenschaft,* March 1980:96)]; Collins 1919, 1925; Doebley 1983, 1990a,b, Doebley, Stec and Hubbard 1997; Doebley and Wang 1997; Galinat 1975, 1985a, 1988b, 1992, 1995; Iltis 1971]. Implicit in this view is that the ear of maize was directly derived from the ear of teosinte.

The OTH was concisely summarized by me 30 years ago, at the tumultuous 1969 Illinois Corn Conference (see Iltis and Doebley 1984: 604; Mangelsdorf 1974:180, footnote), in my first attempt to come to grips with the morphological origin of maize, a view I have since, first abandoned (1980–1994) and then more recently returned to, but with modifications. I proposed then, in *The Maize Mystique* (Iltis 1971:1; reprinted in Goodman 1988:205), that

> Corn is domesticated teosinte (*Euchlaena mexicana, sensu lato*), differing *not at all* in any of its basic vegetative, floral, or genetic attributes [except for the ear and the thickened, central tassel spike]. All the unique peculiarities of corn are concentrated in the structure of the female inflorescence, the corncob, and all can be easily interpreted as the result of human selection for human needs for more food: for greater quantity, and for greater, more efficient harvestability. Thus, compared with wild teosinte, the increase in the volume of harvest sub-units, namely in grain size, in grain row number through activation of aborted spikelets and [rarely] aborted florets, in rank number [polystichy] and in cob length were all selected for by primitive man to produce more food. The decrease in the number of primary harvest units (female inflorescences) to one or two giant, apically dominant, terminal inflorescences per plant; the coordinated protection of these inflorescences by many husks, these liberated from their old function of protecting the many, now suppressed, lateral [ear clusters]; and the change [by loss of abscission layer] from a fragmenting, disarticulating rachis (cob axis) and rachilla to one that is shatterproof, were all selected for by primitive man to increase the ease and efficiency of harvesting. In addition, the reinforcement in the corn plant of teosinte's . . . single, gigantic stem are likewise due to human selection. The resulting cultigen is easily grown, easily harvestable and abundantly yielding.

While here the OTH addressed three of the four or five main genetic and morphological differences between teosinte and maize (doubling of grain by pedicellate spikelet activation, polystichy, loss of abscission layers), as well as the obviously multigenic increases in grain size, grain number and protection, it did not deal in any way with the complex architecture of either the whole teosinte plant (i.e., tillering) or the teosinte ear clusters, namely the fact that most teosinte ears are borne in crowded axillary *lateral* ear branches and the maize ears are solitary and *terminal* at the end of the *primary* branches.

There are, of course, those who believe that primary teosinte branches may be tipped by an ear which would thus be in a position to evolve straight into a maize ear. For them, there is no problem. But, except possibly in some abnormal depauperate plants (?), the primary branches of open- and well-grown teosinte plants always have a tassel at their apices (see Iltis 1983b:894, footnote 66, regarding abortion/suppression of primary branch axes under crowded conditions). In fact, the typical "candelabra" growth form of open-grown wild teosinte was unknown to most botanists who struggled with maize evolution, so that the morphological difficulties of translocating lateral femininity to the terminal position of the male tassel had over the years bothered only those few who had seen live plants growing in their native habitat (e.g., Kempton 1937, pl. 17). To me, however, it presented a conundrum in need of resolution. Thus, to solve this one problem, and over-emphasizing the direct homology of the maize ear and the teosinte primary branch tassel spike, as well as the well-known but less-direct homeology between the maize ear and the maize tassel spike (e.g., Iltis 1911), I presented in the 1980's the following hypothesis:

2. *The Catastrophic Sexual Transmutation Theory* (CSTT), which derived the ear of maize from the tassel spike of teosinte (Iltis, in Doebley and Iltis 1980; Iltis 1983b, 1987; Iltis, in Iltis and Doebley, 1984; Gould 1984). In other words, "the *Catastrophic Sexual Transmutation Theory proposed that the maize ear is the feminized, condensed central spike of the tassel that terminates primary teosinte branches*," the feminization having reactivated a vestigial ovary in both of the already soft-glumed male spikelets of the Andropogonoid pair (Iltis 1987:197). While it seemed a simple way to solve the problem of the terminal maize ear, it was illogical and wrong on many counts (see abstract!). Nevertheless, it contained useful mistakes, however, in that it not only stimulated research by others (Sundberg and Orr 1986, 1990; Orr and Sundberg 1994) and served as a whipping boy for valid criticisms (e.g., Galinat 1985b), but brought valuable information about teosinte together in one place. Yet the problem it tried to solve remains still with us.

3. *The Sexual Translocation Theory* (STLT), here presented in print for the first time, attempts to explain how (or why) the female morphology of teosinte that terminates secondary or tertiary branchlets lateral to the primary branches was able to become translocated to the apex of the primary branch in maize by stepwise increases in apical dominance through increases in ear size by a process of sexual homeotic translocations or conversions (Sattler 1988).

Though certain aspects resemble the CSTT, the STLT is based on new information regarding the basic branching architecture of the teosinte ear cluster, which heretofore has been an unknown, or ignored, entity (Cámara-H. and Gambino 1990).

Teosinte ear cluster morphology appears to be very important, even though the complexly-branched, much compacted architecture of teosinte ear clusters, and their role and meaning in the evolution of maize has never really been seriously considered and is even now all but ignored. Because of their usually extreme condensation and bewildering complexity, especially if several of them are compounded into a super-cluster containing as many as 20 or more ears in various stages of maturity, and an equal number of bracts (spathes) and prophylls to boot, teosinte ear clusters have defied proper interpretation by even competent plant morphologists. Thus, though often discussed as an adaptive seed protection, storage and dispersal device, and as a preadaptation leading to the creation of the maize ear (Galinat 1975, 1985a), their internal structure had remained uninvestigated. The few illustrations that have been made are all misleading. They are either incomplete and show only older ears, what with the slender, younger, still soft and fragile ears remaining hidden within the prophylls and ear spathes (Weatherwax 1935:29), or they are simply wrong, the ears being mistakenly shown as binary, that is, in pairs, with one ear sessile and the other pedicellate, in an erroneous analogy to the typically sessile-pedicellate Andropogonoid male spikelet pairs of the tassel (Galinat 1975, 1985a:251). Beadle never worried about this, and I (Iltis 1987), though spending fully five pages of discussion on various aspects of ear cluster biology, from gross morphology to reproductive ecology and CO_2 and H_2O sequestering within the tightly husked ear clusters, and finding the subject intuitively important and tantalizing, had no understanding of the complex morphology within either. In fact, in my otherwise exactly proportional drawing of a large teosinte plant (Fig. 1), the ear clusters are illustrated simply in a diagrammatic, symbolic fashion to show their correct position on the plant and nothing more. To this day, there exists no careful, accurate, faithfully executed illustration of even a simple teosinte ear cluster.

But all is not lost. Recently, Julian Cámara-H. and S. Gambino (1990), two Argentinian morphologists, published "Ontogeny and Morphology of *Zea diploperennis* Inflorescences and the Origin of Maize," in which the architecture of the teosinte ear cluster is interpreted as a typical Andropogonoid inflorescence (as found in *Andropogon, Tripsacum* and other less specialized genera, and thus, not surprisingly, also in *Zea*) characterized by a staggered sequential maturation of its branches (i.e., ears). Though these authors presented only diagrammatic, not actual representations, their insights were helpful in the present context and are fully explained in the following discussions and illustrations (Figs. 1–17).

In their conclusions, to my distress, however, they reject both "... those theories [OTH] attributing the origin of the ear of cultivated maize to the pistillate inflorescence [i.e., the ear] of teosinte or ... as the more recent [CSTT] postulates, as stemming from the teosinte tassel," but opted instead to "... support the origin of [maize] as deriving from wild maize ...," namely Mangelsdorf's (1974, 1986) view long since abandoned by almost all others who have worried about the origin of maize. But this should perhaps surprise no one, if one recalls Cámara's long association with Mangelsdorf, their joint experiments to select out of *Z. m. mays* × *Z. diploperennis* hybrids perennial maize (Cámara-H. and Mangelsdorf 1981), and Mangelsdorf's powerful personality that had a way of dominating both his students and associates.

These disagreements aside, the insights of these botanists has now led me to postulate still another explanation to account for the evolution of maize, specifically for the terminal position of the maize ear at the end of the primary branches, where it takes the place of a tassel. *The Sexual Trans-Location Theory* (STLT) derives the maize ear from the teosinte ear by partly incremental, partly more stepwise morphological changes, very much as the OTH, but tries to explain the change in sexual position, not by a one-step feminization of the tassel as in the old CSTT, or by a direct gradual transformation of a single teosinte ear already terminating a primary branch, but by invoking one or two homeotic sexual translocations, replacing first the secondary branch tassels and finally the primary branch tassel (i.e., its spike) with a female structure. All these changes are concurrent with steady but punctuated increases in ear complexity and ear size, these made possible, first, at the expense of the less mature ears within an ear cluster, and eventually of all the ear clusters themselves, which became suppressed by the apical dominance exerted over the primary branch by the terminal maize ear. Based on Cámara-H. and Gambino's (1990) recent interpretation of the elusive branching pattern of teosinte inflorescences within the ear clusters, which they were able to discern from the more open, less complicated, less congested ear clusters of the most primitive species within the genus, *Zea diploperennis* (cultivated by Cámara for Mangelsdorf in Buenos Aires), the basic simple ear cluster turns out to be an Andropogonoid *rhipidium* (Figs. 3, 4), a cymose, sympodial, sequentially maturing branching system, composed of one to six or more tertiary, quaternary, etc. branches (rames) developing alternately in opposite directions, each tipped by a teosinte ear.

According to the STLT, the evolution of the maize ear from teosinte may thus be visualized as a phylogenetic homeotic process, that is, in the broad sense, one body structure replacing another, or "The assumption by one part of an organism of the likeness of another part" (Sattler 1988:1609–11), as follows: A rare genetic mutation (e.g., Dorweiler et al. 1993; Dorweiler and Doebley 1997) exposed the teosinte grains from their now reduced fruitcases and opened the door to human utilization and the initiation of human selection (Fig. 6d, 7c, d). By its very nature, the sequentially-maturing branching system would have allowed mutations for increased grain size and/or doubling of grain number (all requiring increased nutrients and all first expressed in the earliest maturing ear of each ear cluster) to cannibalize the resources needed from the later-maturing, younger, subsidiary ears even without any major structural changes or increases in photosynthetic output, simply by an increase in apical dominance. This explains how human selection would have induced competition for nutrients, first within and soon between teosinte ear clusters and, by suppression (abortion), eventually genetically fixed, reduced within a primary *Zea* branch the number of ears from ca. 100 to only one, and within a whole *Zea* plant, from a large candelabra-branched plant of cultivated teosinte to a modern plant of maize, the number of functional ears from an initial, let's say, 100 teosinte ears, to 20 proto-maize earlets, to 10 small maize ears and eventually, to two maize ears, all within plants of the same size producing the same 1000 grains each (100 × 10; 20 × 50; 10 × 100; 2 × 500). All this would be accomplished without any major structural changes in the *basic* architecture of the plant except ±gradual internode condensation, loss of ear disarticulation, apical I° branch meristem proliferation leading to ear polystichy, and this in turn, and correlated with it, to a gradual husk polystichy and husk proliferation in the branch nodes closest to the ear "butt," the husks of the ear-bearing maize branch grading from maizoid polystichy at the apex to teosintoid distichy at the base (Kiesselbach 1949:51; pers. obs.). In short, there is then no need to hypothesize any *major,* instant mutations shortening primary branches or other radical changes in plant gross architecture as being essential (See Sect. IV).

The evolutionary sequence proposed by the STLT thus envisions the development of a gradually increasing apical dominance that comes with ever larger grains, and ever larger, but fewer ears terminating ever shorter I° branches (each ear having control over an ever larger nutrient source), until only one large ear terminates the tip of the primary branch as the ultimate nutrient sink. The sexually mixed (distal-male, proximal-female) inflorescences hypothesized for the Tehuacán archeological maize and often seen in contemporary material offers additional evidence for the STLT (Sundberg and Orr 1986; cf. Benz and Iltis 1990:507; Benz and Long 2000, in press).

In a way, the STLT combines parts of the older OTH and some ideas of the rejected CSTT: namely, that the teosinte ear evolved directly into the maize ear, but along the way, by one (or two) homeotic sexual translocation(s), allowing it thus to eventually occupy the terminal position held within the primary branch tassel by the tassel "spike," its homologue.

IV. AN ILLUSTRATED GUIDE TO THE SEXUAL TRANSLOCATION THEORY (STLT)

Better than words, the following diagrams (Fig. 1-17) outline the basically incremental but nevertheless somewhat stepwise evolution of the maize ear from the teosinte ear, as visualized in this modification of the Orthodox Teosinte Hypothesis, the STLT, by which increased apical dominance was achieved in the following hypothetical sequence: 1), a one-time, rare, grain-projecting, glume-thinning mutation induced grain utilization and thus, human selection; this, in turn, resulting, 2), in larger grains and grain doubling by spikelet reactivation (i.e., termination of pedicellate spikelet abortion; Sundberg et al. 1995); leading, 3), automatically to the earliest-maturing ear within each ear cluster intercepting the nutrients going to the younger, later-maturing ears, and their suppression; then, eventually, 4), to competition for nutrients between ear clusters and, eventually, ears; and finally and concurrently, 5), to one or two sexual translocations by way of homeotic sexual conversions, allowing female morphology to be expressed at the apex of, first, the secondary branches and, ultimately, the primary branches. The idea revolves around the basic, untillered, candelabra architecture of the annual teosinte plant as well as the sympodial cymose branching of the axillary teosinte ear clusters, which for far too long has been misunderstood. Recently, Cámara-H. and Gambino (1990) clarified this problem, and have allowed, in my view, to make the rise of the teosinte ear to absolute apical dominance a morphologically more intelligible process. [Nota Bene: Cámara-H. and Gambino's (1990) codifiction of stem and branches is followed here (i.e., A^0-main axis/stem, A^1-primary branch, A^2, A^3, etc.-lateral branches of higher order), but conflicts with that of Orr and Sundberg (1994) (i.e., A^1-main axis/stem, A^2-primary branch, A^3, A^4, etc.-lateral branches of higher order).]

V. WHY WAS TEOSINTE DOMESTICATED?

Agriculture, it has been said, was the first act of civilization. But only an agriculturalist would be guilty of so fraudulent a claim. Horticulture came before agriculture, and the garden itself came before both. (*Gardens, Plants and Man* by Carlton B. Lees 1970:52)

A. AN ETHNOBOTANICAL MYSTERY IN SEARCH OF AN ANSWER:

The origin of agriculture has been for the past 100 years a popular "bandwagon" (Flannery 1973) for theorizing in both the social and bio-

Open-grown Annual Teosinte from the Valley of Mexico
(*Zea mays* ssp. *mexicana,* Race Chalco)

Fig. 1. Annual Teosinte (*Zea mays* ssp. *mexicana,* Race Chalco): Open-grown, robust, candelabra-form individual collected 5.5 km NE from Los Reyes on the road to Texcoco, Valley of Mexico (alt. ca. 2000 m). In teosinte plants from dense stands (e.g., fields of maize or teosinte), the lower primary branches tend to become suppressed (as is the 3rd branch from the base in Fig. 1). Plants of *Z. mays* ssp. *parviglumis,* the ancestor of maize, though somewhat more slender, are nearly identical. Box (a) corresponds to diagram (a), box (b) to diagram (b) in Fig. 3. Though the ear clusters as shown on the right-hand side of the plant are simplified diagrammatic abstractions, the internode and branching pattern is based on exact measurements of an actual plant. The gentleman serving as a scale in the picture is Stephen Solheim, 6′3″ (1.9 m) tall, one of my field companions on the fall, 1980 teosinte hunt (H. H. Iltis del. 1980).

Open-grown Annual Teosinte (diagrammatic)
(ear clusters not shown except in insets)

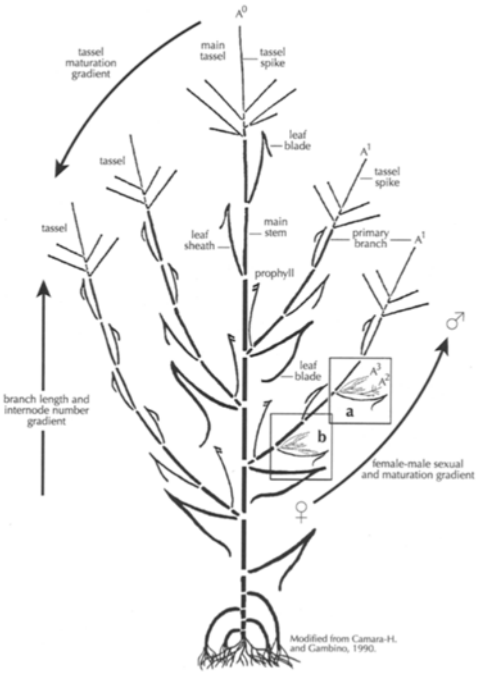

Fig. 2. Annual Teosinte (*Zea mays* ssp. *parviglumis* or *Z.m.* ssp. *mexicana*), Diagram of Branching Pattern: Ear cluster in box (a), terminating in a small tassel, enlarged in Fig. 3a; that in box (b), being closer to the main stem and the zone of female hormonal expression, hence all female, enlarged in Fig. 3b (modified from Cámara-H. and Gambino, 1990).

logical-ethnobotanical sciences. Increasing human populations causing drastic decrease in large game (Cohen 1977) and the concomitant increase in utilization of small mammals (Iltis 1987:212; 1989); increasing seasonality in a wildly fluctuating post-glacial climate; the perfection of food storage [in the Old World perhaps by imitating hamsters, e.g., *Cricetus cricetus* (cf. Iltis 1987:212; 1989, where editorial discretion deleted a section on the "storage teaching" role of Near Eastern, seed storing rodents), in the New World, pocket gophers, e.g., *Geomys* spp. or *Orthogeomys grandis,* the ravagers of the two local perennial teosintes in the Sierra de Manantlán, Jalisco, Mexico (Iltis pers. obs.; Benz pers. com.)], and the consequent need for permanent settlements, all seemed to have played their interrelated roles (Iltis 1987:211–213; 1989). The problem has more recently been properly reformulated as the "Origin*s* of Agriculture" (Sauer 1965; Reed 1977; Flannery 1973; Iltis 1987; Cowan and Watson 1992; Smith 1998); for aside from somewhat analogous, highly seasonal climates, that both necessitated the need for human food storage but also furnished the dry-season-adapted species, namely, the indispensable botanical infrastructure which, adapted to survive the dry season, is thus preadapted for domestication, the Old World (Near Eastern) and New World (Mexican) "agricultures" were autochthonous, independently evolved phenomena, with drastically different

Teosinte Secondary (A^2), Tertiary (A^3) Branches, etc., with Compound and Simple Ear Clusters

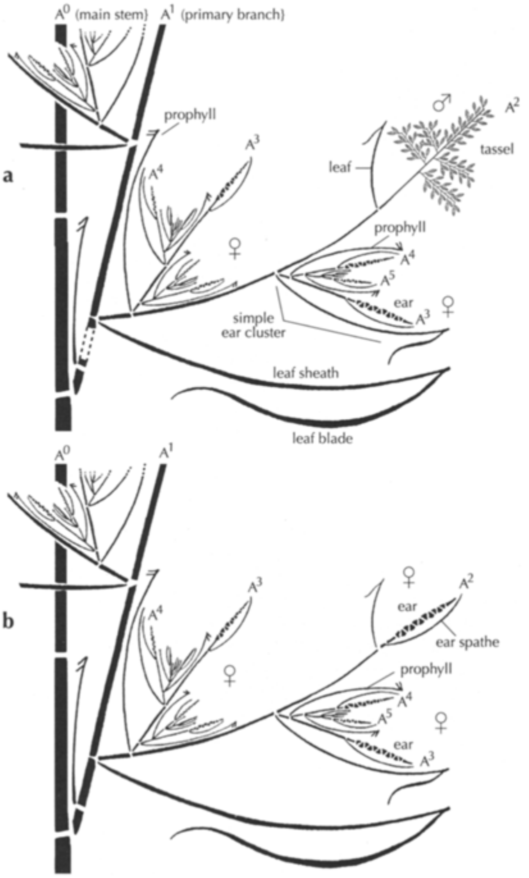

Fig. 3. Branching Pattern of Teosinte Axillary Inflorescences (Ear Clusters): Diagram based on ear clusters of *Zea diploperennis,* the most primitive teosinte, drawn as if uncondensed for easier interpretation. (a) Secondary branch (A^2), arising from a primary branch (A^1), bearing a compound ear cluster near its base, a simple ear cluster in the middle, and a small tassel at the tip. Each ear cluster is composed of a series of branchlets of higher order (A^3, A^4, etc.) in a cymose sympodial arrangement, the branchlets tipped by sequentially maturing ears. The lower (distal) simple ear cluster, enlarged in Fig. 4a, shows branching at its most basic. (b) Ear cluster from near base of primary branch axis (A^1), hence all female, with the secondary branch (A^2) tipped by an ear. [Such ear clusters would presumably skip the first of the hypothetical homeotic sexual conversions (translocations), with their terminal ears becoming maizoid more directly (cf. Figs. 9–14)]. (Both diagrams modified after Cámara-H. and Gambino 1990). In actuality, both in the perennial and especially annual teosintes, the internodes of A^3, A^4, etc. are extremely short, with several ear clusters often so tightly telescoped into a congested, compound cluster, and with all ears, prophylls and leaves so tightly em-

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braced by the subtending leaf sheath, that the ear cluster morphology becomes very difficult to interpret or illustrate.

cultigens, methodologies, climates and trajectories (Clark and Piggott 1965:171–181).

The many small grains of the Near-Eastern *true* agriculture [from the Latin *ager,* genitive singular *agri,* a field] are all long-day (lengthening-day; cf. Iltis 1987:204–206), winter-rain germinating, spring-and early summer-maturing, cool-temperate, small and slender, monocephalic, perfect-flowered and selfing ephemeral annuals that can be easily mass-collected, hence mass-selected, and, ranging originally in dense stands from deserts to upland woodlands, were pre-adapted to be eventually mass-sown in the flood plains of streams, these relatively weed free, yearly rejuvenated and ready-made seed beds. That these seeds are also easily stored is no small consideration. In many respects, much the same can be said of the Near Eastern legumes.

The key species of the Mesoamerican food triumvirate, on the other hand, beans, squash and maize, are all large, short-day (i.e., shortening-day; cf. Iltis 1987:204–206), summer-rain germinating, unisexual-flowered (except beans) and out-crossing, fall-maturing subtropical annuals, that must be individually hand-planted, individually cared for, individually hand-harvested—plant by plant—and for the most part individually selected (Sauer 1965) and except for beans, individually stored. They are, in short, basically garden plants and subject to a horticulture (from the Latin, *hortus,* a garden) that began their domestication in the disturbed, weedy and highly fertilized kitchen middens near campsites and shelters, often near water sources, of the Mesoamerican hunter-gatherers. With the exception of minor (Chenopods, Amaranths), local, or unsuccessful attempts, true seed agriculture never took hold in the New World (till much later and not until implemented by technology) for lack of appropriate species to grow and appropriate climates to grow them in.

Flannery's (1973:287, 296) question of *why* the people of Mesoamerica brought these species into domestication, more specifically, "Why . . . such a plant [as teosinte was] domesticated in the first place?" is, despite his protestations,

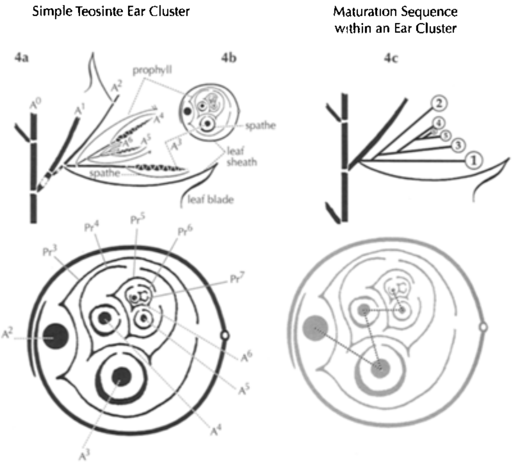


Fig. 4. Branching and Maturation Sequence Within a Simple Teosinte Ear Cluster: (a) Diagram of a simple teosinte ear cluster (from Fig. 3a or b, right-hand cluster): Technically, this is a *rhipidium,* a fan-shaped, sympodial, cymose, typically Andropogonoid branching system, with the lateral branches (tipped by ears) developing alternately in opposite directions. Each ear is subtended by a bladeless bract (spathe), each ear-bearing axis by a 2-nerved prophyll (indicated by 2 "flags" at tip), each cluster enclosed by a blade-bearing leaf-sheath. Each triangle represents a cupule (a hollowed-out rachis segment, or rachid), closed-off by the hard outer glume of its single fertile spikelet, the whole structure called the cupulate fruitcase, which permanently imprisons its solitary grain (4a and 4b after Cámara-H. and Gambino 1990). (b) Simple teosinte ear cluster, in cross-section. Each ear is surrounded by a spathe; each new branch by a 2-keeled bract, the prophyll, the whole ear cluster by a leaf-sheath. (c) Diagram of a simple teosinte ear cluster: Numbers indicate the maturation sequence of the ears in (a) and (b). Only after ear 1 (on A^3) is well on its way toward maturity will ear 2 (on A^4), then ear 3 (on A^5), etc., become fully mature, the lowest order ear (on A^3) preempting their nutrient supply. Often the smallest ears do not develop at all, or reach maturity only in favorable, wet years, and eventually disperse as empty, snow-white fruitcases. Of the two bottom diagrams (unnumbered), the left shows axes (A) and prophylls (Pr) in detail; the right, the zig-zag nature of ear cluster branching.

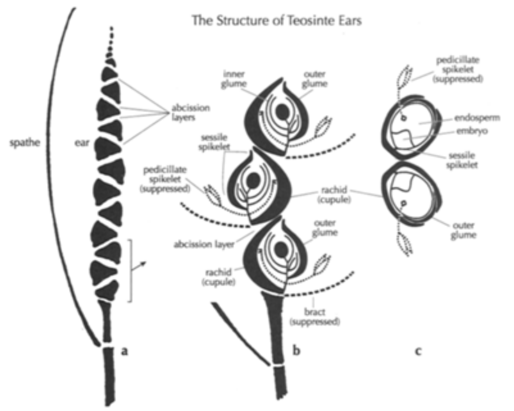


Fig. 5. Teosinte Ears and Fruitcases: (a) Diagram of teosinte ear, in longitudinal section. (b) Diagram of longitudinal section, in front view as in Fig. 6b, of the two basal cupulate fruitcases, each showing the thick, concave axis (rachis) segment (rachid, or cupule *sensu stricto*) and the hard, outer glume (the thinner half-circle), the two together enclosing both an empty floret and, above it, the single fertile floret with its grain (black dot); the suppressed pedicellate spikelet (shown as if developed and male), prophyll and bract indicated by thin, dotted lines (Modified after Cámara-H. and Gambino 1990). (c) Cross-section of two disarticulated cupulate fruitcases, as they would appear relative to each other if such successive fruitcases were transversely sectioned from apex of ear to base, with the position of the suppressed pedicellate spikelets shown correctly as originating from underneath the fertile spikelet (see Fig. 5b) (left side is adaxial, or back, as in Fig. 6a). Outer glume *margins* are very thin and surround more of the grain than shown, inner glume not shown at all. Note: The embyros in all the cross-section figures of individual grains (as in 5c) are diagrammatic abstractions and do not reflect either their exact position or extent.

relatively easy to answer, at least at one level, for who would not encourage the growth of plants one likes to eat in order to have them available six months later, near the end of the rainy season, when food is scarce and hunger great.

With time, accidental planting soon led to habit, and habit to selection, inadvertent or deliberate. In fact, wild (?) beans (Gentry 1968; Kaplan and Lynch 1999) and cultivated squashes (Smith 1997, 1998) have been found way back in the archeological record in Mesoamerica, so growing plants was nothing new by the time some people, somewhere, in Southwestern Mexico began to grow teosinte.

But, here now, a reformulation of Flannery's (1973:296) question has all of a sudden enormous implication: "*Why was teosinte chosen to be domesticated*?" It is an old, old question already asked by many others, such as Kempton (1937) and Mangelsdorf (1974), who could not imagine why anyone in his right mind would deliberately domesticate such a uniquely useless and inaccessible grain.

While, so far, the archeological evidence of teosinte grain as food is overwhelmingly negative, there are other interesting facts that suggest the initial use of teosinte was as a source of sugar and as a vegetable, two nutritional virtues of this giant green grass that may have initiated deliberate, if somewhat haphazard, cultivation, leading eventually, in plants with mutated fruitcases, to the domestication of teosinte for its grain. While this heterodox theory has never even been suggested, it may hold the key to finally resolve this seemingly intractable problem.

B. TEOSINTE AS A POTENTIAL CEREAL, THE NEGATIVE EVIDENCE:

But teosinte *is* the ancestor of maize, and was domesticated, and hence its paradoxical domestication must be discussed in detail. Given sufficient moisture, teosinte (*Zea* spp.) is a rapidly-growing robust annual that grows well even in dense stands. From the ethnobotanical standpoint, it is an abundant yielder of easily harvestable, easily storable fruitcases, each of which contains a relatively small grain. Not only that, but studies in Guatemala by Melhus (1953; cf. Iltis, Kolterman and Benz 1986) clearly showed that the nutrient value of wild *Zea* grains is more concentrated, hence much higher than that of maize (Robson et al. 1976).

If there ever was a grain *not* pre-adapted to be domesticated as a cereal, teosinte certainly would take first place. Unlike grains of all other domesticated grasses [excepting Job's Tears (*Coix lacrymae-jobi*), a minor crop of Southeast Asia], teosinte grains are permanently imprisoned in a hard, woody shell, made up of a hollowed-out, cup-shaped inflorescence internode, the *cupule*, or rachid, and a hard bract that closes its narrow opening, the *outer glume*, these two together, forming the *cupulate fruitcase* (Fig. 7a, b). This structure is so hard and indestructible that human use of the grain is out of the question. Even during grain germination, when the swelling coleoptile forces the glume outward to a slight degree, the cupulate fruitcase permanently encloses its solitary grain, quite unlike the relatively accessible free grains of wheat, barley, rice or sorghum. "Popping" of the grain

Teosinte Ears (Normal and Mutated) and Teosinte Tassel Branch

Fig. 6. Teosinte Ears, Normal and Mutated, and Teosinte Tassel Branch: (a–c) Female (ears) and (e) male (tassel) inflorescence branches of *Zea mays* ssp. *mexicana*, race Chalco, the annual teosinte of the Valley of Mexico: (a) side view of ear (left is adaxial); (b) front (abaxial) view of ear; (c) longitudinal section of (b), showing a single grain enclosed in each of the eight fertile cupulate fruitcases; (e) front (abaxial) view of a tassel spike *or* tassel branch, which are identical in teosinte and readily disintegrate by abscission layers, while maize tassels, with a much thicker spike and lacking abscission layers, do not. (d) Female inflorescence (ear) of *Zea mays parviglumis* (adaxial view) homozygous for maize allele *tga1* (*teosinte glume architecture 1*), (Dorweiler et al. 1993; cf. Roush 1996): rachids are less developed, shallower (1.5–3 mm), narrower and more open, encasing less than ⅓ of the spikelet, allowing the outer, and part of the inner glume and, within, most of the grain, to be exposed (see Fig. 7). The outer glume (partly overlapping the inner glume and both together the grain), less thick on the back but thin on its margins, is hinged to the cupule at its base, where it can be broken off ± easily together with the grain, thus presumably allowing human utilization of the grain for food. This, or a similar mutation reducing rachid size and shape, softening the outer glume, and exposing the grain, must have been the critical first step leading to the domestication of maize (see Fig. 7c, d). (a–d) Female inflorescence: *ra*, rachid (cupule); *og*, outer glume, which together with *ra*, forms the cupulate fruitcase; *em*, embryo; *en*, endosperm; *ig*, inner glume, visible only in (d); *pd*, peduncle; *sp*, spathe (most of the spathe removed); *ab*, abscission layer. (e) Male inflorescence: *ra*, rachid; *og*, outer glume; *ig*, inner glume; *ss*, sessile spikelet; *ps*, pedicellate spikelet. (a–c) from Ixtapaluca (Iltis and Doebley 10b), (e) from 5.5 Km northeast of Los Reyes (Iltis et al. 769); (a–c, e) to same scale, drawn by Lucy C. Taylor, (d) from material and photograph (Dorweiler et al. 1993) courtesy John Doebley, drawn by Kandis Elliot [(a–c; e) from Iltis 1983b].

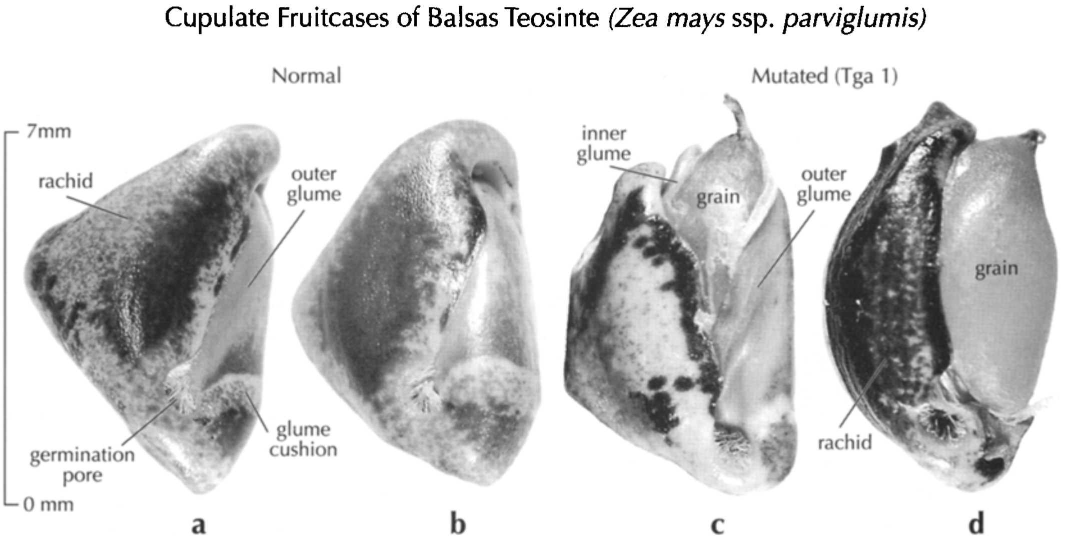


Fig. 7. Cupulate fruitcases of Balsas Teosinte (*Z. mays* ssp. *parviglumis*), Normal and Mutated: (a, b) Normal fruitcases of Balsas Teosinte, showing massive, deep and indurated rachid (rachis joint or cupule), embracing the outer glume, of which only a narrow, hard and indurated strip is left exposed, with the glume cushion and germination pore (through which the root emerges) visible at the base. (c) Mutated fruitcase homozygous for the maize allele *tga1*, a locus that "represents a single gene with a dramatic phenotypic effect . . . and a key step in maize evolution" (Dorweiler et al. 1993), showing a narrower, shallower rachis joint, with the grain, thinly hidden by the inner and outer glumes, pushing the outer glume and the cupule apart, and thus exposing both the outer glume's thin margins, the thin inner glume and the grain tip. (d) Mutated fruitcase, as above, with both glumes removed (the outer broken off at the glume cushion), showing most of the grain exposed due to the shallowness of the rachid (rachis joint or cupule). (a, b) Normal fruitcases, from El Aguacate, 40 km w of Teloloapan on road to Arcelia, Guerrero, Mexico, Iltis and Cochrane 97; (c, d) *tga1* mutated fruitcases, courtesy John Doebley, all photographed by Claudia Lipke.

has been repeatedly cited as how teosinte was first used, but, to this day, there is no archeological evidence that this ever happened (see below).

Furthermore, although Chalco Teosinte, *Zea mays* ssp. *mexicana,* Race Chalco, the high altitude population abundant around Mexico City, has arguably the largest grain of any Mexican annual teosinte, or for that matter, of any New World annual grass, it is the small-grained Balsas (Guerrero) Teosinte, *Zea mays* ssp. *parviglumis,* native to the lower, warmer, moister, southern slopes of the Mexican plateau, with a *seed* weight half as much (0.056 g vs 0.026 g, fide Wilkes 1967), that is the ancestor of maize. In fact, its grains (when removed from the fruitcase) are not all that much larger than those of a large-seeded millet (*Setaria*), the archeological use of which has been amply demonstrated at Tehuacán. Moreover, since the early 1980's, there has been full agreement, based on biochemical evidence (Smith, Goodman and Stuber 1984; Doebley, Goodman and Stuber 1984), that the central population of Balsas Teosinte (between Volcan Toluca, Iguala, and Arcelia, Guerrero) is directly ancestral to maize, verifying earlier suggestions on ecological and cytological grounds (Miranda 1966; Wilkes 1979; McClintock, Kato and Blumenschein 1981; McClintock, pers. comm. 1972: cf. Iltis 1987:213). But for anyone who knows teosinte well, there remains the perennial vexing question: Why would anyone bother to collect or try to grow this utterly useless grain when the grain itself is permanently imprisoned in a hard fruitcase. "There are hosts of wild grasses which have never been domesticated, any of which would seem more promising material for the primitive plant breeder than teosinte" (Collins 1919). In short, in all other wild cereals, one can directly utilize the grain, domesticated or not; in teosinte, there is no such option.

Many people have struggled to resolve this conundrum and a goodly number had simply solved the problem by opting for a "wild maize" other than teosinte, a plant no one had

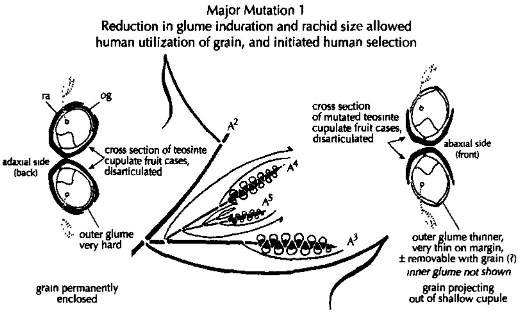


Fig. 8. Major Mutation 1, the Liberation of the Grain: Diagram of simple teosinte ear cluster (as in Fig. 4) after a mutation (e.g., *tga1*) reduced cupule depth and outer glume induration, projecting outward a now much more exposed and more lightly held grain, permitting its separation from the cupule and, thus, its utilization for food (cf. Figs. 7c, d). Human selection would soon result in larger grains, their size increase enhancing the apical dominance within each ear cluster of the earliest maturing (i.e., largest) ear (on A^3). Harvesting would automatically focus on this ear, and neglect the later maturing ears (on A^4, A^5, etc.), which, deprived of nutrients, would never mature. At this early evolutionary stage, ears would still have been disarticulated, and after having been mass collected in late fall, the individual fruitcases might have first been ground gently to break the grain away from the cupule and outer glume (in teosinte, the rachilla attaching the tightly held teosinte grain being essentially without any structural function and extremely weak), and then ground up into flour. Admittedly, a highly hypothetical scenario!

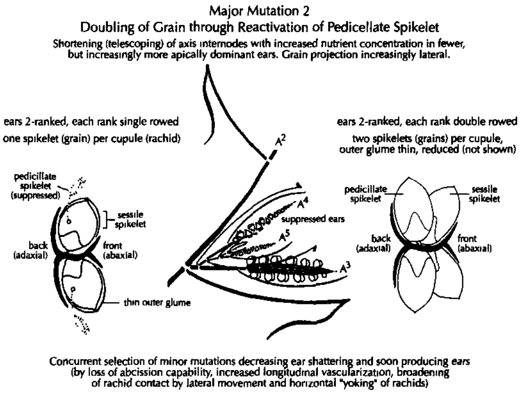


Fig. 9. Major Mutation 2, the Reactivation (termination of abortion) of the Pedicellate Spikelets: Doubling of spikelets (i.e., grains) from one per cupule to two, automatically doubled the harvestable yield per ear (e.g., from 12 to 24!), but also further increased (1), nutrient demand, and thus apical dominance, of the earliest maturing ears (on A^3) at the expense of all other ears within the cluster, these eventually, by indirect selection of pertinent mutations, becoming suppressed; (2), the opening of the cupule and fruitcase further by pushing the glumes apart; concurrently, (3), after generations of harvesting and inadvertent selection, the ±gradual degeneration of the abscission layer, and, also concurrently, the accumulation of diverse structural mutations counteracting fragmentation, such as greater ear size, which, together with the doubling of the grains/cupule, greatly increased strength and extent of longitudinal vascularization and inter-cupule contact, both laterally and horizontally, due to increased condensation. Whole *ears* could then be harvested, the ecological adaptive significance of the abscission layers in the wild species having gradually given way to the practical aims of harvesting the cultigen. Partial abscission layers survive to this day and can sometimes still be seen between the cupules and in the pith of young, dried out maize ears or old and dried out corn cobs, but are overridden by the enormous strength of the longitudinal primary vascular cylinder within the maize ear, this eventually evidently a prime but inadvertent target of human selection, and reflected in the propensity of year-old, rotting or dried-out, shelled corn cobs, laying around a farm yard, to longitudinally split part way between the rows of cupules into four or five narrow, out-arching segments.

ever seen. Others accepted teosinte as the "madre de maíz," and hypothesized that people had ground the fruitcases between stones in a metate, grain and lignified, silicified cellulose both, and separated the flour by sifting, or the woody parts by floatation in water (leading to fermentation—and maize beer?). But then, 6000 or more years ago, these early agriculturalists were already utilizing and perhaps even growing millet (*Setaria* sp.), the archeological abundant, more or less naked "grains" of which were freely available without any woody enclosures.

Admittedly, ripe fruitcases of teosinte are very easy to harvest, this well known not only from experimental harvests by ethnobotanists and anthropologists, such as Beadle, Wilkes and Flannery, but from my own experiences. In Guatemala, I once obtained neary one kilo of ripe "seed" from a single, exceptionally giant, open-grown, abundantly-branched *Zea luxurians* with hardly any effort, by simply uprooting the plant and shaking it upside down over a blanket, and was instantly rewarded with a shower of lovely, polished, speckled disseminules pouring out of their spathes (Iltis 1987:208).

The calculations of Flannery (1973:297) clearly show that a considerable amount of potential food could thus be gathered in a very short time with the expenditure of little energy, provided—and that is the big If!—one can then liberate the grain and use it.

Selection for Fewer, Larger Ears
Increase in apical dominance, ear size,
internode condensation, and ear husking (not shown)

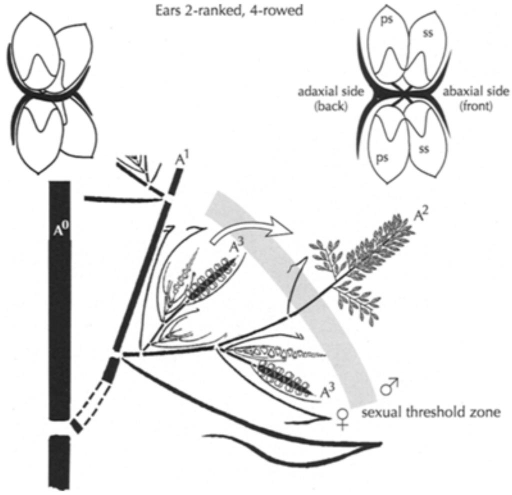


Fig. 10. Selection for Larger but Fewer Ears: Teosintoid secondary branch (on A^2) with condensed internodes bearing 2 proto-maize "earlets" (on A^3) in compound ear clusters, but with all other teosinte ears suppressed [compare to Fig. 3, 8 and 9: these clusters are the same as the distal (right-hand) ear cluster in Figure 10]. By this stage, "earlets" are still 2-ranked, but 4-rowed, with ca. 20–30 grains each. This increase in earlet size would not only further suppress all subsidiary ears of a cluster into empty, atavistic structures, but the central spike in each tassel (as the homeolog of a lateral "earlet") would not only become more condensed (i.e., thicker), but the whole tassel would gradually lose its abscission capabilities, leading to the non-fragmenting tassel of maize, both of these tassel phenomena indirect (secondary) effects of ear selection. Increased condensation of ears, as well as of branch internodes, gradually bring the tassel closer to the zone of female expression (hollow arrow here represents the sexual translocation coming in Fig. 11).

Despite the lack of any evidence whatsoever, the culinary use of ground up fruitcases, grain and woody cellulose milled together, are to this day continually hypothesized. Thus Flannery (1973:296) states as fact that teosinte fruitcases ". . . can be ground up to produce coarse but rather pleasant-tasting unleavened cakes when cooked on a hot flat rock . . .," this to me a highly questionable proposition and a matter of opinion. George Beadle (1939) hypothesized that teosinte plants were burned or the fruitcases roasted, causing the grains to pop like popcorn to make pop-teosinte (!). While teosinte grains do pop and so partly escape their fruitcases, they

Homeotic Sexual Conversion (Translocation)
(hollow arrow; cf. also Fig. 10)

Proto maize ear replaces tassel terminating secondary (A^2) branch (crossing of hormonal threshold due to mutations shortening the branch internodes, correlated with increased apical dominance.) Terminal ears probably with male "tails." Doubling of husks in the node(s) just beneath the ear. Atavistic buds of suppressed ears not shown.

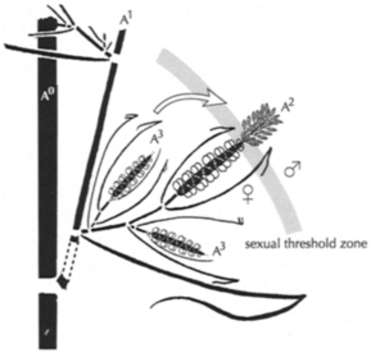
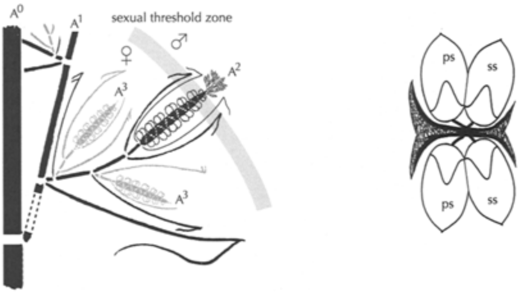


Fig. 11. Homeotic Sexual Conversion or Translocation No. 1: Increased ear size (grain size, grain number) and, reciprocally, reduction in ear number in each branch, accompanied by *branch* condensation, moved secondary branch (A^2) tassels across the hormonal threshold into the zone of female morphological expression, with each tassel becoming gradually replaced by a distichous proto-maize "earlet" (i.e., a feminized tassel spike). Such homeotic translocations of female morphology onto male branches are not uncommon in terminal tassels of maize tillers or, rarely, of main stems, that have been (1), infected with corn smut (Iltis 1911); (2), exposed to herbicides; (3), growing in low, cold ditches, or (4), in greenhouses under abnormal illumination or shade (Schaffner 1930; Ritchey and Sprague 1932); or (5), are often found terminating short (but not long) basal tillers (Montgomery 1906). Here now, abundant nutrients, concentrated by the increasingly stronger apical dominance, would have allowed mutations for an increase in the number of rachids (cupules) to become expressed, and for these to become rearranged into opposite, yoked pairs, producing a 2-ranked, 4-rowed, flat ear much like that of an F_1 maize × teosinte hybrid. At the same time, the subsidiary ears on A^3 may very likely have had their nutrient supply reduced by the apical dominance of the ear on A^2 resulting first in non-development of the pedicellate spikelet (which would explain some odd archeological material) and eventually in their total suppression.

Concurrently, the alternate distichous ear husks on the uppermost node(s) just beneath that newly enlarged ear would have split into opposing, still distichous pairs, increasing ear protection. Variability in genetic feminization potential of maize populations has been experimentally shown (Schaffner 1930, 1935; Richey and Sprague 1932), with certain maize races not ever becoming feminized, others highly susceptible. From the ethnobotanical standpoint, by this stage human selection must have greatly intensified.



Increased Apical Dominance

Increase in number, condensation and "yoking" of rachids, and strengthening of longitudinal vascular system in terminal ear, with lateral ear supression and continued increase in ear husking

Fig. 12. Apical Dominance and Increase in Size of Ear: The proto-maize ear, in a terminal position on A^2, the secondary branch, is now able, because of its increased apical dominance, to cause a local revolution in resource allocation, to wit, to commandeer all nutrients of that branch, including, with time, of those going to the ears beneath it, of those produced by the subtending leaf (and other leaves) on its primary branch and of some leaves of the main central stem. It is, therefore, within the limits set by its "source" field, an increasingly effective nutrient "sink," and, *because it is the first to mature,* in a position to take nutritional advantage of any mutation for increased ear size, grain size and/or grain number. All leaves (leaf sheaths plus decreasingly reduced blades) of the secondary branch and one prophyll will enclose the ear as "husks," these probably doubled in the upper 1 or 2 nodes and opposite but still distichous.

All ears of *Zea,* wild or domesticated, are apically dominant over the branch on which they sit, the degree depending on their size and position within the ear cluster. It has been suggested (Doebley and Wang 1997) that increase in apical dominance is due to multiple effects of a particular gene (tb1), but the gradual selection of mutations shortening and strengthening the branch internodes, and so bringing the ears into the zone of female sexual expression (perhaps positively correlated with increased weight of the ears), may be another way of looking at the same phenomenon. Somehow, morphology and developmental genetics must be brought into closer harmony.

Secondary Branches Tipped by Ears,
Primary Branch by Tassel (low apical dominance)

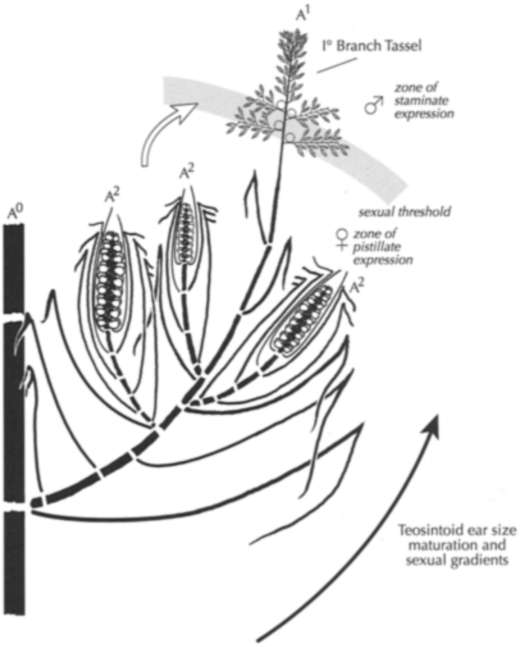


Fig. 13. Initiating Homeotic Sexual Conversion No. 2: As ears became heavier and primary branch condensation increased under human selection, the terminal tassel of each primary branch (A^1) would move across the hormonal zone of female expression, and some of its basal spikelets would become feminized. By now, the terminal tassel of the primary branch (on A^1) has acquired a condensed, ±thickened central spike, a secondary effect of mutations increasing condensation, grain number and size selected by humans in the ears, what with this tassel spike and lateral ears being homeologs (Sattler 1988). The diagram shows the main, central stem (A°), a primary branch (A^1) ending in a tassel, with a few of the sessile spikelets of a pair at the base of the tassel branches bearing grains, and three secondary branchlets A^2, each bearing a small, terminal (probably 2-ranked and 4-rowed) proto-maize earlet, each enclosed by "husk" leaves (i.e., leaf sheaths) and a prophyll (leaf with 2 "flags"). Compare this drawing to Fig. 1 [and Fig. 3, where the A^2 branch—though with fewer internodes—is the same as the A^2 branch on right-hand side of A^1 in Fig. 13].

It is likely that all through this condensation process not only did the husks double in number by proliferating at the highest several nodes of the shanks (I° branches) just beneath the ear butt, but that the whole "super cluster" (in our illustration all 3 small ears) was enclosed by protective sheaths of the large I° branch leaves.

are hardly edible. During the Great Teosinte Mutation Hunt of November 1971 in Guerrero, Mexico, Beadle delighted in bringing with him a bag of Chicago-baked "teosintillas" into the field and "experimentally" feed them to his captive associates, with an encouraging "not bad-tasting, eh?" [Oh yeah? Made up of ground up grains but also woody fruitcases (cupules and glumes), they tasted nothing so much as salted, dry, brittle brown cardboard, an unacceptable candidate for human food, even if fed to us by

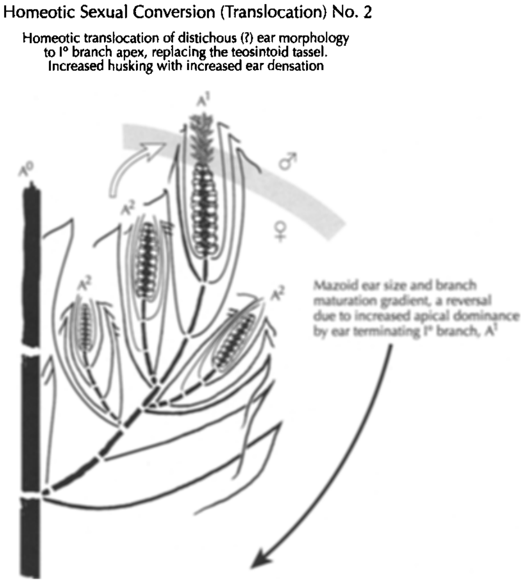


Fig. 14. Homeotic Sexual Conversion (Translocation) No. 2: Whether gradual or fairly sudden, the continuing human selection for branch condensation (telescoping) and larger, heavier ears moved the primary branch tassel across the sexual threshold into the field of female expression (i.e., closer to the main stem, A^0, and root) and translocated the proto-ear morphology to the apex of the primary branch tassel, feminizing its spike—this, we need to remember, the direct homolog of the maize ear (Iltis 1987; Cámara-H and Gambino 1990; Orr and Sundberg 1994), with basal tassel branches gradually becoming suppressed. The terminal ear would probably have carried a small male, or mixed male-female, "tail" (pedicellate spikelet, male; sessile spikelet, female), a case of incomplete homologous substitution. Tail "stubs" are present on some of the earliest archeological maize from Tehuacán (Galinat in Mangelsdorf 1974: 180, Fig. 15.24). Though labeled "wild corn" (sic!) and reputed to have had freely dispersing grains (sic!), Galinat's prescient conclusion on the presence of hypothetical "male tails" in several of these small ears fits in well with the STLT as here proposed. Mutation(s) (Sundberg and Doebley 1990) for polystichy, from distichous 2-ranked, 4-rowed ears to polystichous 4-ranked, 8-rowed ears, was beginning to be selected initially at this point. ["The homeosis in maize is an example of homeosis occurring during ontogeny (Sattler 1988: 1609–1611); the sexual conversion in teosinte to maize is homeosis as it is usually understood, i.e., as occurring during phylogeny" (R. Sattler, pers. com. March 24, 1995).]

a kindly Nobel Laureate!]. Beadle (1977:621–622) experimented on himself, eating substantial amounts of ground up teosinte fruits to make his point, but, as Mangelsdorf has emphasized (1974:50), no teosinte fruitcase material *of any sort* (with one or two minor, archeologically recent exceptions, no older than 2000 years) has ever been found in archeological sites, human coprolites included (see below).

To put it quite simply, neither corn beer making, nor "teosintillas," nor popped teosinte, explain the maize domestication we so wish to understand. Based on current evidence, the early agriculturists could not, and did not, use teosinte grains for food, or for anything else—hence could not have domesticated teosinte according to any of the time-honored Old World mass-selection scenarios of grain domestication that ethnobotanists often cite.

C. The Case of the Missing Teosinte Fruits, Positive Clues From Negative Archeological Evidence:

Teosinte fruitcases are hard as rocks and virtually indestructible, and ought to be especially well-preserved in dry caves. Direct archeological evidence for their human utilization should therefore be abundant. But it is a most peculiar, but highly significant fact that teosinte fruitcases, despite their being extremely durable objects ideal for storage and, hence, archeological preservation, large enough and peculiar enough to be easily spotted and identified, abundant in nature and very easily collected, *have never been found,* except in two totally insignificant instances: in a preceramic horizon near Chalco in the Valley of Mexico, a site ca 9500 years old (Lorenzo and Gonzales Q. 1970; Niederberger 1979), which yielded only two (sic!!) individual fruitcases assigned to *Zea mays* ssp. *mexicana* (this *not* the ancestor of maize and still very abundant in the region); and one teosinte fruitcase fragment in a presumably human coprolite found jointly with a large number of chewed maize (teosinte?) quids from a much later horizon (ca. 2000 ? BP.) in La Perra Cave in Tamaulipas (Mangelsdorf, et al. 1967), this of course from long after maize had become commonly cultivated throughout much of Mexico. To repeat, except for these two trivial, basically meaningless pieces of evidence as far as maize domestication is concerned, *teosinte fruitcases have so far never been collected in any archeological horizons!*

Surely, that would be a peculiar omission had teosinte fruitcases been mass-collected and utilized for human consumption! Why, one must ask, is any and all evidence for teosinte "grain"

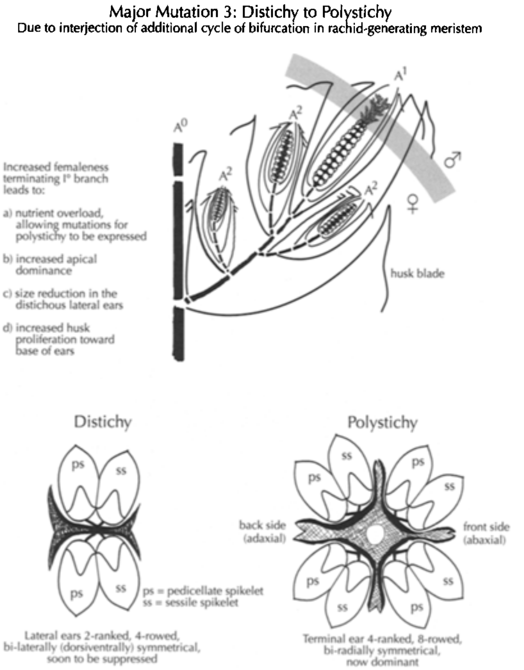


Fig. 15. Major Mutation 3—Teosintoid Distichy to Maizoid Polystichy, the Birth of the Maize Ear: An ear terminating a primary branch (A^1), replacing the teosintoid tassel, would be the first to mature and thus, being female, would gradually become the branch's primary nutrient sink by virtue of the ear's increasingly, and eventually enormous apical dominance. The concentration of all primary branch nutrients into a single ear must have been favored by early agriculturists because of the greatly enhanced harvestability that apical dominance allows, with the single-headed giant sunflower (*Helianthus annuus* var. *macrocarpus*) an analogous example (Iltis 1971; Doebley and Iltis 1980). Not until this stage, with an overload of nutrients available, would mutations for polystichy (identified as a gene on chromosome 2; Doebley and Stec 1991) be allowed to be effectively expressed. While the lateral, hence later-maturing, and thus more nutrient-deprived distichous ears (on A^2) would continue to be produced (sometimes in modern maize as well!), as archeological maize from Tehuacán demonstrates, with time only the terminal ear would survive. Human selection for increased rank number (polystichy), grain number, grain size, ear length, and husking (see below), but also decreased number of ears per plant, finally resulted in that magnificently monstrous marvel, the massive ear of modern maize. Mutations leading to polystichy involve a second (or several) bifurcation in the ear primordia of an enlarged apical meristem, leading to a simultaenous doubling or tripling of the rachid (cupule) initials (Sundberg and Doebley 1990; Sundberg and Orr 1996; Cámara-H. and Gambino 1990; R. Rutishauser, pers. com.), a model verified by SEM studies and replacing the erroneous condensation-twisting model of Collins (1919; Galinat 1975: 323; Iltis 1983, 1987). In maize, the earliest polystichous meristem is still weakly bi-laterally symmetrical, to become bi-radially symmetrical by pressure displacement in the mature ear (Sundberg and Doebley 1990), a symmetry still easily seen in most 8-rowed maize ears, where the gap between the ranks (rows of cupules; i.e., double rows of grain!) is greatest on the adaxial side between the two adjoining rows of pedicellate spikelets, one each from two adjoining ranks (ps:ps in Fig. 15, lower right-hand diagram).

gathering missing? Had teosinte been collected for its grain, one would expect to find many bags full and large caches of it in the archeological record. But since this is not the case, other explanations must be sought.

That even small amounts *accidentally* associated with human settlements have never been found may well be due in part to the ecology of teosinte, a giant grass which grows most luxuriously in summer-flooded, fall-dry stream beds, arroyos and alluvial fans, a quite unsuitable habitat for human occupation. Early agriculturists no doubt planted crops in such seasonally wet habitats (with teosinte, in particular, the perfect annual adapted to a seasonally-dry climate), but did their living in upland caves or shelters nearby. Perhaps if archeologists would look at sediments in ancient fields not associated with potsherds and other human artifacts, scattered fruitcases might eventually turn up. Nevertheless, the total absence of fruitcases in rock shelters, caves, or anywhere else makes a powerful statement.

The question thus arises, if teosinte was not grown for its grain, then why was it domesticated? Why would people have taken the trouble to deliberately grow teosinte, if they could not, and did not, utilize the grain in any shape or form? Flannery's (1973) famous question does deserve a plausible answer.

D. TEOSINTE AND MAIZE AS A VEGETABLE OR SUGAR SOURCE:

> The New World afforded no greater delicacy than the green ear of corn, the 'roasting ear' of modern times. In season this was a favorite food everywhere. It was eaten raw, boiled, or roasted; and the Indian was the inventor of the mixture of green corn and beans known as 'succotash'. The juice of the stem, especially in subtropical climates, was often extracted and boiled down to a syrup, or fermented and used as a drink." (Weatherwax 1923:212). ". . . the principal lux-

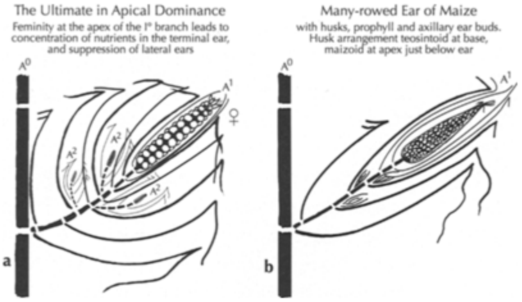


Fig. 16. The Triumph of Apical Dominance: (a and b). With a polystichous ear terminating the primary branch (A^1) exerting very strong apical dominance, the lateral ears of that branch (maturing progressively later as one descends, with the teosintoid maturation gradient now reversed) will be reduced to "nubbins," minute ears that do not fully mature, or, in some modern maize races, do not even develop, what with the secondary branchlets on which they sit as well as the leaves and ears, reduced to vestiges. Polystichy in some maize races developed to such a high degree that the 12 or more ranks themselves seem to disappear, the tight packing of the cupules reminiscent of fasciation, as in "strawberry popcorn."

> ury of the New World, the sweet, green ear of maize . . . ." (loc. cit:214).

One logical explanation to that conundrum is simple: *Teosinte, at least initially, was not grown for its grains,* but for other culinary virtues, three of which come quickly to mind:

1. SUGAR-CONTAINING PITH: As I discussed thoroughly elsewhere (Iltis 1987), plants of the genus *Zea,* like many large annual tropical grasses that grow in a short-day regime (i.e., in a shortening-day regime, as I prefer to call it, that is, in the northern hemisphere late summer and fall) are characterized by a sugar-storing and secondary nutrient-transference system, where sugar is stored in its massive pith during the early, high sun-energy period of the life cycle, only to be shunted to the grains when the ears are close to maturity and ready to be filled, this at a time when the days have become steadily shorter and sunlight energy weaker.

To this day, families on a September Sunday outing to the countryside near Mexico City will eat a picnic lunch on a roadside near a maize field and, once finished with their maíz, tacos or enchiladas, may cut down a young maize or teosinte plant for the kids, peel back the hard outer cortex and let them chew on the raw sugary pith (See cover, this issue of Economic Botany; cf. Crosswhite 1982a:197). Humanity has done such chewing for a long time with sorghum and sugar cane, and no doubt with teosinte as well: surely not a staple food, but a pleasant culinary interlude, nevertheless. Of course, there are fibers (vascular strands) in and on the edge of the pith, fibers that one must chew on for a while to get the sugar out, and which, eventually, tightly compacted into a wad or *quid,* have to be spit out.

One does not see *quids* of chewed stems lying around very often these days, for most sugar comes from sugar cane via the grocery store, a commodity abundant in the world today and proof that *Homo sapiens* loves sugar above almost anything else. But once upon a time, sugar was rare and much prized, and hence these quids are not uncommon in certain archeological sites.

2. *ZEA* QUIDS IN THE ARCHEOLOGICAL RECORD: It is a fascinating fact that quids of chewed green maize ears and maize stems are known from Mexican archeological sites, both in Tamaulipas and Puebla, here in the same cave as the earliest known maize ears. Excavations by R. S. MacNeish at La Perra Cave, Eastern Tamaulipas, Mexico, not only yielded a coprolite with some teosinte fruitcase fragments, but also maize stems, cobs, husks, and quids ". . . composed of thoroughly chewed young ears. After seeing these we tried chewing young ears enclosed in husks and found them tender, succulent, and sweet. Consuming maize in this way is a quick and simple method of obtaining a little sugar; no equipment of any kind is required" (Mangelsdorf 1974:154). Almost the same may be said for teosinte stems and ears, although the ears are much smaller. With several in an ear cluster one could find it worthwhile to go through the same procedure, again and again.

Perhaps even more significant were the remains from the famous San Marcos Cave site near Tehuacán, Puebla, where maize ears, the earliest so far collected in Mexico, have now been recalibrated to ca. 4500 B.P. cal. (Long et al. 1989). In its Palo Blanco horizon (Zone C and B, 850–700 B.P.), together with 581 corn cobs, MacNeish found remains of 58 quids, of which 32 were chewed stalks and 26 chewed husks. These are illustrated by Mangelsdorf (1974:177, fig. 15.21), who comments on their rather common occurrence, without suggesting any significance to it in terms of initial maize domestication:

> We had previously found from studying the quids from La Perra Cave . . . that young ears enclosed in husks are quite sweet. Also . . . it is well known that growing corn stalks from which the ears have been removed, or which are barren for other reasons, often accumulate sugars and are about as sweet as sugar cane . . . when chewed. Since a 'sweet tooth' is almost universal in the human race, it is not surprising to find that the Tehuacán people made use of the sweetness derived by chewing young ears and stalks of corn.

Again, human use of teosinte would surely have been similar, though again, admittedly, the ears of teosinte are smaller and the amount of stored sugar in the teosinte stem less concentrated, what with the sugar-releasing phenomenon in teosinte being more gradual (as compared to the sudden "filling" of ears in maize), in synchronization with the gradual, sequential maturation of the teosinte plant, stretched out as it is over many weeks (cf. Iltis 1987:210–211).

In summary, one may predict that future archeological exploration of earlier sites in regions where teosinte is indigenous (as it was not in Tamaulipas or Tehuacán, Puebla) will find teosinte quids, though to tell them apart from maize quids will be a problem since, for all practical purposes, vegetatively the two cannot be told apart.

Nevertheless, the presence of these archeological quids, even though from later horizons, informs us of the ancient Mexicans' knowledge of *Zea* as a source of food, a presence that speaks volumes!

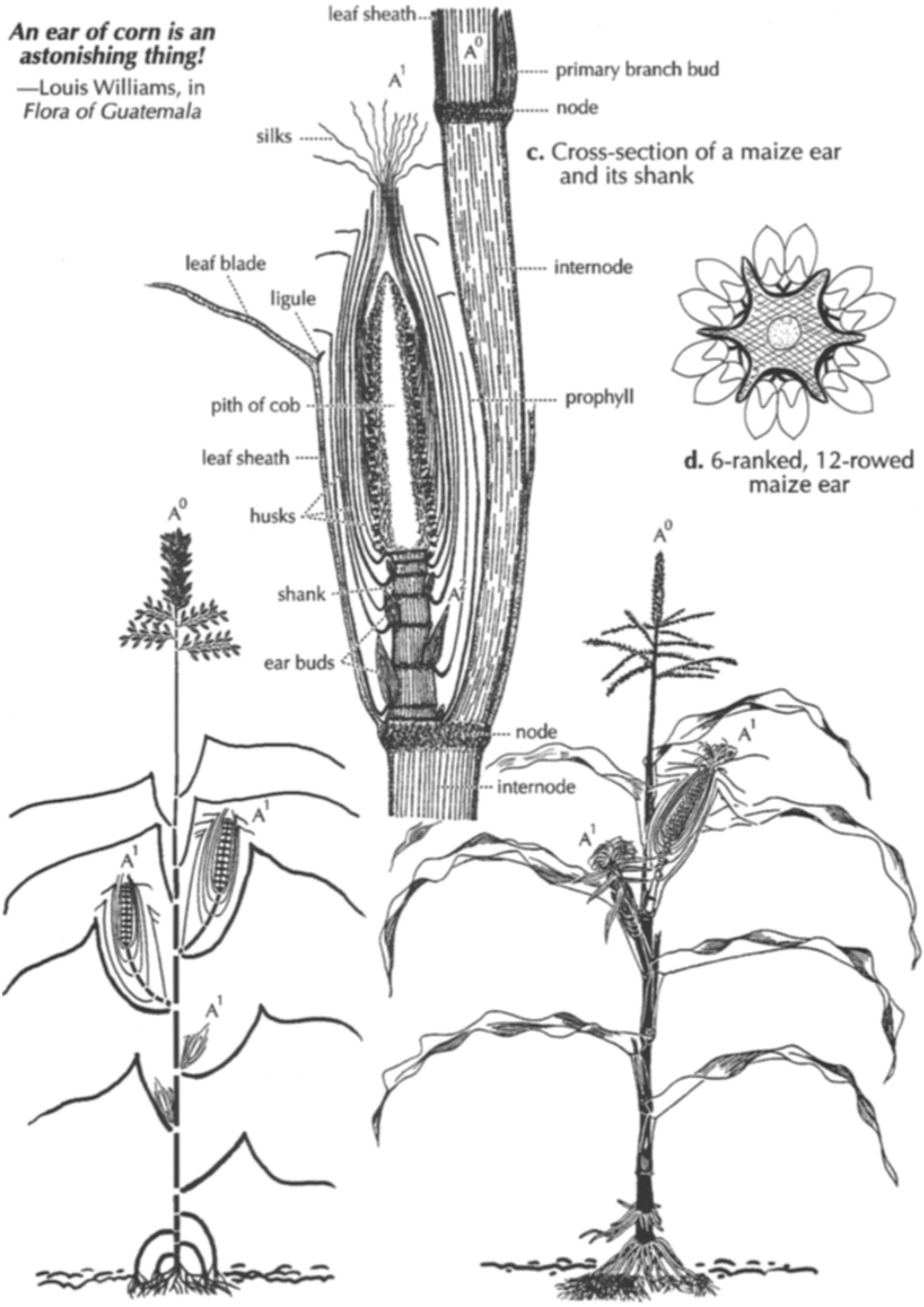
3. GREEN EARS AS RAW VEGETABLE: Teosinte plants, especially large ones, produce many ear clusters, within each of which the ears mature in a staggered fashion, over many weeks and even several months, depending on available moisture. As a consequence, in Mexico in early fall, when teosinte is still green and shedding pollen, one plant will have many green ears. These, when in the sugary phase, are soft, crisp, and sweet, and most all of Beadle's "teosinte hunters," and Mangelsdorf's archeologists as well (see above), picked out a young ear now and then to chew on. The ancient Mexicans no doubt did the same—not as a major part of their diet, but as an extra, seasonal delicacy. Still, like everything else about teosinte, the local folks must have been well aware of teosinte wherever it grew, and for several reasons, this one among them (Wilkes, in a personal communication, informs me that he and his wife once served George Beadle teosinte chicken soup with green, young, female teosinte spikes, which were quite tasty).

4. CORN SMUT, THE "HUITLACOCHE" OF THE MEXICAN CUISINE: Teosinte, like its derivative, maize, gets infected now and then with corn smut [*Ustilago maydis* (DC) Corda], a fungus which turns infected grains into rapidly-growing, often large and shapeless monstrosities, these at first white to gray-speckled, crisp but soft, but later deliquescent black masses of spores. Not only are these smutted grains and their parasitic fungal bodies edible, but corn smut may also infect the tassels, where often it may turn male spikelets into abnormal diseased naked grains, producing this sex change through the production of growth hormones, such as giberellins (cf. Iltis, 1987). Such feminized tassels, resembling the various maize mutations called "tassel seed," have long been of special interest not only because of their evolutionary implications, as my father, Hugo Iltis (1911), never tired of telling us children during one of our many Sunday field trips into the Moravian countryside, but because their grains, borne between the soft male glumes and on the flat tassel rachids, are naked, and in an early sugary state present themselves as still another object of human interest.

Stephen D. Koch, agrostologist and Professor-Investigator at the Colegio de Postgraduados, Montecillos, Edo. de Mexico, had long ago pointed out to me the possibility that corn smut may have had an important role in the initial domestication of maize. He wrote me, alas within the context of my earlier Catastrophic Sexual Transmutation Theory (Iltis 1983), that "It is possible that smutty grains in the central spike of teosinte was what first attracted man to teosinte as a food plant, perhaps even leading to its cultivation on a limited scale. Selection for tassels that produced more infectable grains could have lead to the necessary feminization. Somewhere along the way, it would have been discovered that the uninfected [naked, tassel] grains are edible, too, perhaps in the milk stage at first, since it is at this stage that *huitlacoche* is eaten" (S.D.K. to H.H.I., December 7, 1983). Even though I have abandoned my old theory, Koch's comment, coming from one who knows Mexico and its grasses well, is worth noting.

In fact, *huitlacoche,* or *cuitlacoche* from in-

An ear of corn is an astonishing thing!
—Louis Williams, in *Flora of Guatemala*



c. Cross-section of a maize ear and its shank

d. 6-ranked, 12-rowed maize ear

a. Diagramatic modern maize plant, much simplified

b. A modern maize plant

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Fig. 17. Part 1: The Modern Maize Plant: (a) A diagram. [Not clearly shown is the increase in the number of husks per node, the decrease in the length of "shank" (primary branch) internodes, and the change from a basal teosintoid, distichous to a maizoid, polystichous arrangement of the husks as one moves up towards the ear (see below)]. (b) A habit sketch. (c) Modern maize ear, showing the telescoped (condensed) internodes of A^1 and the vestigial secondary branches, or ear buds, in the axils of the husks decreasing in size upwards (After Weatherwax 1923:57, modified).

Fig. 17. Part 2: On the Ancestry of Maize from Teosinte: Atavistic Clues in Seedlings and Ear Shoots.

1. Axillary shoots of maize seedlings: In annual teosinte (Fig. 1), the lowest primary branches are the longest, have the most internodes [as many, exactly, as the main stem has above their point of origin (Montgomery 1906; Iltis 1983a:83)], and in the very young seedling are the earliest to develop. Unlike teosinte, in maize the uppermost branch (shank) is always the longest (Fig. 17a, b), but, *as in teosinte,* has the fewest internodes. What is most interesting, however, is that in the very young maize seedling, *the initial development of the branches (axillary shoots) is exactly the same as in teosinte,* in that the lowest branch buds develop first, hence are soon the largest and longest, while those that follow become gradually reduced upward in size as they develop on the minute seedling stem. But that is true only up to a certain specific point (V9 stage; Ritchie, Hanway and Benson 1986), when the growth of the lowest seven or eight axillary shoots is inhibited, and the growth gradient reversed, with successive upper axillary ear shoots (i.e., primary branch buds) soon developing ever more rapidly in the opposite direction, to eventually produce the maizoid pattern, with the longest primary ear-bearing branch (but with the fewest internodes) bearing the highest ear (Fig. 17b). Thus, the teosinte ancestry is betrayed by the atavistic maize ontogeny, and accounts for the anomalous developmental pattern in the maize seedling, never before explained, though well described and beautifully illustrated (Ritchie et al. 1986). To return full circle to Fig. 17, the teosintoid pattern of the branch buds developing from the base of the minute seedling stem on upwards, as just described, is reiterated in Weatherwax's (1923) careful drawing (Fig. 17c) of the maize ear, showing the upward reduction in the size of the suppressed secondary ear buds, a size gradient that here, however, is frozen by the apical dominance of the primary ear. Despite the occasional, and still continuing, confusion about the ancestry of maize, the fingerprints of teosinte survive everywhere.

2. The Phyllotaxy of Husks on the Shank, a Subject in Need of Study: The arrangement of the *husks* (I° branch leaves) on the *shank* (the ear-bearing I° branch), their phyllotaxy, gives us additional clues to the teosintoid ancestry of maize. While husk phyllotaxy has been generally misunderstood (e.g., Bonnett 1954:78; Weatherwax 1923:57), it can best be studied by a very simple technique which I applied last summer to some local sweet corn:

A. Obtain complete husk-covered ears from the grocery store or field, but make certain that they all include the 2-nerved prophyll on the adaxial side, for only then can you be sure that you have a whole husk system in hand. Get at least half a dozen ears, for no two are exactly alike, even though all follow the same pattern.

B. Split the prophyll in half by pulling the two sides apart all the way to the bottom, and there, on the shank, mark its *center of attachment* with a marker pen, or with a needle or pin pushed into the shank. Then tear the prophyll off and discard it.

C. Split the tip of the outer-most husk with your fingernails exactly in the middle and then tear its two equal, parallel-nerved sides apart all the way down to the base of the husk; and there again mark the shank at the center of attachment, which will be ±90° to the left or right to that of the prophyll, and then discard the husk. Repeat this procedure with every husk up to the very last. [Pick, if you can, a few-ranked (8- or 10-rowed) ears with a long (20 cm or more) shank at the start. Very thick, short shanks are much harder to interpret].

D. To count the nodes, it is best to slice the shank lengthwise, for they are best seen by their inner nodal plates.

Once the shank has been stripped of its husks and the centers of their attachment marked, one can discover several significant facts. First of all, comparing several shanks, there is enormous variability in their length, in the number of nodes and internodes (ca. 5–9), in the number of husks (in Wisconsin sweet corn, from 8 to 24), and, finally, in the arrangement of the husks, in their phyllotaxy. Nevertheless, from my studies of sweet corn, the most significant generalization that can be made is that *the phyllotaxy of the husks on ear-bearing shanks is purely teosintoid at the base and purely maizoid at the apex,* that is, at the base of the ear, with all intermediate stages found in between. In other words, the *husks are distichous at the base and increasingly polystichous toward the top.*

To be specific, and I am here describing a not uncommon, but idealized situation: the two or three lowest, usually most widely separated, nodes carry husks that are *solitary, alternate* and *distichous,* one per node, first on one side, then on the other, exactly as the leaves on a teosinte branch; the next one or two nodes may have two husk leaves each that are still distichous and laterally disposed, but *opposite* to each other; the next node or two carry husks that are *decussate* to these; that is, again opposite but perpendicular to the pair below (i.e., at 90°) and, if on two nodes, to the pair above; then follow one or two nodes that are, for lack of a better word, *tricussate* (tristichous?); that is, with three, by now narrower husks/node followed by one to three very crowded nodes (with hardly any internodes between) just below the ear, which are fected maize ears, and in the right stage for eating, is still much prized by modern Mexican country folks as a delicacy, and many a tortilla and soup stand along rural roadsides, and several fancy Mexico City restaurants as well, will feature *sopa de cuitlacoche* or *tacos, enchiladas, quesadillas, empanadas,* or *crepas de cuitlacoche,* all filled with corn smut mixed with honey and other ingredients as one of their specialities (Peterson and Peterson 1998). There can be little doubt that the use of *huitlacoche* is a very ancient one, and for the sake of argument, may well predate the domestication of teosinte. During the moister and warmer periods of the deglaciation (e.g., 8–6000 years B.P.), it may even have been much more common than today. But all this is theory, for *Ustilago maidis* does not keep, and records of its early existence do not exist except as spores in the ground for which no one, as far as I know, has as yet searched.

E. THE RARITY OF TEOSINTE FRUITCASE MUTATIONS:

Narrowly canalized morphological structures tend not to be subject to many mutational changes. It would be therefore reasonable to assume that *Tga1* (Dorweiler et al.1993; Dorweiler and Doebley 1997), or any mutation with similar effects on the teosinte fruitcase, was a one-time, rare event. Mutations in teosinte fruits must be exceptionally rare, no doubt in part because the cupulate fruitcase and its enclosed grain are highly adaptive structures and deeply canalized for both animal, water, and gravity dispersal. They must, in addition, be of a great age, for they are practically identical in all the five wild taxa, implying that their distinctive morphology dates back to the origin of the genus *Zea* several million years ago.

The invariability of teosinte fruitcases was demonstrated by the Teosinte Mutation Hunt of

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quadricussate or even *quintucassate*; that is, with four or five crowded, very narrow, thin, flimsy, pale husks, that overlap and are difficult to decipher.

There is only one reference that I have been able to find that halfway correctly describes this situation:

> "The outer husks [of maize] are distichous like ordinary leaves while the inner are polystichous, there sometimes seeming to be as many ranks [of husks] as there are double rows of kernels" (Kiesselbach 1949 [1980]:51).

In short, we see here, in this phyllotactic husk transition from basal teosintoid distichy to apical maizoid polystichy, the developmental influence of maize *ear* polystichy transferred downward to the upper region of the shank, a no doubt *indirect,* inadvertent result of human selection aimed at ear polystichy, but nevertheless probably of some adaptational value in producing a nearly airtight jacket around the ear that keeps out voracious insects and hungry birds as well as rain, and possibly keeps *in* scarce moisture and high, potentially useful CO^2 concentrations (Iltis 1987:206–210).

As a further generalization, very long shanks (ea. 21 cm) are more likely to be teosintoid with, to use an actual example, the first five husks, one per node, distichous and widely spaced-out to nearly the end of the shank, followed by two nodes with four husks in two decussate pairs, and just beneath the ear by one tricussate-husked node—which adds up to eight nodes with 10 husks on this one shank. Very short, thick, greatly condensed shanks of multi-ranked ears are, not surprisingly, strongly maizoid, with only one or two distichous husks, these quickly grading into decussate, tricussate, quadri- or quintucussate nodes, the whole husk system highly congested and composed, in some ears of sweet corn, of up to 19 husks on nine nodes or, in another, of 23 husks on eight nodes. In such situations, but even in less crowded ones, an occasional husk is inserted irregularly at an angle between two nodes, which may have suggested a husk phyllotaxy in maize that is spiral (Doebley and Wang 1997:361), a most unlikely arrangement in *Zea.*

In addition to the teosintoid-maizoid *phyllotaxy gradient* described above, an *internode gradient,* from long internodes at the base of the shank to very short ones just beneath the ear, well illustrated in Weatherwax's (1923) fine drawing (our Fig. 17c), and a *husk width* and *texture gradient* as well, from the outermost (lower) being tough and very wide to the innermost (upper) husks being very thin and narrow.

Finally, the total number of shank nodes are somewhat independent of the usually higher total number of husks, and appear to be precisely as many as predicted on theoretical grounds by Montgomery's (1906:61; cf. Iltis 1983a:83) diagram, (or, if anything, fewer by coalescence), namely, the same as the number of nodes on the main axis (A°) of the maize plant above the point of insertion of the shank, and not, as Kempton (1937: 397) thought, the same as the number of husks, a mistake (had he only bothered to longitudinally section a shank!) that cost this otherwise brilliant maize worker the pleasure of deriving the maize ear from the teosinte tassel by a sexual homeotic translocation, and thus discovering the true nature of maize.

November, 1971, organized by George Beadle, during which a dozen maize or teosinte specialists collected teosinte fruitcases in Guerrero for two weeks, one group at "El Salado" near Mazatlán, not far from Chilpancingo, the other west of Teloloapan, during which we examined a total of over 70 000 teosinte plants and probably a million fruitcases for any and all mutations leading toward maize, such as "soft glume" or "shallow cupule," *but did not find a single one.* [We did find two plants with "fat glumes," that is, with glumes pushed out a little by the enlarged grains, but judging from several rare maize × teosinte F_1 hybrids in the maize field nearby, we considered them to be hybrid backcrosses to teosinte. Galinat (1992:214) reports a similar discovery, collected on the same expedition by L. R. Randolph of the other group, who too thought that its peculiarities were due to maize introgression, which Galinat questions. The plant apparently was not saved.] According to Mangelsdorf (1974:51), this trip was an exercise in futility, for even then, in 1974, he refused to acknowledge teosinte as the ancestor of maize. But his snide scorn and derision were misplaced, for Beadle's huge experiment made it crystal clear that even "minor" mutations, such as non-shattering ears or soft glumes, are *extremely* rare; and that is surely worth knowing.

F. WHEN AND HOW WAS MAIZE DOMESTICATED?

The earliest archeological maize remains from Tehuacán, Puebla, recently redated to 4700–4500 B.P., cal. (Long et al. 1989), are clearly domesticated (Benz and Iltis 1990; Benz 1995; Benz and Long 2000), but judging from both the small size of the eight-rowed ears (presumably with male tails) and the smaller, distichous (presumably lateral) ears found with them, this maize was still in the process of shedding some of its teosintoid characteristics. In view of this, domestication must have occurred some time before its appearance at Tehuacán, though when this occurred is purely a matter of guesswork at this point. So are the various hypotheses that, because of a supposed great climatic cooling depressing the modern geographic ranges, place the beginnings of maize domestication well before 9000 B.P., with "... coastal people cultivating teosinte to maintain populations near the coast"; and that, because this ancient age is based in part also on molecular studies indicating slow evolution, "... the founder population of maize was large" (Buckler, Pearsall and Holtsford 1998).

I would like to suggest an alternative hypothesis: namely that the ranges of the taxa of teosinte have not changed to any great extent in the last 10 000 years, especially that of Balsas Teosinte, considering the enormous species endemism in that valley; second, that Balsas Teosinte was first grown by hunter-gatherers somewhere in Guerrero, Michoacan or Jalisco, not exactly in the same area as these modern teosinte populations, but yet not too far from where it is found now either, and then at elevations lowered at most by only 500 to 600 m, and not 1000 to 2000 m, perhaps in the flatlands around Arcelia at 600 m, or elsewhere in the Rio Balsas region (Doebley, Goodman and Stuber 1984; Benz and Iltis 1992); third, that because of the extremely rare occurrence of mutations in teosinte, the "founder population" leading to maize was initially extremely small, in fact more likely only *one* large mutated "founder plant" (cf. Goodman 1987:213), albeit producing many fruitcases, and not a large, genetically heterogeneous founder "population," in short, a maizoid "Eve," and that this extremely small effective population size facilitated the fixation of mutant alleles, and then "... acquired ... over the centuries, ... its cytological, enzymatic, and morphological variation by a combination of mutations and backcrossing to the parental taxon" (Goodman 1987:213); fourth, and in concordance with the habits of the still mobile, minute bands of hunter-gatherers becoming incipient horti-agriculturalists, that there must have been multiple occasions when, while being moved from place to place, captive (i.e., non-indigenous) teosinte populations where repeatedly forced through the eye-of-a-needle, experiencing repeatedly dramatic reductions in size (i.e., subject to founder effects), favoring easy fixation of alleles by random genetic drift; and fifth, that genetic variability of maize came about not by multiple domestications, or by large populations of teosinte being mass-selected, but by occasional or rare backcrosses of the mutants to nearby plants of less-mutated or even pure parental Balsas teosinte "hanging on" in the wild or even in the same "garden" (or whatever one may wish to call sporadic cultivation on kitchen middens by these foraging hunter-gatherers).

I am not a subscriber to exceptionalist theories, but *Zea,* being monoecious, subtropical, and with an initially inedible fruit, is certainly an exceptional crop ancestor. Thus, one must agree with Doebley (1990a:16) that "... because any transformation of teosinte into maize must have involved a series of improbable mutations (Galinat 1983; Iltis 1983b, 1987), it seems more probable to hypothesize that this transformation occurred only once." And if only once, why not only from a single mutated seed that grew into a single, multi-seeded, mutated plant? I am neither a molecular geneticist nor a population biologist, but the reported lack of any detectable differences between maize, *Z. mays* ssp. *mays,* and the two teosintes, *Z. m. mexicana* and *Z. m. parviglumis,* in the maternally inherited chloroplast DNA is evidence in support of this notion (Doebley, Goodman and Stuber 1987), of which there is very little variation even between teosinte taxa and even less in maize, which has its own subset. Mitochondrial DNA, which is also inherited strictly maternally, could also be cited in support of such maizoid "Eve" arguments, but appears to be unstable, very variable and "in a flux" in *Zea.*

It is certainly clear, also, from all that I have read, that "the inhabitants of Guilá Naquitz and Coxcatlan [caves] were predominantly foraging on the most abundant local plants and that cultivation appears to have been insignificant at those locations ..." (Buckler, Pearsall and Holtsford 1998). In fact, "The Archeological record in various regions of Mexico and North America shows that people did not switch from hunting and gathering to food production as soon as they had maize [read teosinte]. Rather, they planted some corn [read teosinte], probably as more of a snack than a staple, and remained primarily reliant on wild food sources for centuries" (Sauer 1993), or even millennia. The substitution of teosinte for maize in the above quote, grown not for grain but for sugar and vegetable, and, as Jonathan Sauer says, "more for a snack than a staple," thus gives us a hypothetical picture of what the initial domestication scenario of *Zea mays* in some messy kitchen midden proto-garden might have been like (cf. Clark and Piggott 1965:171–172; Lieberman and Lieberman 1980).

To reconstruct a scenario of the earliest teosinte *grain* domestication is hazardous. Though the mutation that projected the grain from the fruitcase (*Tga1,* or one with similar effects) may have started with *one* plant, that rare mutant very likely could have had many "seeds," many hundreds in fact, that would of course have been perfectly capable of starting a small local population all by itself by self-seeding. But it is perhaps much more likely, however, that such a population was perpetuated with aid from an garden-minded imaginative person, since until then "seeds" (fruitcases) were not utilized, and teosinte plants, once past the sugar stage, abandoned and used, if at all, only for kindling.

In any case, by reducing induration, such a mutation would have reduced nutrient demand by the cupule, which concurrently opened up to release from narrow confinement the atavistic pedicellate spikelet and thus would have soon allowed the now excess nutrients and the changed morphology to allow a mutation for doubling the grain to become activated. Doubling the grain number would have opened the cupule even more and, in addition, vastly strengthened the longitudinal vascularization of the ear and thus its non-fragmentation, countermanding at the same time its abscission layers. Finally, by exposing the grains, alleles for anthocyanins, already present but hidden in the teosinte fruitcases, became visible (Hanson et al. 1996), leading to their use as genetic markers and the explosive evolution of the races of maize under intense human selection. In short, the one mutation that liberated the grain would seem to have started a small cascade of morpho-physiological events that previously would not have been possible, at least not without destroying the whole, highly canalized adaptive syndrome that the cupulate fruitcase represents. But, once domestication for grain took over, and now decoupled from teosintoid morphological constraints, that syndrome unraveled quickly to slowly give way to one closely tailored to human needs: the polystichous, many-seeded, firmly husked and human-dependent ear of maize.

VI. DISCUSSION AND CONCLUSION

The case has here been made that teosinte, the direct ancestor of maize, was initially domesticated not for its grain but for its sugary pith or other edible parts. Under what conditions, then, and where, did maize evolve?

First of all, and in general agreement with many anthropologists and ethnobotanists, most Old World cultivated grains may have initially been *gathered* in the region of their greatest abundance, but the actual effective *domestication* probably occurred away from the region of nativity, for who would take the trouble to plant and care for a crop that grows wild in abundance in your own backyard and can be had for the asking? The corollary of this hypothesis, of course, is the notion that selection for a particularly useful mutation, one that would be favored by selection for more food and easier harvestability, would have to occur far from the vast fields of wild plants, so that speciation could proceed in geographic isolation, away from contamination by indigenous pollen, a principle that holds for cultigens as much as it does for most any other plants and animals. Thus, for both reasons, the absence of the resource in the region making it valuable, and the geographic isolation leading to effective genetic isolation, we may suppose that the mutated teosinte was first cultivated ±*away* from its enormous wild populations that at least 20 years ago were still clothing the limestone hills between Teloloapan and Arcelia in Guerrero, a domestication that may even have occurred near some watercourse near Tehuacán where the earliest archeological maize so far known has been discovered, an area where teosinte does *not* now occur, nor presumably thousands of years ago, but where some unknown hunter-gatherers may have grown it for its sugary pith from Guerrero seeds. Clearly, we don't know, and much more aggressive archeology is needed in Mexico.

In order for teosinte to have become domesticated anywhere away from its native populations, someone had to gather its "seeds." It is evident from all that has been said that teosinte was probably even better known to local people then as it is now—it is a grass that cannot be ignored. Gathered from one plant at a time, small amounts of "seeds" must have been carried to the new location and sown, grown, and the new seed saved for the following year, or often even self-sown, for generation after generation, with no aim for *grain* improvement, conscious or unconscious, in mind. After generations of association, someone, somewhere, must have noted a mutation (Dorweiler et al. 1993; Dorweiler and Doebley 1997) one that by reducing the depth of the cupule, projected the grain and made it visible, and, if dried or parched, brittle and separable by abrasion, and thus usable and open to human selection.

It may, initially, have been only one plant that started teosinte out on its long journey, a plant grown from a seed with a single mutation for soft glumes and shallow rachids, spotted probably by some bright-eyed young woman engaged in mothering the few crops on which their germinating civilization soon learned to be dependent, someone who then planted (or allowed to self-seed) these, by comparison, rather peculiar grains the next year, and the long tortuous morpho-genetic journey towards *Zea mays mays* would have been on its way.

Teosinte is an enormously complicated plant, structurally and physiologically (Iltis 1987), and it took a long time to reach the stage of domestication shown by the primitive, yet fully evolved *maize* ears found at Tehuacán, these, alas, yet burdened with many tell-tale indications of the as yet not quite completely canalized maize morphology: polystichous ears with male "tails" and small grains, and distichous ears (these presumably lateral on the primary branches) not all that uncommon. As of now, it may well be said that the reason agriculture came to the New World much later than in the Old was a reflection of both the absence of any large-grained Hordeae in the Americas, and of the difficulty mankind had in taming teosinte, its only large-seeded annual grass, and even then one with dubious agricultural potential. After all, with wheat, barley or rye, all that was needed were some simple genetic changes, gained by mass-harvest, automatically selected in a short-day climate (Iltis 1987). This must have been true to some extent even with beans and squash, hence their postulated earlier utilization or domestication (Kaplan and Lynch 1999). But teosinte, in its enormous structural complexity, and its long-day (lengthening-day), subtropical life-cycle, was in every way different, this said despite vehement protestations to the contrary (Harlan 1975). The belated discovery of alkali processing of maize grains may have also contributed to the 5000 year lag in Mexican agriculture and civilization (Katz, Hediger and Valleroy 1974).

Maize, in all its glory, is indeed a reflection not only of the intelligence devoted to its domestication—no automatic mass selection here, as in the Old World, only individual plant-by-plant, eye-to-eye becaring (Sauer 1965)—but to the love of color, shape and taste of this most marvelous of all human agricultural creations, which not only fed the bodies of the New World farmers, but their spirits and souls as well: for as the old campesino from near Toluca, one Vincente Gilberto, said to me in answering my questions about why he grew such an incredibly variable maize crop: "Ah, Señor, porque los mazorcas son muy lindas!" ["Ah, señor, because these ears are so very beautiful!"] (Crosswhite 1982b).

It is not for nothing that "teosinte" or "teocintle" meant "God's grain" in the ancient Nahuatl language of the Aztecs, or that it was a local farmer's wife, a pretty feisty young waitress at CIMMYT's (Centro Internacional de Mejoramente de Maíz y Trigo) cantina bar (but *not* any of its visiting Ph.D.'d plant breeders), who, in 1981, when shown some freshly gathered teosinte, knew it right away, calling it "madre de maiz," the mother of maize!

Teosinte survives in Mexico, but some populations have been lost, others are barely hanging on (Iltis 1974; Sanchez and Ordaz 1987; Wilkes 1985), and no concerted effort to preserve *in situ* this great gift of the gods is in the offing except in our beloved Sierra de Manantlán (Vázquez G. et al. 1995; Guzman and Iltis 1991; Benz, Sanchez-V. and Santana-Michel 1990). Since the story of maize has not yet all been told, and since the genetic erosion of its land races, too, continues unabated (Iltis 1974), we ethnobotantists might well want to reconsider our priorities, both scientific and personal, as we move pell-mell and thoughtlessly into a second Green Revolution, which promises to have consequences even more destructive of wild nature, native cultures and precious cultivars than the first. It is thus for many good reasons why Wade Davis (1994:339), the author of *One River*, Richard Schultes' biography, felt compelled to remind all of us that "... the ultimate role of ethnobotany lies not in the identification of new natural products for the benefit of the modern world, but rather in the illumination of a profoundly different way of living in relationship to nature, a folk wisdom that may temper and guide the inevitable development processes that today ride roughshod over much of the earth."

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