From Teosinte to Maize: The Catastrophic Sexual Transmutation

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Summary. An alternative to the theory that the ear of maize (*Zea mays* ssp. *mays*) evolved from a slender female ear of a Mexican annual teosinte holds that it was derived from the central spike of a *male* teosinte inflorescence (tassel) which terminates the primary lateral branches. This alternative hypothesis is more consistent with morphology and explains the anomalous lack of significant genetic and biochemical differences between these taxa. Maize, the only cereal with unisexual inflorescences, evolved through a sudden epigenetic sexual transmutation involving condensation of primary branches, which brought their tassels into the zone of female expression, leading to strong apical dominance and a catastrophic shift in nutrient allocation. Initially, this quantum change may have involved no new mutations, but rather genetic assimilation under human selection of an abnormality, perhaps environmentally triggered.

A commonly accepted aspect of Darwinian evolution by natural selection is the gradual change of species over time. This has been challenged recently by the view that basic structural change occurs during a rapid macroevolutionary phase followed by long periods of relatively little change (*1*). That nearly instantaneous morphological revolutions can occur is shown by the evolution of maize, the subject of this article.

The hundred-year controversy surrounding Indian corn or maize (*Zea mays* L. ssp. *mays*) revolves around two questions: Where, when, and from what species did this obligatory crop evolve? In what way and from what structure did the uniquely polystichous maize ear arise?

With few dissents (*2, 3*), the first question has recently been resolved in favor of Mexican annual teosinte, either *Zea mays* ssp. *mexicana* (Schrad.) Iltis or *Zea mays* ssp. *parviglumis* Iltis & Doebley. Archeological material from Tehuacán suggests that domestication occurred about 7500 years ago (*2, 4*). The relationship is supported by morphology (*5–10*), genetics and cytology (*11–14*), and phytochemistry (*15*). Maize and Mexican annual teosinte have ten pairs of chromosomes with nearly identical structures. They are often 100 percent interfertile with the hybrids showing regular meiotic pairing, and segregates include all conceivable intermediates in their ears. So close is this relationship that these taxa are now all classified as subspecies of *Zea mays* (*7, 9, 16*).

Although support for teosinte as the direct ancestor is overwhelming, valid questions have been raised which lack satisfactory answers (*2, 17, 18*).

1) If maize evolved gradually from teosinte, why have no intermediates (excluding hybrids) been found in nature or in the archeological record?

2) If Indians domesticated teosinte for its "grains," why has no one ever found their extremely durable fruitcases contemporaneous with or predating the earliest archeological maize? Had teosinte grains been gathered, one would expect to find quantities of them in Mexican archeological sites. Yet, except for only two fruitcases, these probably not used by man (*19*), such have never been found (*2*, p. 52). In fact, teosinte is a most unpromising grain source (*2, 17, 20*).

3) Given the extreme hardness and concavity of teosinte fruitcases, why are the glumes of the earliest archeological maize soft and thin and its cupules relatively shallow?

4) If teosinte ears became transformed into maize ears, why do both modern and archeological maize ears so often exhibit staminate "tails" (*2*, pp. 128 and 180)?

5) Compared with the gradual evolution documented for all other cereals, how did maize arise so suddenly, from ancestors difficult to identify?

The question of exactly how the maize ear arose also continues to perplex botanists and geneticists (*21, 22*). Clear-cut Mendelian factors distinguishing maize from teosinte are yet to be found, despite 80 years of searching (*11, 14, 18*). Maize and teosinte are practically indistinguishable except for their female inflorescences. To say that maize evolved from teosinte in the usual Darwinian fashion is hardly enough, and a plausible explanation integrating morphology with genetics is needed. However, if the maize ear is derived from the male inflorescence of teosinte, rather than from the female, all these difficulties can be resolved (*6–8, 23, 24*).

The Origin of the Maize Ear: A Plethora of Theories

The teosinte hypothesis (*5, 10, 11, 13, 14, 16, 25*) identifies annual Mexican teosinte as the ancestor of maize. The polystichous maize ear is derived from the distichous teosinte ear by gradual enlargement, condensation, and twisting of the inflorescence axis (*5, 10, 26 pro parte*) (Figs. 1, 2, and 3, a–k).

The uninterrupted series of hybrid intermediates linking distichous (with two rows of single grains; Fig. 2b) teosinte ears to the polystichous (with four to many rows of paired grains; Fig. 3, d–e and i–k) maize ears has made this twisting easy to visualize (*10, 17, 26–29*). Nevertheless, Weatherwax (*30*, p. 113) sensed that something was amiss: "Hybrids between maize and teosinte will always exhibit suggestive series; but, until we are more sure of the homologies between these two genera, it is futile to expect much information from the hybrids, for they will be speaking in a language that we cannot understand." The crucial difference in the position of the female inflorescences escaped his notice: clustered and lateral on the stout primary branches in teosinte, terminal in maize. In other words, in a well-grown, branched teosinte, the position of the maize ear is always occupied by a tassel (Fig. 1). Additional confusion has come from a misinterpretation of ear clustering in teosinte, often considered as the first step in maize domestication (*10, 11, 14, 21, 31, 32*) (Table 1).

The homology of maize ear and tassel spike hypothesis is based on the fact that both are polystichous and can readily change from one into the other by proper

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experimental technique (*33*) or corn smut infection (*34, 35*). From this arose two misconceptions: (i) the maize ear is a feminized central tassel spike of maize and (ii) several distichous tassel branchlets of some ancestral grass fused or fasciated to form a polystichous structure.

The homology of maize ear to tassel spike is an accepted fact: "All authorities recognize that the ear of corn is a transformed terminal inflorescence of a lateral branch and that its covering of husks came about through a shortening of the internodes," said Kempton (*17*, p. 396). [Though not realizing its significance, he showed a picture of a teosinte plant with all lateral branches tipped by tassels (*17*, plate 17, figure 2).] "The ear is obviously the terminal inflorescence of a lateral branch whose internodes have, probably during the course of domestication, become dramatically contracted. . . . [T]here can be little doubt that it is the homologue of the central spike of the staminate inflorescence, the tassel," said Mangelsdorf (*28*, p. 35). Like Montgomery (*36*) and Kellerman (*37*), however, he had the wrong parent.

It is easy to transform the already polystichous maize tassel spike into a polystichous maize ear, as seen in a common teratology (*35*). But how did the tassel spike itself become polystichous? For in the 97 genera and more than 900 species of the subfamily Andropogonoideae, "except for maize, and maize alone, . . . polystichy of any sort is totally unknown, and distichy the universal rule" (*8*, p. 983; *38*).

Another teratology (*17, 27, 36–41*) is branched corn—a normal polystichous (Fig. 3, d–e and j–k) ear of maize subtended at its base by several distichous grain-bearing branchlets (Fig. 3, c and h). Enclosed with the central ear in the same husks, such branched ears are but feminized tassels, with polystichy and distichy on the same inflorescence. This suggests that polystichy is a position effect related to apical dominance (*5, 10*) and not to specific genes for polystichy (*28*, p. 65).

The branch reduction hypothesis proposes that maize ears and tassels evolved from panicles with perfect-flowered spikelets by differential suppression and condensation. The panicle of the main stem became the male tassel, those of the lateral branches the female ears. In either sex, polystichy was achieved by reducing the many uppermost panicle branchlets to one spikelet pair each (*17, 36–38, 42–45*). But sexual dimorphism was already fully established long before the origin of maize, both in teosinte and in the related genus *Tripsacum*.

The extinct wild maize hypothesis, that maize was domesticated in the nick of time from a now extinct, polystichous wild species, was the basic assumption of the tripartite hypothesis of Mangels-

Chalco teosinte
Zea mays mexicana

Protomaize
based on maize
X teosinte hybrid

Maize
Zea mays mays

Fig. 1. The origin of the maize ear by catastrophic sexual transmutation. The contraction of branch internodes was coupled to a shift of the terminal male inflorescences (tassels) into the hormonal zone of female expression and the suppression of lateral female inflorescences of teosinte. Shaded bands indicate the threshold zone below which only female inflorescences form. The left-hand side of each plant is shown as a habit sketch, the right-hand side as a diagrammatic cross section of internode patterns and exposed ears. Note increases in apical dominance associated with the feminization of the male inflorescences of primary lateral branches and the secondarily correlated thickening of the maize tassel spike. The sketch of Chalco teosinte is based on a plant growing 5.5 km from Los Reyes on the road to Texcoco, Valley of Mexico, that of the hypothetical protomaize on Chalco teosinte × maize hybrids grown by G. W. Beadle and J. H. Lonnquist. Recent work indicates that the direct ancestor of maize was probably subspecies *parviglumis* rather than *mexicana*.

dorf and Reeves (*2, 4, 44, 46*), as well as the remote common ancestor hypothesis of Weatherwax (*47*) and Randolph (*48*), which proposed the parallel evolution of wild maize (*Zea*), teosinte (as *Euchlaena*), and *Tripsacum*. Neither theory addressed the origin of polystichy. Today, most workers agree that (i) annual Mexican teosinte and maize are conspecific (*9, 16, 25; 49*, p. 240), (ii) the teosintes are clearly differentiated into several taxa (*7–9, 12, 50*), and (iii) the teosintes are not hybrids of any ancestral wild maize with *Tripsacum* (*2; 44*, p. 172). Furthermore, biochemical (*15*) and morphological evidence (*7, 8*) precludes any possibility that the annual teosintes are segregates of a hypothetical cross between *Zea diploperennis* Iltis, Doebley & Guzman and wild maize, as recently proposed (*3*). Although these truly wild theories caused much controversy, both stimulating and otherwise (*2, 3, 14, 51*), they did lead, indirectly, to the remarkable discovery of the 7000-year-old protomaize of Tehuacán (*4*).

The Catastrophic Sexual Transmutation Theory: A New Synthesis

The catastrophic sexual transmutation theory (CSTT) states that the maize ear is the transformed, feminized, and condensed central spike of the teosinte tassel that terminates the primary lateral branches (*6–9, 23, 24; 42*, p. 18). From previous theories, it accepts the following assumptions (Table 1):

1) From the shortening, yoking, and twisting hypothesis of Collins (*26*) for the origin of polystichy, that axis contraction [condensation, compaction (*28*)] led first to lateral displacement of rachis segments (rachids), then to their yoking, horizontal twisting, and alternate stacking according to principles of optimal packing—all this on the male background of the teosinte tassel spike. [Collins used—for sake of clarity only, as he emphasized—a distichous maize tassel branchlet to illustrate the genesis of polystichy in the ear (Fig. 3, o–r)].

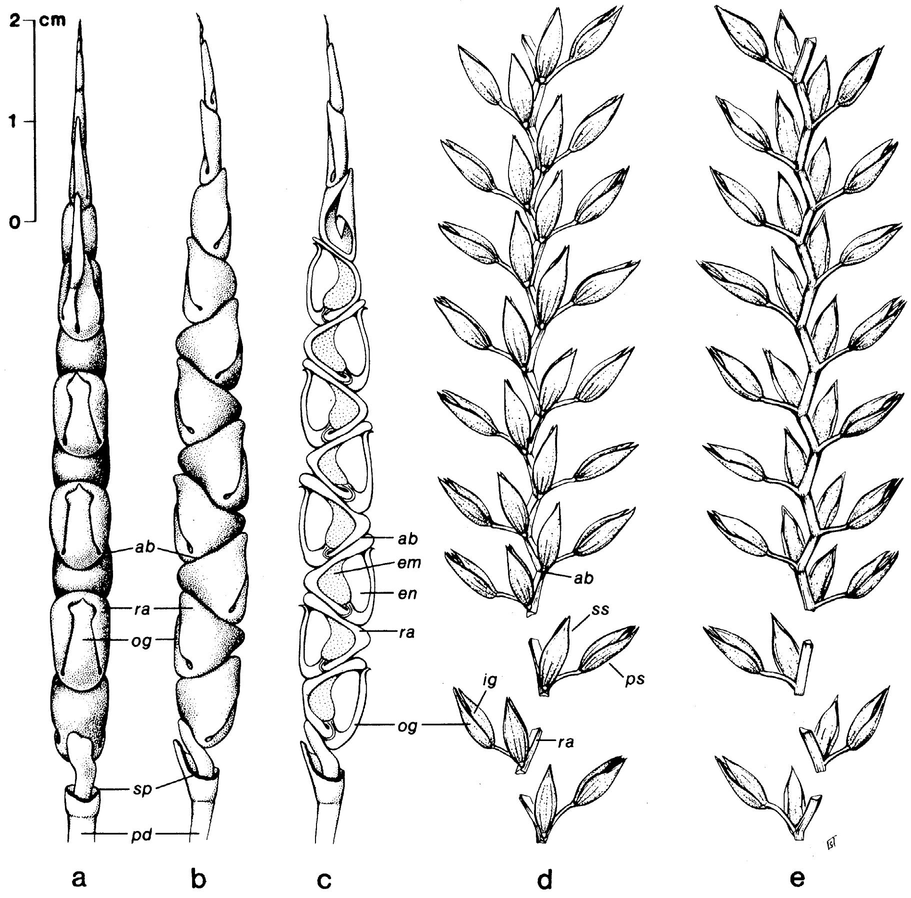

Fig. 2. Female (ears) and male (tassel) branches of *Zea mays* ssp. *mexicana*, race Chalco, the annual teosinte of the Valley of Mexico: (a) side view of ear (left is back); (b) front (abaxial) view of ear; (c) longitudinal section of (b); (d) front (abaxial) and (e) back (adaxial) view of tassel spike or branch. (a–c) Female inflorescence: *ra*, rachid (cupule); *og*, outer glume, which, together with *ra*, forms the cupulate fruitcase; *em*, embryo; *en*, endosperm; *pd*, peduncle; *sp*, spathe scar (most of the spathe removed); *ab*, abscission layer; papery inner glume, lemmas, and paleas of both suppressed and grain-forming spikelets are not shown; in (a) the eighth rachid from the base shows also a nonsuppressed pedicellate spikelet, a rare abnormality. (d–e) Male inflorescence: *ra*, rachid; *og*, outer glume; *ig*, inner glume; *ss*, sessile spikelet; *ps*, pedicellate spikelet; *ab*, abscission layer; lowest three rachids with their spikelets are shown disarticulated. Female ears from Ixtapaluca (*Iltis and Doebley 10b*), tassels from 5.5 km north of Los Reyes (*Iltis et al. 769*); all drawings to same scale; note that 11 female rachids equal about 17 male rachids; hence feminization of the latter will result, automatically, in condensation and deflection of grain away from the rachid.

2) From the teosinte hypothesis of Ascherson (*39*) and Harshberger (*52*), later elaborated by Beadle (*13, 14*) and others (*5, 10–12, 16*), that maize evolved from annual Mexican teosinte, but the maize ear derived from the teosinte tassel spike (Fig. 2d) and not from the teosinte ear (Fig. 2, a–c). Although the CSTT was developed independently in 1979 (*6, 23*), the idea was anticipated in 1913 by Montgomery (*42*), who was a student of Bessey's at Nebraska commemorated in the "Montgomery effect" (*53*), and among the first to invoke sexual transformations in the origin of maize (*54*). Similar sexual transformations were noted by Torres in 1938 (*55*).

3) From the maize ear–central tassel spike homology hypothesis proposed by Kellerman in 1895 (*37*), Montgomery in 1906 (*36*), and Iltis in 1911 (*35*), that the maize ear was derived from a central tassel spike (Fig. 3, n and r), however not from the polystichous one of maize, but from the distichous one of teosinte terminating each primary lateral branch (Figs. 1, 2d, and 3f).

4) The CSTT accepts the various botanical and genetic objections (*2, 10, 17, 18, 21, 43, 44, 47; 56*, pp. 183–187; *57; 58*, p. 17) to the teosinte hypothesis regarding the assumed simplicity of Mendelian inheritance of the critical maize characteristics as postulated by Emerson, Langham (*59*), Rogers, and Beadle (*13, 14, 60*). But the CSTT shows that, except for polystichy, the basic traits differentiating maize from teosinte are simply those that differentiate the teosinte tassel spike from the teosinte ear. The unique characters of maize are nothing more than the sexually transmuted, primitive characteristics of the teosinte tassel, accompanied by the suppression of all lateral ears. (When occasionally such do occur in maize, they are often distichous.) The CSTT also accounts for the anomaly that no key genes differentiating maize from teosinte have ever been found. This is because, in fact, they do not as such exist.

5) The CSTT envisions hormonal mechanisms at early developmental stages to be of prime importance, perhaps initially triggered by environmental or biotic factors (*35, 38*). A hormonal model proposed by Chailakhyan and

Khryanin (*61*, figure 6, p. 340) may be applicable to the CSTT: the masculinizing influence of gibberellins produced in the seedling leaves would be overcome by the feminizing influence of cytokinins produced in the seedling roots. Sexual transmutations are easily induced experimentally in *Zea mays* ssp. *mays* (*33, 61–64*) and in greenhouse-grown plants of the ancestral subspecies *mexicana* (*65*).

The CSTT is based on a complex of physiological interactions and evolutionarily mandated predispositions (Table 1 and Figs. 1 to 3):

The apical dominance hierarchy. A branched plant of annual teosinte has an outer male zone of tassels and an inner female zone of ears (Fig. 1). Its central stem is terminated by a tassel. This tassel, the first to bloom, physiologically dominates primary branch inflorescences of both sexes beneath it, these in turn those of still lower order (*27*). Within each tassel, the central spike blooms in advance of the lateral branchlets.

In open-grown teosinte plants (Fig. 1), each of the five to ten primary branches is terminated like the main stem by a tassel which develops before subsidiary tassels or ears of that branch (*38*). The apical dominance of that tassel is weak, however, being constrained by its limited use of resources: some material for pollen, the rest for the thin flowering bracts—glumes, lemmas, and paleas. In contrast, the dominance of a female inflorescence, if terminal on a primary branch, is very strong.

The feminization of the branch tassel. Should primary branch internodes become shortened (*66*), the branch tassels would soon find themselves in the female hormonal zone and start producing female instead of male flowers. Certain abnormal environmental conditions also trigger tassel feminization which then, in turn, could have induced branch internode condensation. In either case, feminization increases primary branch condensation, secondary branch suppression, and tassel branchlet, peduncle, and branching space deletion. The critical zone of hormonal initiation is evidently the base of the tassel spike (that is, the butt of the ear), with condensation proceeding from there both upward into the tassel spike (ear) and downward into the primary branch (shank). This is especially well shown in cultivars such as Conico (see cover). Concurrently, feminization likewise proceeds from the base of the tassel spike and branchlets upward and is expressed, to begin with, in the sessile spikelet of each pair only (*27, 35, 36*) (Figs. 1b and 3, b and g).

Sex expression in Zea. All *Zea* flowers are characterized by relic bisexuality, each with the potential of developing the vestigial parts of the opposite sex (*33–36, 41, 47, 67*). Sexual switches in either direction are common in plants subjected to unusually wet or cold summers, disease or injury, or, in greenhouses, to the shorter growing seasons and colder nights of winter (*33, 62, 63*). The propensity for sex reversal is genetically determined, as shown by dramatic differences in sex expression under abnormal environments between different inbred maize cultivars (*62*). Hormonal explanations for sex expression in maize imply the involvement of a seasonal (*38*), shifting balance between cytokinins produced by the seedling roots causing feminine expression and gibberellins produced by the leaves causing masculine expression (*61*). Perhaps significantly, root growth in corn is promoted by cool temperatures (*65*).

Branch condensation in Zea. Tassel feminization and primary branch condensation are intimately related (Fig. 1). The role of condensation has been stressed before, but only as a supposed consequence of human selection (*10, 21, 31, 66*). However, teosinte grains borne on a male background will result auto-

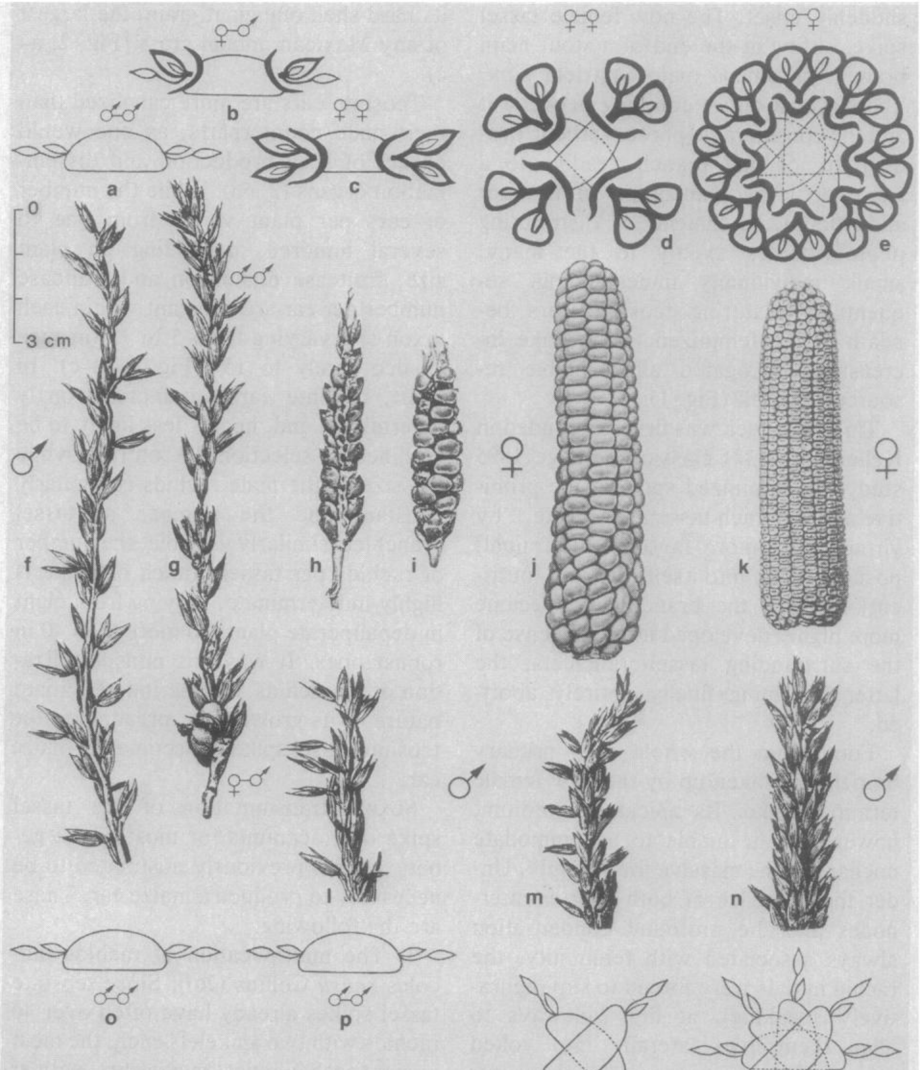

Fig. 3. The evolution of the maize ear by sexual transmutation [(a–e) cross sections of (f–k) following Collins' (*26*) diagrams of the male sequence] leads from a distichous central tassel spike (f), becoming feminized at base (g), to a distichous (h), then polystichous 8- (i and j) to 16-rowed (k) ear, with condensation (contraction of internodes), twisting, compaction and [after (i)] multiplication of the processes involved. The homologous male sequence [(o–r) from Collins (*26*), are cross sections of (f) and (l–n)] leads to the polystichous tassel spike of maize (n and r) consequent to human selection in the female sequence [(f) Chalco teosinte (*Zea mays* ssp. *mexicana*); (g) Chalco teosinte × maize; (h and i) Chalco teosinte × Argentine popcorn hybrids, grown by G. W. Beadle in Mexico; (j and k) maize; (f–j and l–n) same scale; (k) reduced by half].

matically in some ear condensation (Fig. 2), because in a given length of inflorescence there are about 60 percent more male rachids than female rachids.

Apical dominance, nutrient sink, and structural revolution. Because tassels are developmentally precocious, *Zea* is protandrous. Tassels are slender and nutrient-undemanding, unlike the ears evolved from them, which exert vigorous apical dominance over all later-developing structures. This dominance is especially strong over the many ears of the secondary and tertiary lateral branchlets. When the central spike of the primary branch tassels changed sex, the whole physiological balance in the dominance system of the teosinte plant was suddenly upset. The now female tassel spike, sitting at the end of a stout main branch, became a major nutrient sink. There was a direct coupling between it and the considerable photosynthetic productivity of that branch, leading to a catastrophic reorganization of nutrient allocation (*23*). Instead of distributing photosynthates evenly to the many, small, individually undemanding, sequentially maturing teosinte ears beneath it, the feminized tassel spike increasingly arrogated all available resources to itself (Fig. 1).

This basic idea was first expounded in Kellerman's (*37*) classic one-page 1895 study: the feminized spike of the primitive maize branch tassel, she wrote, "by virtue of its more favorable [terminal] position, drew into itself the main [nutrient] force of the branch, and became more highly developed at the expense of the surrounding tassel-branchlets, the latter becoming finally entirely aborted."

Food from the whole of a primary branch was taken up by the now female terminal spike. Its apical primordium, however, was unable to accommodate unchanged the massive food supply. Under the influence of both shorter internodes and the profound condensation always associated with femininity, the rachid initials were forced to slip (figuratively speaking), at first sideways to align themselves laterally into yoked pairs to form a compact distichous ear (Fig. 3h), which then, with still greater condensation, twisted spontaneously into a still more compact polystichous maize ear (*26*) (Fig. 3i). Thus, "a threshold in torsion created by a basal gradient of twisting from condensation [was] suddenly relaxed by slippage into a higher order of ranking" (*10*, p. 323).

The teosinte tassel spike, preadapted to become a maize ear. Among cereal genera, *Zea* alone has unisexual inflorescences. Without this specialization, there could never have been a sexual transmutation. Nevertheless, the teosinte tassel is otherwise unspecialized, its branchlets nearly identical to those of such primitive andropogonoid genera as *Erianthus*, *Ischaemum*, or *Andropogon* (Table 1 and Fig. 2, d and e). The basic structural design (spikelets in sessile-pedicellate pairs, each with two florets; rachids slender; glumes soft) is evidently ancient. In contrast, the teosinte ear (Fig. 2, a–c) is structurally highly modified (spikelets solitary, each with one floret; rachids and outer glume hard) and clearly recent. When mature, it disarticulates into 5 to 12 "cupulate fruitcases" (*11–12*), each permanently enclosing in its hard shell one giant grain, the largest of any Mexican annual grass (Fig. 2, a–c).

Teosinte ears are more canalized than their male counterparts, as one would expect of seed production and dissemination organs (*7, 68*). While the number of ears per plant varies from one to several hundred, depending on plant size, fruitcase dimension and fruitcase number per ear are constant within each taxon (*7*), varying from 5 to 12 (in race Chalco rarely to 15) (Fig. 2, a–c). In short, teosinte ears are more strongly determinate and, hence, less likely to be modified by selection. In contrast, while the size of the male rachids is similarly constant and the number of tassel branchlets similarly variable, the number of rachids per tassel branch or spike is highly indeterminate, varying from eight in depauperate plants to more than 40 in robust ones. It was this nonspecialization of its rachids and the indeterminate nature of its growth that preadapted the teosinte tassel spike to become the maize ear.

Sexual transmutation of the tassel spike thus accounts for most of the genetic events previously postulated to be necessary to produce a maize ear. These are the following:

1) The multiplication of rachids [alicoles *sensu* Collins (*26*)]. Since teosinte tassel spikes already have often over 40 rachids with two spikelets each, the most ancient archeological maize ears, with at most 36 rachids (72 grains), are easily derived. Because the number of rachids in tassel spikes are relatively indeterminate, the proliferation of rachids to 500 or more in modern maize does not present much of a morphogenetic problem.

2) The reactivation of the pedicellate spikelet, suppressed in the teosinte ear. This is unnecessary since each male tassel rachid already carries a pair of fertile spikelets (Table 1 and Figs. 2 and 3).

3) The initial condensation of the ear, the liberation of the grain from the cupulate fruitcase, and the occurrence of free, hence harvestable, grains already in the oldest archeological maize. The sexual transmutation produced female spikelets on the shorter, more slender rachids of the tassel, that is, on a male background (Fig. 3g). Even with the condensing, hardening effects of feminization on the rachid (*35*) (Table 1), the grains were subtended by short, shallow, empty cupules and, enclosed in soft male glumes, were thus free from the start. The maize (rarely teosinte) mutants of tassel-seed allow us a glimpse of this ancient state.

4) The paradoxical male tail at the tip of the female ear, common in archeological (*4, 69*) and contemporary maize, and illustrated in Mangelsdorf and Galinat's reconstruction of wild corn (*2, 4, 70*). Feminization of the tassel spike proceeded gradually upward (Figs. 1b and 3f) and, if incomplete, left an as yet unmodified tassel tip as a phylogenetic reminder. Primitive types of maize (for example, Pollo) still have long shanks, hence frequently such atavistic male tails, and even ordinary corn ears are usually tipped by a few sterile or male spikelets.

In summary, out of a preadapted structure, with minor spatial and vascular adjustments, feminization automatically produced first a distichous four-rowed ear resembling a popcorn × teosinte hybrid (Fig. 3h), and later a small, polystichous maize ear (Fig. 3i). Occurring over only a few generations, hence phylogenetically instantaneous, these events resulted in a plant which, while easily harvestable, was totally dependent on man. Thus, the old system of reproduction by way of a thousand naturally dispersed grains produced over several months in a hundred small, disarticulating inflorescences was replaced by several nondisarticulating, multigrained and naked-grained inflorescences which mature in synchrony. This structure, initiated by accident but preserved, improved upon, and dispersed by human culture, evolved into that most remarkable of all agricultural artifacts, the modern ear of maize.

Threshold selection and phenotypic response. The sexual transmutation came about when male inflorescences crossed a hormonal threshold and became subject to feminization. To quote Mayr (*71*, p. 110): "The same genotype may produce different phenotypes under different environmental conditions. An extreme environment may bring out developmental potencies that are not expressed under normal conditions; it permits genetic factors to manifest themselves that do not normally reach the threshold of phenotypic expression." Such threshold effects underlie Waddington's (*72*) concept of "genetic assimilation."

Threshold effects could help explain the origin of maize in central Mexico 7500 years ago, as suggested in the following scenario. A wild population of teosinte subjected to abnormal conditions (such as accidental irrigation during the winter dry season, with grains germinating in a physiologically unorthodox regime) produced plants with feminized tassels, hence free grains, which gained

Table 1. Evolutionary criteria in *Zea mays*.

Teosinte hypotheses (*5, 10, 11, 13, 14, 21*): a female structure of teosinte is ancestral to the female structure of maize	Catastrophic sexual transmutation theory (*6, 23, 24*): a male structure of teosinte is ancestral to the female structure of maize
Assumptions	
The ear of maize evolved from a teosinte ear lateral to a primary branch or from an ear terminating a very short branch of an ear cluster lateral to the main stem, by the usual microevolutionary Darwinian processes.	The ear of maize evolved from the central spike of the terminal tassel of a well-developed, elongated, primary lateral branch, by way of a catastrophic sexual transmutation, a unique macroevolutionary event.
The ear of maize became apically dominant gradually through human selection; no sudden reallocations of nutrients within the branch system are hypothesized. Sudden appearance of maize in the archeological record, and the lack of teosinte fruitcases therein, are not explained.	Tassel feminization led to apical dominance: the central spike of the primary branches (having developmental priority and hence potential for preempting nutrients by suppressing ears on branches of lesser rank) changed from a nutrient-undemanding "governor" to a nutrient-requisitioning "dictator." This sudden nutrient reallocation explains the sudden appearance of maize in the archeological record.
Domestication was initiated by harvesting ripe teosinte grains for food. Unbranched teosinte plants with strongly clustered ears represent the crucial intermediary steps leading to maize: ear clustering and loss of long tassel-bearing branches are due to selection for easier harvesting.	Ripe teosinte grains were not used for food. Openly branched teosinte plants were ancestral to maize, their stout and long primary branches bearing ear clusters and terminating in tassels; nonbranching is the normal response of teosinte to high competition or shading.
Domestication of maize, initiated by a stepwise accumulation of single-gene mutations typical of human crop selection, is analogous to that of Old World Hordeae such as wheat or barley. All basic characteristics distinguishing maize from teosinte (such as reactivation of pedicellate spikelet, doubling the grain number per rachid) are due to mutations favored by human selection.	Domestication of maize, only in a minor way analogous to that of Old World Hordeae, began after a sexual transmutation produced free-grained proto-ears, allowing grain utilization. All basic traits distinguishing maize developed simultaneously with tassel feminization. Doubling grain number was automatic with male rachids already possessing two spikelets. Only nonfragmentation, husking, and various increases (in condensation, grain size, and rachid number beyond that of tassel spike) are due to human selection.
"The cupule [of the female teosinte ear] provides the connecting link between the maize cob and the fruitcase of teosinte" (*10*, p. 317); the cupules of maize and teosinte are homologous, and this represents the strongest morphological argument that the maize ear evolved from the teosinte ear. The morphological differences in the cupules are not explained.	"In the oldest known archaeological maize cobs, the cupule is obsolete" (*10*, p. 317). Cupule homology is only partial. Maize cupules were derived from the rind hypodermis of the triangular tassel rachids (that is, from the flat, thin evascular hypodermis of the side facing the spikelet pair, with the wings reinforced on the back by that of the outer two vascularized sides) by buckling, lateral expansion, and induration, all induced by feminization. Maize cupules are thus parahomologous to those of teosinte, which represent whole rachids—pith, central vascular strands, and all.
The so-called "freeing of the grain" from the hard teosinte fruitcase, a prerequisite to human use and subsequent grain enlargement, was due to deliberate selection for alleles of *Tu* ("tunicate"), which suppressed abscission layers, softened the glumes, and flattened the fruitcases, allowing easy removal of grains. The soft papery glumes of the earliest archeological maize and of modern primitive maize are due to "tunicate" genes.	The "freeing of the grain" from the teosinte fruitcase did not occur. Grains in maize were free from the beginning, a consequence of femininity expressed on a male background; each tassel rachid, already shorter than that of the female, folded back upon itself, forcing the now much larger, paired spikelets (grains) out. Tunicate genes induce atavistic abnormalities and are not involved in the origin of maize; archeological maize ears are modified soft-glumed tassel spikes.
Variability in teosinte ears allowed selection for an increase in the number of rachids (fruitcases), leading to the evolution of the maize ear. Increase in the number of rachids above that found in teosinte ears (from 5 to 12 in teosinte to 18 or more in primitive archeological maize) was due to a gradual accumulation of mutations analogous to the grain-increasing mutations in wheat, barley, or rye.	The maximum number of rachids per teosinte ear is limited and under strict genetic control. Male teosinte spikes are more indeterminate, varying greatly in length depending on plant size. Increase in the number of rachid units above that of teosinte ears was initially due to feminization of the 40 or more rachids of the tassel spike, the comparison to Old World grains again based on false analogy. As the only cereal with unisexual inflorescences, *Zea* is unique.
The genetic explanation for the evolution of the maize ear is to be found in about five or six simple mutations, each responsible for one major distinguishing character; most such genes are yet to be identified.	Most distinguishing characteristics of maize are based on fundamental and ancient andropogonoid character syndromes; these, retained unmodified in teosinte and maize tassels, are extremely well canalized by polygenes unlikely now to be identified individually.
Results of assumptions	
The standard teosinte hypothesis creates paradoxes for which no solution can be found (such as soft-glumed primitive maize and the inability to find the monogenes differentiating maize and teosinte), does not permit establishment of consistent criteria by which valid phylogenies for races of maize can be developed, and precludes any plausible interpretation of maize morphology and anatomy.	The catastrophic sexual transmutation theory resolves almost all paradoxes in maize evolution and archeology, establishes consistent morphological criteria by which valid maize phylogenies may be developed, allows a plausible interpretation of maize ear morphology and anatomy, and promises experimental verification by environmental and genetic manipulation.

the attention of local farmers. In all likelihood, the majority remained normal, for the simple presence of genes allowing tassel feminization, even at low frequencies, would not have been sufficient under normal conditions [adapting a quote from Mayr (*71*, pp. 110–111)], "to lift the phenotype above the threshold of visibility. The [abnormal] treatment, however, reveals the carrier of such genes, and their continued selection [in our case, by man] permits an increasing accumulation in the gene pool of genes contributing to [feminization] until they express themselves phenotypically even without the treatment. The term 'genetic assimilation,' which Waddington [(*72*)] uses for such situations, seems [to Mayr] poorly chosen, because it fails to bring out the essential point that the treatment merely reveals which among a number of individuals already carry polygenes or modifiers of the desired phenotype. What we really have is *threshold selection*," which allows certain cryptic genes (*2*, pp. 127–131) to become expressed.

Alternatively, the initial expression of feminization may have been related to infection with a virus or with corn smut (*Ustilago maydis*) which regularly induces tassels to bear grains (*35*). Subsequent human selection could have canalized the grain-bearing potential independent of such infection.

The great variability in feminization potential of maize has been shown experimentally (*33, 62*). Certain lines never become feminized, others are highly susceptible. Thus, if phenotypic sexual responses differ both within a maize cultivar under different selection pressures and between different cultivars under identical selection pressures, there is every reason to expect homologous responses within wild teosinte populations.

In the timing of phenotypic expression, the altered sexual states were initially due to genes affecting late stages of development (*71*, p. 110). However, as facilitating genes accumulated in the gene pool, the critical points of modification were pushed back into earlier stages of ontogeny, so that, in maize, spikelets lose their potential for either maleness or femaleness by the end of seedling development (*33, 67*).

Only in abnormal environments would rare feminization-facilitating genes have revealed themselves. Without human intervention, these genes would never have accumulated. However, near human habitations, where any free grains would quickly have been noticed as potential food, these genes would have accumulated rapidly. In addition to sexual transmutation, then, human selection was the second factor favoring the super-rapid evolution of maize. Abundant remains of maize stem quids in Tehuacán and other cave deposits (*4, 19*) suggest that pre-Columbian Indians chewed on the sweet teosinte stems and ate green teosinte ears, just as modern rural Mexicans still do today. Since they were engaged in agriculture already, and must have known teosinte well, it would have been but a small step for them to plant seeds of these abnormal individuals, and maize domestication would have been on its way.

The ecological factor—selection under competition. Monopodial annuals growing in dense stands tend to suppress lateral branches, a splendid preadaptation for field domestication. Thus, in annual teosinte, branched types (Fig. 1) are usually found in noncompetitive situations, unbranched plants in thickets, dense teosinte stands, or maize fields. Loss of branches has been attributed to human selection (*10, 14, 31, 32, 50*) (Table 1). But both Guerrero teosinte (*Zea mays* ssp. *parviglumis*) and Guatemala teosinte [*Zea luxurians* (Dur. & Asch.) Bird] show the same reactions to crowding, even though these are mostly wild. While human selection could have had an influence, as it has in other weeds (*73*, pp. 123–134), and as suggested by Wilkes (*50*) for weedy forms of teosinte [but see Doebley (*7*)], both growth form and ear clustering in teosinte seem to be largely if not exclusively normal reactions of this pioneering annual to its own peculiar ecological realities.

The human factor—selection under domestication. The following major traits emerged under domestication: (i) increase in row number and grain and ear size; (ii) hardening of cupules and glumes; (iii) development of tough, nondisarticulating cobs; (iv) naked, free-threshing grains; (v) decrease in primary branches, that is, ear number; (vi) condensation of primary branch and ear internodes; (vii) increase in leaf sheath size and number; (viii) total deletion of tassel peduncle and branching space; (ix) suppression of all lateral tassel branchlets; (x) suppression of all lower order lateral branches, including inflorescences; (xi) synchronization of grain maturation within an ear, a plant, and a field (*25*); and (xii) evolution of ecogeographic and genetic isolating mechanisms preventing backcrossing to the ancestral teosinte and leading to race formation.

As the homolog of the maize ear, the central tassel spike is indirectly affected by many of the same genes (*45*). Thus, subsequent to the initiation of the sex change, human selection aimed at the ear resulted in indirect effects in the tassel. Selection for increased row number led to a thickening of the central spike and branchlets (*45*) (Figs. 1 and 3, m, n, q, and r). Selection for nondisarticulation led to loss of abscission layers not only in the target structure, the cob, but in the tassel as well.

Evolution at two levels in maize—the organismal-biochemical paradox. Teosintes are dissimilar enough from maize that they were classified as a separate genus, *Euchlaena*, for over 100 years. Yet, Mexican teosintes are often completely interfertile with maize, lacking not only any major genetic differences but biochemical ones as well. The latter are often much greater between the morphologically similar races of teosinte (*50*) than between the very dissimilar subspecies *mexicana* or *parviglumis* and maize (*15*). In fact, subspecies *parviglumis* and the several maize races tested so far are isoenzymatically indistinguishable (*74*). Although a recent revision of *Zea* recognized several races as full taxonomic species (*8, 9*), these are nevertheless difficult to distinguish. To paraphrase King and Wilson (*75*, p. 107): "The intriguing result . . . is that all biochemical methods agree in showing that the genetic distance between [the taxa] is probably too small to account for their substantial organismal differences."

Cataclysmic change. Almost every scientist who tried to understand the origin of maize came independently to the conclusion that, especially if teosinte were ancestral, (i) the evolution of maize must have been most rapid, (ii) all characters would have had to evolve simultaneously, (iii) a once useless grass would have had to become useful all at once, and (iv) the origin of maize was somehow unique (*76*). Mangelsdorf (*56*), in a remarkably prophetic statement (but disavowed in the very next sentence), wrote: "[I]t does not seem possible that maize could have been derived from teosinte *during domestication* by any genetic mechanism now known. If maize has originated from teosinte it represents the widest departure of a cultivated plant from its wild ancestor which still comes within man's purview. One must indeed allow a considerable period of time for its accomplishment or one must assume that cataclysmic changes, of a nature unknown, have been involved."

The rapid evolution of new structural types. Two contrasting modes of rapid morphological evolution are demonstrated by a comparison of maize and *Oxysty-*

lis lutea (Capparidaceae) (*77*), an annual which evolved under extreme selection in the Death Valley desert in the past 15,000 years or less.

According to Mayr (*71*, pp. 361–363; *78*), such macroevolution may arise by two major modes: (i) intensification of function of a preexisting structure through an "intensification of selection pressure" (for example, aridity or human selection) directed against existing structures, resulting in changes which may not lead to the emergence of anything basically new but may be dramatic enough to produce a new genus (*Oxystylis*) or a new crop (tetraploid wheat); and (ii) change in function of a structure, which "depends on two prerequisites: the capacity of a structure to perform simultaneously two functions and the duplication of one of these functions by another structure" (*71*, pp. 362–363). Preadaptation of a duplicated structure (for example, tassels of the lateral branches) for a radically different function (grain production) was evidently critical in the evolution of maize.

These two models are different in rather fundamental ways. Evolution due to intensified selection is based on the gradual accumulation of individual mutations, hence genetic differences can be traced one by one. But morphological evolution due to a change in function (especially if simply due to a positional effect as in maize) may not only be infinitely more rapid and pronounced but will initially lack discrete and identifiable genetic differences because (i) the switch in function may not have a direct genetic cause; (ii) it may effect many changes concurrently; (iii) it may be triggered by minor multifactorial, quantitative changes (for example, shortening of internodes); and (iv) the genetic foundations of the ancestral structures that determine the new morphology may lie very far back in time. This is critical. Since the basic architecture would have an archaic polygenic foundation buffering it against any drastic developmental deviations, its continuing expression may have no relation whatever to the development of a new function and hence cannot be used to explain it.

Among several factors, "shifts in sexuality" are cited by Mayr as promoting macroevolution in animals (*71*, p. 254; *78*, pp. 435–439). One may suppose that sexual shifts are of far greater importance in plants, especially in the mystery-shrouded pathways of phyletic evolution that led to cones and flowers (*79*).

While macroevolution due to intensified selection is still basically a gradualistic (if accelerated) model in the Darwinian mode, macroevolution in the maize ear [as in the panda's thumb (*80*)] represents a rare cataclysmic switch in function, a gross and sudden quantum evolutionary emergence of a "hopeful monster" somewhat on the Goldschmidtian mode. With punctuated equilibria (*1*, *80*) now in the air, can morphological catastrophes be far behind?

Conclusions

There are lessons here beyond the enormous economic implications that almost any insight into the evolution of one of the world's most important crop plants may have. Had the ancestral teosinte died out, we would not only have been forced to place *Zea mays* in its own subtribe (on account of the ears), but we would also have been quite unable to reconstruct its remarkable evolution. Extinction of species, and with it of knowledge, is forever, and many teosinte populations are now in danger and some have become extinct. Biotic preservation thus is an ultimate concern not only for all biologists, but also for agricultural scientists and politicians as well.

The sexual transmutation of teosinte into maize is "fascinating from a purely botanical standpoint. Morphologically, the seeming extraordinary evolutionary explosion that accompanied the beginnings of maize are almost unthinkable, no matter how firmly the homologies and transformation series are established, and may be the most spectacular series of changes ever to be documented" (*81*). The CSTT should stimulate a reinterpretation of much of the vast literature on maize, as well as allow new approaches to maize phylogeny, morphology, and genetics. But more importantly, it promises to throw light on broader problems—of morphogenesis and sexuality, punctuated equilibria and genetic assimilation, morphological and genetic transmutations, and perhaps even the origin of the angiosperm flower. Supported by much previous physiological work, and resolving most archeologic, morphologic, and genetic paradoxes of maize, the new model is amenable to experimental verification. In fact, it may be possible to repeat the processes of this sexual transmutation and produce a protomaize in controlled growth chambers. Finally, by modifying Beadle's (*14*) teosinte hypothesis to accommodate some of Mangelsdorf's (*2*) criticisms, the CSTT can now lay to rest over 40 years of debate (*51*) on the origin of maize and its wonderful polystichous ear.

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Law and Science Policy in Federal Regulation of Formaldehyde

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Formaldehyde, one of the more widely used chemicals in modern industry, has recently become one of the more controversial as well. A plethora of lawsuits, congressional hearings, and scholarly analyses have centered on formaldehyde, and more particularly on federal agency responses to new data indicating that it may be a carcinogen. These developments were sparked by an October 1979 report from the Chemical Industry Institute of Toxicology (CIIT) that formaldehyde causes cancer in rats.

On receiving the CIIT findings, the Environmental Protection Agency (EPA), the Occupational Safety and Health Administration (OSHA), the Consumer Product Safety Commission (CPSC), and other agencies undertook several joint actions, the most important of which was to form the Federal Panel on Formaldehyde. The panel was composed of top scientists from the federal government and was directed to evaluate all available information on the long-term effects of exposure to formaldehyde and to assess the human health risks. In November 1980 the panel pesented its report to the agencies. Based on its review of the available data, the panel concluded that "formaldehyde should be presumed to pose a carcinogenic risk to humans" (*1*). Thereafter, CPSC issued a ban against the use of urea-formaldehyde foam insulation. EPA and OSHA, however, declined to take regulatory action against formaldehyde.

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