

BOTANICAL MUSEUM LEAFLETS

HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, APRIL 3, 1959

VOL. 18, No. 9

THE ORIGIN OF CORN

III. MODERN RACES, THE PRODUCT OF TEOSINTE INTROGRESSION

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THE third postulate of our tripartite hypothesis (35) that certain modern races of maize are the product of teosinte (*Zea mexicana*) introgression has been the least controversial of the three. There is now almost unanimous agreement among those who have studied the problem that corn and teosinte are constantly hybridizing in Mexico and Guatemala and that this introgression of one species into the other necessarily has had substantial genetic effects. The exception to this unanimity is represented by Randolph (41) who has offered the following objections: (A) There is little natural crossing between maize and teosinte. (B) The extent to which hybridization between the two species has resulted in gene exchange is open to question. (C) There is no cytological evidence of the introgression of teosinte into maize. (D) There is no evidence that introgression, if it occurs, leads to improvement. (E) Characters found in maize varieties which have been attributed to teosinte introgression can be equally well explained as the result of parallel mutations.

How valid are these objections and to what extent are they supported by the evidence?

The first objection is plainly contrary to the facts. It may be true, as Randolph suggests and as others have recognized (8), that there are partial genetic barriers to the free hybridization of corn and teosinte in nature. Certainly the number of recognizable hybrids found in localities where the two species are growing together in the same fields, and flowering at the same time, is less than might be expected in view of the fact that both species are monoecious and wind pollinated and that abundant opportunities for hybridization apparently exist. But the barriers, whatever their nature, are by no means complete, and every student of the problem from Harshberger on has been aware of natural hybridization of corn and teosinte (8, 16, 18, 30, 41). Randolph, himself, has furnished the most convincing evidence of this hybridization, when he counted 45 F_1 hybrids in five days of travel in a limited region near the villages of Nojoyá and San Antonio Huixta in Guatemala. If this small sample is representative, there must be thousands of new hybrids produced each year. That Randolph personally failed to find hybrids near Chalco in Mexico is of no significance, for others (18, 30) have done so.

That maize and teosinte hybridize in Mexico and Guatemala must be accepted as an established fact and, if the frequency of that hybridization is less in any one place at any one time than some botanists expect, it must be remembered that it has been going on in countless localities for many centuries.

The extent to which this hybridization results in gene exchange is not easily measured with precision, but it cannot be denied that there is some exchange. This would be expected on the basis of the following well-established facts: (a) The F_1 hybrids of corn and teosinte are usually vigorous and highly fertile and are easily backcrossed to either parent to produce fertile progeny; (b) The chro-

mosomes of the two species are morphologically similar and synapse more or less normally in the hybrids (2, 3, 4, 19, 20, 21); (c) The arrangement of the gene loci although probably not identical in the two species is certainly similar (11); (d) Crossing over between linked loci in maize and teosinte chromosomes is, with few exceptions, of the same order as it is in corn (11). In view of these facts, it is difficult to see how, once hybridization has occurred, gene exchange could be prevented; and there is ample evidence that it has not been.

Collins (8) noted many years ago that the teosinte in the vicinity of Chalco in Mexico is quite maize-like in its characteristics, including plant color and pilosity of the sheaths. The first of these characters involves at least one gene either *B* or *R* and the second at least two (39). In being transferred from maize to teosinte, these genes have undoubtedly carried with them blocks of closely linked genes which accounts, at least in part, for the fact that the teosinte of Chalco is among the most maize-like varieties in many other respects. Randolph (41), himself, has found yellow endosperm, a maize character, in teosinte, and Mangelsdorf (28) has reported both yellow endosperm and colored aleurone.

There is no doubt that the teosinte of Mexico is more maize-like than that of Guatemala in its general aspects (18), in cytological features (21, 24, 25) and in genetic characteristics (47, 48, 49). Reeves (44) found a hybrid of the Mexican teosinte Nobogame x New to have uniformly paired spikelets, a so-called "generic" character of *Zea*, distinguishing it from teosinte. These facts require explanation, and the simplest and most commonly accepted one is that the Mexican teosintes have, on the average, undergone more admixture with maize than have the Guatemalan varieties. Longley's explanation of the cytological differences as the product of "gradi-

ents'' has been pretty thoroughly demolished (32, 45).

Since some varieties of teosinte have obviously been modified by admixture with maize, it is almost inevitable that some varieties of maize have likewise been modified by admixture with teosinte. Weatherwax concedes this in the same chapter in which Randolph attempts to deny it. And if this conflict of opinions proves to be confusing to some readers, it at least demonstrates an admirable independence of mind on the part of the two joint authors.

Wellhausen *et al* (53), in an important paper which both Weatherwax and Randolph have repeatedly overlooked, report the results of an intensive study, over a period of seven years, of more than 2000 collections of maize from all parts of Mexico. Of the 25 races of maize which they describe, they recognize teosinte introgression in 22, primarily on the basis of the induration of the rachis and the lower glumes of the ears. Their scores for teosinte introgression proved to be strongly correlated with chromosome knob number; and more recently, they have shown a remarkable correlation with resistance to a virus disease, corn "stunt" (7). Here may be another case, similar to that reported by Venkatraman and Thomas (57), of one of the lower forms of life being more perceptive than botanists in recognizing the true nature of populations.

Randolph's conclusion that there is no cytological evidence of the introgression of teosinte into maize is correct only if his assumption that the chromosome knobs of maize are not derived from teosinte is valid. But apart from chromosome knobs, what cytological evidence of introgression could there be? Randolph has repeatedly emphasized the remarkable similarity, except for the knobs, between maize and teosinte chromosomes. If they are indeed as similar as he regards them to be, then even

the most extensive introgression of teosinte into maize would not be detectable, and the lack of cytological evidence of which he speaks would have no significance. On the other hand, if our assumption is valid—that the chromosome knobs of maize have been derived from teosinte and are good indicators of teosinte admixture—then there is abundant cytological evidence of teosinte (or *Tripsacum*) introgression in the maize varieties of practically all parts of this hemisphere (5, 32, 42, 46, 53).

There is no longer any doubt that the knobs of teosinte can be transferred to corn. Cytological studies by Ting (unpublished) of the modified strains of inbred A158 developed by Mangelsdorf have shown that knobs have been introduced into various modified strains from chromosomes 1, 2, 3, 5, 8 and 9 of Durango teosinte and from chromosome 4 of Nobogame teosinte.

Nor can there be any doubt that chromosome knobs are associated with tripsacoid characters. Mangelsdorf and Cameron (32) showed that in the maize of western Guatemala the number of chromosome knobs is associated with several characteristics which may have been derived from *Tripsacum*, including denting of the kernels, fibrous seminal roots, and resistance to shattering, lodging, and smut infection. Brown (5) found high knob numbers to be positively correlated with high row numbers, denting, absence of husk leaves, many seminal roots and irregular rows of kernels, all of which are characteristic of Southern Dents; but he concluded that more data are needed before chromosome knobs can be regarded as reliable indicators of *Tripsacum* germplasm, since the Northern Flints, apparently the most tripsacoid maize in the United States, have the lowest knob number. Brown added a comment, however, which Randolph, in discussing the results, seems to have overlooked, that the tripsacoid nature of Northern Flints

may be a superficial one. This is probably the case. We expressed the opinion some years ago (36) that the flint-flour corns of the Plains Indians, some of which are included in Brown's Northern Flints, show little admixture with *Tripsacum* in spite of their straight rows. Additional experience has confirmed this earlier impression. The origin of the Northern Flints is still obscure, but the corn in Latin America which most resembles them occurs at high altitudes in Guatemala, is non-tripsacoid, and has low chromosome knob numbers (55).

The question whether or not corn is improved by teosinte introgression is answered in part by circumstantial and in part by direct evidence. Vachhani (56) found no correlation between chromosome knob number and various morphological and agronomic characteristics, including yield, in 20 inbred strains, but added that these results are not necessarily in conflict with those of Mangelsdorf and Cameron since only relatively low knob numbers were involved. Three additional papers (overlooked by Randolph) contain evidence which suggests or shows that teosinte introgression, in some instances at least, results in improvement.

Wellhausen *et al* (53) concluded that the more productive races of maize in Mexico had undergone introgression from teosinte and that some of the most valuable races, such as Tuxpeño and Celaya, are the product of several independent introductions of teosinte germplasm into maize. More recently, Wellhausen and Prywer (54) showed that among inbred lines developed from Mexican varieties adapted to elevations from 4500 to 6000 feet, those with the higher knob numbers tended to be the parents of the more productive hybrids. The reverse was true at higher altitudes. These results are consistent with those of Mangelsdorf and Cameron which showed that, in Guatemala, teosinte introgression is slight at altitudes

of more than 6500 feet presumably because it confers no advantage at these elevations. Wellhausen and Prywer's conclusion is as follows :

. . . these data suggest that there is a relationship between knob number and yield factors. At low altitude, the high-knobbed inbred lines tend to be better combiners than the low-knobbed ones. At high altitudes, the reverse seems to be true; the low-knobbed lines tend to be the best combiners. It is now almost certain that many of the good, high yielding, open-pollinated varieties in Mexico during their evolution picked up some favorable characters from teosinte or *Tripsacum*. The number of knobs a variety has may well be indicative of the amount of germplasm it has received from these two species.

It is possible that the Indians of western Mexico have long recognized the beneficial effect of teosinte introgression, for Lumholtz (27) reported their practice of interplanting *maizillo* (probably teosinte) and maize for the purposes of improving the latter. This, however, is quite in contrast with the attitude of the natives of the Valley of Mexico who contend that the presence of teosinte plants in the field causes the maize to "run down." Here again it may be a matter of altitude.

The question may be raised whether or not the introgression of teosinte into maize which has occurred in Mexico and Guatemala has any influence on corn beyond the borders of these countries. There is little doubt that it has. Practically all of the corn varieties of the United States owe their origin to Mexican and Guatemalan races. The Corn-Belt Dent, the principal type in the United States, is a hybrid of the Southern Dents and Northern Flints (1). The Southern Dents in turn are derived from Mexican lowland corns (6) which are highly tripsacoid races believed to be the product of teosinte introgression (53).

The only direct evidence of the improvement effected by controlled introgression of teosinte is furnished by the data of Reeves (43), who introduced teosinte germplasm

into two Texas inbred strains, 4R3 and 127C. Some of the modified strains of 4R3 showed significantly greater tolerance to heat than the controls but were not appreciably changed with respect to yielding ability of their hybrids. Similar modification of 127C, however, increased the yielding ability of its hybrids quite significantly. Reeves concluded that some inbreds can be improved by the addition of teosinte genes but others can not. He postulated that, so far as yield is concerned, 4R3 already has the optimum assortment of teosinte genes. He might have added that 4R3 is actually one of the most tripsacoid inbreds in the United States.

The contention that the tripsacoid characters found in maize varieties can be attributed to parallel mutations rather than to admixture with teosinte has no foundation in the evidence now available. It merely substitutes an untestable hypothesis for the well-established fact that maize and teosinte are hybridizing today and have probably been doing so for almost 2000 years as the evidence from prehistoric corn shows.

ARCHAEOLOGICAL EVIDENCE OF TEOSINTE INTROGRESSION

Virtually all of the archaeological maize from Mexico and North America which has been studied recently includes specimens which are highly tripsacoid and which are quite similar in their general appearance and certain botanical characteristics to modern ears derived from experimental maize-teosinte hybrids. This is especially true with respect to the induration and lignification of the glumes which are known from genetic studies to be among the most common and conspicuous effects of the introduction of teosinte germplasm into maize. Mangelsdorf, for example (28), has shown that the genes for indurated glumes occur on at least four chromosomes of

Nobogame teosinte and on at least five chromosomes of Durango teosinte. Rogers (48) has found linkages between glume score, which is mainly concerned with induration, and marker genes in hybrids involving five varieties of teosinte, the strongest linkage in four of the five hybrids being with the marker gene on chromosome 4. In view of these facts, the occurrence of highly lignified specimens of prehistoric cobs immediately raises the suspicion of previous contamination with teosinte. When lignification is accompanied, as it is in some specimens, with single spikelets, also a teosinte characteristic, the suspicion virtually becomes a fact.

Tripsacoid prehistoric maize was first clearly recognized in a collection of archaeological corn from Bat Cave, a rock shelter in New Mexico excavated by Mr. Herbert Dick (37). Weatherwax (52) was skeptical of this evidence and, since he had seen illustrations of only a limited number of specimens, his skepticism may have been warranted. The data are however quite convincing. Of the 471 cobs studied, 250 or more than half were scored as being intermediate or strong in teosinte introgression. The fact that all but two of these were found in the four upper levels of the deposit was regarded as highly significant and as an indication that teosinte admixture appeared on the scene only after maize cultivation had become well established in the area in which Bat Cave is located.

The second expedition to Bat Cave by Mr. Dick turned up many additional tripsacoid specimens not yet described and has confirmed one of the most significant features of the collection from the first expedition: non-tripsacoid cobs in the early levels, a high frequency of tripsacoid cobs in the later ones.

In addition to those found in the two Bat Cave expeditions, tripsacoid cobs have now been identified in collections from the following caves: Richards and Tonto

Caves in Arizona (14); La Perra Cave in northeastern Mexico (34); Swallow, Tau, Slab, and Olla Caves in northwestern Mexico (33); Cebollita Cave in New Mexico (Galinat unpublished). Additional collections not yet studied but obviously containing tripsacoid cobs have been received from Mr. Herbert Dick from a site in Colorado; from Mr. Dick Shutler from sites in Nevada; and from Dr. Robert E. Bell from a site in Oklahoma. Highly tripsacoid cobs can also be recognized in a photograph of prehistoric specimens from Tularosa Cave in New Mexico published by Cutler (9) and in the illustration of specimens from the Hueco Mountain Caves in Texas published by Cosgrove (cf. 14).

That these tripsacoid cobs are the result of teosinte admixture, which probably occurred in northern Mexico, and not of parallel mutations is strongly indicated by the fact that some of them have more than one character of teosinte, such as distichous spikes, single spikelets and highly lignified rachises and glumes. Simultaneous mutations producing all of these tripsacoid characters are difficult to imagine, but genetic recombinations involving all of them are common in segregates from maize-teosinte hybrids. Both Mangelsdorf (28) and Rogers (48) have shown that there is genetic linkage between all of these characteristics.

Perhaps the strongest evidence that these prehistoric tripsacoid cobs are the product of admixture with teosinte lies in the fact that virtually all of them can be matched quite closely, sometimes almost exactly, with modern specimens derived from experimental maize-teosinte hybrids. Galinat *et al* (14) have illustrated a number of these matched pairs, and we have many others. Until it can be shown that there are other and better ways of synthesizing facsimiles of the tripsacoid prehistoric specimens, we shall continue to assume that

the striking resemblances between the prehistoric and modern specimens reflect a corresponding similarity in their genotypes.

ARCHAEOLOGICAL EVIDENCE OF IMPROVEMENT

These prehistoric tripsacoid specimens not only show that corn crossed with teosinte centuries ago but they also indicate that corn was improved as a result of the admixture. In all of the collections of archaeological maize in which the lower levels comprise non-tripsacoid corn this early corn is small and uniform in type. In higher levels, accompanying the appearance of tripsacoid types, there is an almost explosive increase in variability. This is especially well illustrated in the collections from Bat Cave in New Mexico (37) and from Swallow Cave in northwestern Mexico (33). This increased variability, which involves types both poorer and better (by modern corn-breeding standards) than the original corn, can be attributed both to genetic recombination and to heterosis. This is especially well shown by the data presented by Galinat *et al* (14), based on 433 specimens in which a high correlation, 0.859, was found between length of cob and estimated teosinte introgression. The correlation is strongly curvilinear, both the shortest and the longest cobs being highly tripsacoid. This is explained by assuming that the short, strongly tripsacoid cobs are homozygous for genes introduced from teosinte, while the long cobs are heterozygous for such genes and are the vigorous products of maize-teosinte heterosis.

It is improbable that the large modern ear of corn could have evolved except for hybridization of corn with teosinte which contributed genes for induration and lignification of the tissues characteristic of the prehistoric tripsacoid specimens. On this point Mangelsdorf (29) has expressed the following conclusion:

The elements of strength necessary to support this greatly enlarged inflorescence have come from teosinte, which contributes genes for hardness and toughness when it is hybridized with corn. Teosinte is to the modern ear of corn what steel is to the modern skyscraper.

THE MUTAGENIC EFFECTS OF TEOSINTE INTROGRESSION

Hybridization of maize and teosinte not only produces new genetic combinations, some of which are favorable, but it also has mutagenic effects. These have been recently described by Mangelsdorf (31). Most of the mutations, like spontaneous mutations or mutations produced by irradiation, are deleterious, but some appear to be beneficial. It is entirely possible that these mutagenic effects of teosinte introgression have been an important factor in the evolution of cultivated corn, as important perhaps as the creation of new genetic combinations following hybridization.

INTROGRESSION DIRECTLY FROM TRIPSACUM

After carefully examining the objections to the idea of teosinte introgression, as well as the evidence supporting it, we see no reason to doubt that corn is undergoing introgression from teosinte now and that this process has been going on for centuries. If teosinte is, as we have postulated (35), a hybrid of corn and *Tripsacum*, then the introgression is ultimately from *Tripsacum*. We have not assumed that there has been any direct introgression of *Tripsacum* into maize; our assumption has been that the hybridization of maize and *Tripsacum* which gave rise to teosinte needed to have occurred only once (35). Evidence is now accumulating, however, to indicate that maize may have hybridized directly with *Tripsacum* repeatedly, although only once did such hybridization produce teosinte. The evidence for this is of two kinds: (a) tripsacoid characteristics in races of maize which have not

been in obvious contact with teosinte; (b) chromosomes with tripsacoid effects extracted from races of maize far removed from contact with teosinte.

Evidence in the first category is provided by the studies of Roberts *et al* (46), on races of maize of Colombia, especially the race called Chococéño which they describe as follows:

Chococéño is one of the most unusual races of this hemisphere, both in its characteristics and in the primitive way in which it is grown. Its culture is largely confined to the humid coastal region of western Colombia, where rainfall sometimes exceeds 400 inches annually. The maize is grown without cultivation. The fields are prepared by cutting down the small trees and brush. The seed, which is broadcast and not covered, germinates on the surface of the soil. The plants grow up through the branches of the cut vegetation.

To succeed under these primitive conditions the maize must have unusual characteristics. Chococéño is highly tripsacoid. It has tough, slender stalks with tillers, narrow, drooping leaves and pendulous tassel branches. It has the general aspect of certain segregates from maize-teosinte or maize-Tripsacum hybrids. Since teosinte does not occur in this region, and Tripsacum is common, it has been assumed that Chococéño is the product of the hybridization of maize and Tripsacum.

Roberts *et al* also report that in the Chocó region, from which this peculiar race derives its name, plants of maize and Tripsacum often grow together in the same field and flower at the same time. In a preliminary experiment, varieties of Tripsacum collected in Colombia were crossed with a number of different races of maize, and hybrid seeds, some of them capable of germinating without embryo culture, were produced in all crosses.

All the evidence is consistent with the conclusion that maize and Tripsacum have hybridized in Colombia to produce, not teosinte, but a highly tripsacoid race of maize which, in its vegetative characters, at least, shows some resemblance to teosinte.

Even more tripsacoid, at least in characteristics of the

ear, are some of the specimens of "Maíz Amargo" from the province of Entre Rios in Argentina, collected and described by Ing. Urbano Rosbaco (50). When grown in Massachusetts, plants of this maize, like those of Chococeno of Colombia, have numerous tillers, hispid leaf sheaths and thick, drooping leaves. In Argentina, Maíz Amargo is somewhat resistant to the attacks of grasshoppers, and this fact, coupled with the resemblance of some of its ears to segregates of maize-teosinte and maize-Tripsacum hybrids, led Ing. Rosbaco to suspect contamination with *Tripsacum*, perhaps the South American species *T. australe*. Horovitz and Marchioni (17) had earlier suggested that the resistance of Maíz Amargo to grasshoppers may be due to *Tripsacum* introgression.

There is still some confusion about the origin of Maíz Amargo. Rosbaco mentioned several references to it which state that it was introduced into Argentina from the maize-growing region of the Danube. Rosbaco considers this unlikely, and, since the tripsacoid segregates are extremely late in maturity, it does not seem possible that they could have been introduced from the Danube region, to which only varieties of relatively early maturity are adapted, although the original variety which subsequently became contaminated with *Tripsacum* may have been. *T. australe* has not been reported from Argentina, but it has been collected in the Paraná River basin in Paraguay, not far north of Entre Rios (10).

We have only one determination of chromosome knob number in Maíz Amargo which shows it to be low, five. This is the lowest knob number which we have found in any tripsacoid maize and is consistent with the hypothesis of introgression from *T. australe*, which has been reported to have knobless chromosomes (15) or, occasionally in some forms, a small number of chromosome knobs. Ting (unpublished) has found up to six knobs

in a Colombian *Tripsacum* believed to be a form of *T. australe*.

We have through repeated backcrossing to inbred A158 extracted from Maíz Amargo a chromosome which has almost the same effects upon the lignification of the pistillate glumes as chromosome 4 of teosinte. Other examples of extracted tripsacoid chromosomes are described below.

EXTRACTION OF TRIPSACOID CHROMOSOMES FROM LATIN-AMERICAN VARIETIES

Chromosomes having effects similar to teosinte chromosomes have been extracted through repeated backcrossing to the inbred A158 from the living varieties of maize of various countries of this hemisphere (31). Modified strains of A158 containing these extracted chromosomes are virtually indistinguishable from those produced by introducing chromosomes directly from teosinte. Furthermore, these extracted chromosomes, like the chromosomes from teosinte, are mutagenic when incorporated into A158 and, more significant still, some of the mutations produced are genetically identical with those produced by teosinte chromosomes. Chromosomes with tripsacoid effects have now been extracted from varieties of corn from Mexico, Honduras, Nicaragua, Cuba, Venezuela, Brazil, Paraguay, Bolivia and Argentina. Those extracted from varieties from Mexico, Honduras and Nicaragua can be attributed to teosinte introgression. Those from Cuba and Venezuela may also be the product of teosinte introgression, for, although there is no teosinte in these countries, there has been some introduction of Mexican and Central American maize varieties. But the tripsacoid chromosomes from Brazil, Paraguay, Bolivia and Argentina come not only from countries where teosinte is unknown but from races of

maize which have no counterparts in the maize of Mexico and Central America. The fact that Farquharson (12) found a variety of Peruvian corn to be especially effective in crossing with *Tripsacum* is of particular interest in this connection since it suggests the possibility that in some South American varieties the barriers to hybridization with *Tripsacum* may be weak or lacking.

CONCLUSIONS

A careful study has been made of the objections raised against the theory that many modern races of corn are the product of teosinte introgression, and of the new evidence which has been marshalled since the theory was first proposed. Nothing has been found which is clearly in conflict with the theory, whereas the body of facts in support of it is almost overwhelming. We regard this part of the tripartite theory as now so well established that it can safely be employed by corn breeders as a working principle in developing new methods for the improvement of corn.

SUMMARY

Five objections to the theory that many modern races of corn are the product of teosinte introgression have been examined and found to be unsupported by the available evidence.

1. Hybridization between maize and teosinte is not rare but is common in many localities in Mexico and Guatemala and has presumably been going on for centuries.

2. There is every reason to believe that this hybridization has been accompanied by gene exchange.

3. It has been shown that chromosome knobs can be transferred from teosinte to maize and if knobs are accepted as indicators of teosinte introgression there are abundant cytological manifestations of such introgression.

4. Both circumstantial and direct evidence show that maize can be improved in certain characteristics, including yield, by hybridization with teosinte.

5. No facts have been discovered to support the suggestion that tripsacoid characters in maize are the result of parallel mutations. On the contrary, the fact that several such characters may appear simultaneously points to genetic recombination following hybridization.

New evidence from both prehistoric and living maize support the following additional statements:

6. All recent collections of archaeological maize from caves in Mexico, Arizona, New Mexico, Colorado, Texas and Oklahoma include specimens which can be closely matched by segregates of maize-teosinte hybrids.

7. Archaeological evidence of teosinte introgression is accompanied by increased variability and improvement in certain characteristics.

8. The introgression of teosinte has mutagenic effects, some of which appear to be beneficial.

9. There is some circumstantial evidence of the direct introgression of *Tripsacum* into maize.

10. Chromosomes having tripsacoid effects have been extracted from corn varieties from Mexico, Honduras,

Nicaragua, Cuba, Venezuela, Brazil, Paraguay, Bolivia and Argentina.

11. The part of the tripartite theory on the origin and evolution of corn which postulates that many modern races are the product of teosinte (or *Tripsacum*) introgression is now regarded as well established.

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Mangelsdorf, Paul C and Reeves, Robert G . 1959. "The Origin of Corn: III. Modern Races, the Product of Teosinte Introgression." *Botanical Museum leaflets, Harvard University* 18(9), 389–411. <https://doi.org/10.5962/p.168521>.

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