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SCIENCE

Ancestor of Corn

A genetic reconstruction yields clues to the nature of the extinct wild ancestor.

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Our purpose in reconstructing the ancestor of corn is to retrace, so far as possible, some of the principal steps which have been involved in its evolution under domestication. We do this in the hope of gaining a better understanding of the corn plant as one of those unique biological systems which man employs on a grand scale to convert the energy of the sun, the carbon dioxide of the air, and the minerals of the soil into food. Corn is one of perhaps not more than a dozen species of cultivated plants of world-wide importance—each one the principal source of food of millions of people—which quite literally stand between mankind and starvation.

But corn is something more than an important food plant; it is also a mystery, a fascinating botanical mystery, as challenging to a scientist as is a mountain to an explorer.

A Unique Cereal

Modern corn, our starting point in this study (*1*), is unique among the cereal grasses in the nature of its inflorescences (*2, 3*). The terminal inflorescence, commonly called the "tassel" (Fig. 1*A, C*), usually bears only male flowers, each of which contains three pollen sacs or anthers (Fig. 1*D*) packed tightly with some 2500 pollen grains. These are small, about 1/250 inch in diameter, light in weight, and are easily carried by the wind.

The lateral inflorescences (Fig. 1*A, B*), which when mature become the familiar ears of corn, have only female flowers which bear the pollen-receptive organs commonly known as the "silks." These are covered with fine hairs and are admirably designed to capture wind-blown pollen (Fig. 1*E*). Thus corn, in contrast to the majority of cereals, is a naturally cross-pollinated plant. It is this feature which makes possible the production of hybrid corn, one of the most spectacular developments in applied biology of this century.

Each silk represents a potential kernel and must be pollinated in order for that kernel to develop. The kernels themselves are firmly attached to a rigid axis, the cob, and are not covered as are those of other cereals by the floral bracts which botanists call "glumes" and which the layman knows as "chaff." Instead the entire ear is enclosed, often quite tightly, by modified leaf sheaths, the husks or shucks (Fig. 1*B*). Thus, while in other cereals the kernels are protected individually, in corn they are covered en masse. The result is that cultivated corn has no mechanism for the dispersal of its seeds and hence is no longer capable of reproducing itself without man's intervention. The very characteristics which make corn so useful to man render it incapable of existing in nature, and it is probable that corn would quickly become extinct if deprived of man's protection.

How, then, did corn's wild ancestor differ from cultivated corn in ways which enabled it to exist in nature for thousands, if not millions, of years before man appeared on the scene? This is one of the questions which we hoped to answer by reconstructing the ancestral form. Our reconstruction is based in part upon fossil and archeological remains and in part upon genetic recombination of some of the primitive characteristics which still exist in modern corn varieties.

Fossil Corn Pollen

The fossil evidence comprises a number of pollen grains isolated from a drill core taken from a depth of more than 200 feet below the present site of Mexico City. These were recognized as unusually large pollen grains of a grass by Paul Sears of Yale University and Kathryn Clisby of Oberlin College, who, in connection with charting climatic changes, were engaged in pollen studies of the drill core. The pollen was identified by Elso Barghoorn (*4*) of Harvard University as that of corn, which has the largest pollen of any known grass. Although assigned to the last interglacial period and therefore, on the basis of recent estimates, probably at least 80,000 years old, the fossil pollen is scarcely distinguishable in size, shape, and other characteristics from modern corn pollen (Fig. 2). This fact leaves little doubt that the ancestor of corn was corn and not one of its two American relatives, teosinte or *Tripsacum*.

Oldest Cultivated Corn

The oldest known remains of cultivated corn come from a once-inhabited rock shelter in New Mexico known as Bat Cave, which was excavated by Herbert Dick, of the Peabody Museum of Harvard University and later of the Colorado University Museum, in two expeditions, in 1948 and 1950 (*5, 6*). This cave was inhabited for several thousand years by people who practiced a primitive form of agriculture and an even more primitive pattern of sanitation.

The author is professor of botany at Harvard University. This article, adapted from a paper presented at the annual meeting of the American Philosophical Society in Philadelphia on 25 April 1958, is reprinted, with permission, from the *Proceedings* of the Society.

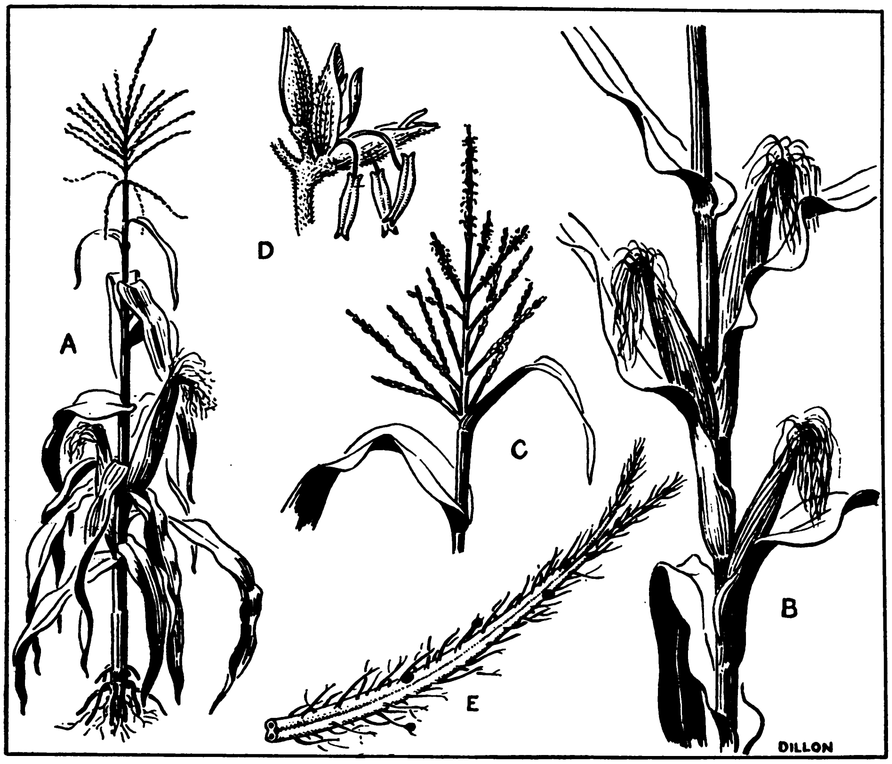

Fig. 1. Botanical characteristics of the modern corn plant. (*A*) The entire plant, showing the male inflorescence, the tassel, at the tip of the stalk and the female inflorescences, the ears, in the middle region; (*B*) young ears enclosed in husks with the pollen-receptive organs (the silks) protruding from the ends; (*C*) typical tassel; (*D*) typical male flower with three anthers containing pollen; (*E*) a single silk magnified to show hairs and adhering pollen grains. [From P. C. Mangelsdorf, "Corn" (*3*), by permission of *Encyclopaedia Britannica*]

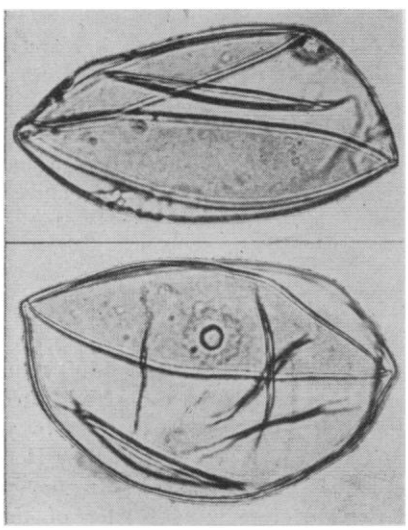

Fig. 2. Fossil pollen of corn (top) from more than 200 feet below the present site of Mexico City compared with a pollen grain of modern corn (bottom) at the same magnification. In spite of some 80,000 years' difference in their ages, these two pollen grains are virtually identical in their characteristics, and they show that the ancestor of corn was corn and not one of its two American relatives, teosinte or *Tripsacum* (×375). [From Barghoorn *et al.*, "Fossil maize from the Valley of Mexico" (*4*)]

During the centuries of their occupancy, garbage, excrement, and other debris accumulated in the cave to a depth of six feet, creating exactly the kind of site which archeologists delight to dig into. At the bottom of this accumulation of trash, Dick turned up some tiny cobs of ancient corn which have been dated, on the basis of Willard Libby's radiocarbon determinations of associated charcoal, at about 5600 years.

Three of these ancient cobs are compared in Fig. 3 with a one-cent piece whose diameter is about equal to their length. One of the tiny specimens is compared in Fig. 4 with ears of two modern races of corn: the dent corn of the United States corn belt and a large-seeded flour corn of Peru. How could a corn like the Bat Cave corn have evolved into these and other modern races even in 5600 years? This is the principal question which we hoped to answer by retracing some of the steps involved in corn's evolution under domestication.

Since there were no living seeds of the Bat Cave corn it was impossible to work forward experimentally from it to modern corn. The alternative was to work backward from present-day corn by combining primitive characteristics still occurring in living varieties. But what characteristics of corn are primitive? My associate, W. C. Galinat, and I sought to determine this by an intensive study of one of the Bat Cave specimens which contained the partial remains of a single kernel. Each part of this cob was carefully dissected out and measured. On the basis of the measurements, Galinat prepared the diagrammatical, longitudinal section illustrated in Fig. 5. The tiny kernels which this cob must once have borne could only be those of popcorn, a type in which the kernels are small and hard and capable of exploding when exposed to heat. The long stems or pedicels on which the kernels were borne and the long floral bracts which almost completely enclosed them show that the Bat Cave corn was also a form of pod corn, a type in which the individual kernels are enclosed in pods or chaff.

It is interesting to note in this connection that the late E. Lewis Sturtevant, a long-time student of corn, concluded many years ago that both popcorn and pod corn are primitive. My former colleague, R. G. Reeves, and I (*7*) later reached a similar conclusion. The ancient Bat Cave specimens provide convincing archeological evidence in support of these conclusions.

Crossing Primitive Corns

What we have done, then, is to cross a number of varieties of popcorn from various parts of the world with pod corn (Fig. 6), which still occurs as a "rogue" or "freak' in some South American va-

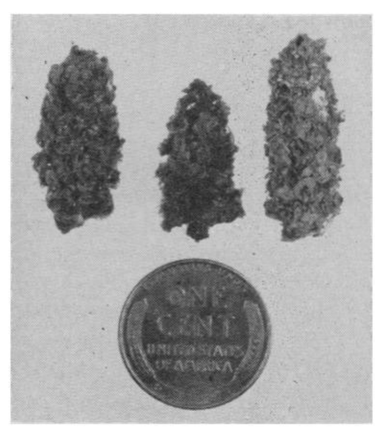

Fig. 3. Three cobs of prehistoric corn from Bat Cave compared with a 1-cent piece. Radiocarbon determinations of associated charcoal date these at 5600 years. Actual size.

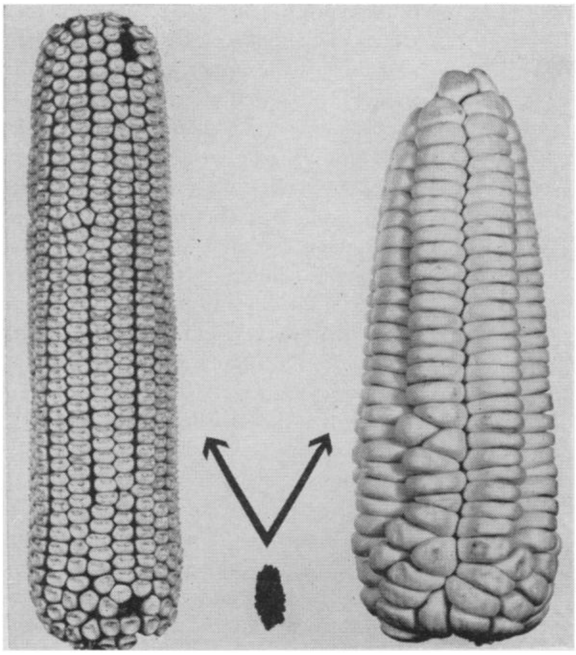

Fig. 4. One of the Bat Cave cobs (center) compared with a modern ear of Cornbelt dent (left) and a large-seeded Peruvian flour corn (right). Extremely rapid evolution has been involved in producing such drastic changes even in 5600 years, the estimated difference in age.

rieties and which in some localities is preserved by the Indians, who believe it to have magical properties. Pod corn has also sometimes been grown in gardens in the United States as a curiosity. Today it is most likely to be found in the experimental cultures of corn geneticists, who maintain it as one of the "marker" genes on the fourth longest chromosome of corn.

There is no doubt that pod corn is primitive in its characteristic of enclosing the kernel in glumes or chaff, as do all other cereals and virtually all other grasses. Despite this fact, and because it is often monstrous and sometimes sterile, it has been dismissed by a number of botanists from any role in the ancestry of corn (*8*). We believe that its monstrousness has been misunderstood—that pod corn is monstrous today only because it is a "wild" relict character superimposed upon modern highly domesticated varieties. Today's pod corn is comparable to a 1900 chassis powered by the engine of a 1958 car. The surprising thing is not that pod corn is sometimes monstrous but that it is not more so—that the particular genic locus which governs its expression is capable of functioning at all in a milieu so different from that in which it was undoubtedly well adapted. We have assumed that pod corn would be less monstrous and would exhibit normal grass characteristics when combined with other "wild" genes, and we hoped to find these in varieties of popcorn.

Our hopes have been realized. Popcorns in general tend to reduce the monstrosity of pod corn when crossed with it, and some varieties do so quite drastically. The varieties Lady Finger and Argentine carry complexes of modifying genes which appreciably reduce the monstrosity of pod corn, and a third variety, Baby Golden, carries a major modifying gene which, on the basis of preliminary linkage tests, appears to be on the sixth chromosome and which acts as an inhibitor of pod corn, reducing its expression by approximately half.

By combining these modifying and inhibiting genes from several popcorn varieties with the pod-corn gene, we have developed a number of strains of popcorn which, having this gene present on both of their fourth chromosomes, breed true for the pod-corn character. Some of these homozygous strains are much less monstrous than the usual forms of pod corn, are completely fertile, and might under suitable conditions be capable of surviving in the wild.

Effects of a Single Gene

The majority of these true-breeding pod-popcorns have other characteristics which we may now regard as primitive. The plants, when grown on fertile soils, instead of having one stalk, as do most modern corns, have several (Fig. 7) and in this respect resemble the majority of wild grasses, including all of the known relatives of corn, both American and

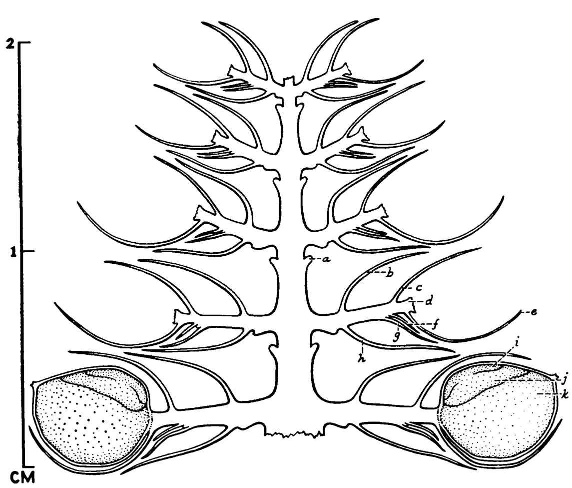

Fig. 5. Diagrammatic longitudinal section of one of the Bat Cave cobs, based on measurements of dissected parts. The tiny kernels show that this was a popcorn; the long pedicels on which the kernels are borne and the bracts which almost enclose them indicate that it was also a pod corn [W. C. Galinat]

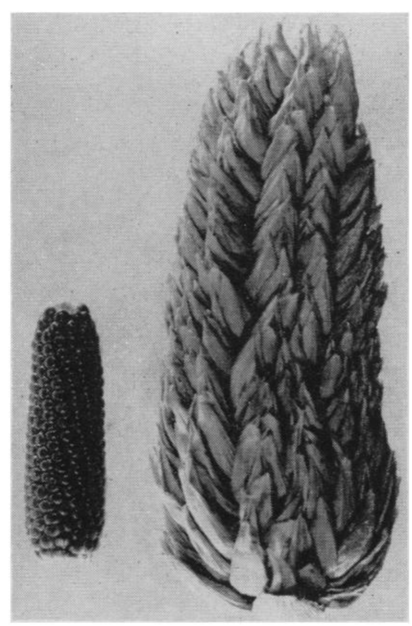

Fig. 6. An ear of Argentine popcorn (left) and an ear of present-day pod corn (right). Popcorn is primitive in having small hard seeds. Pod corn is primitive in having its seeds enclosed in pods or chaff, like the other cereals. These two types were crossed in order to combine their primitive characteristics.

Fig. 7. Three plants of a many-stalked popcorn differing with respect to the pod-corn gene. The first plant (left) lacks this gene; the second (center) has it on one member of the fourth chromosome pair; the third (right) has the gene on both members of the fourth chromosome pair. The progressive decrease in height is associated with the pod-corn gene, which causes, among other effects, a shortening of the internodes of the upper part of the stalk.

Fig. 8. A tassel and ear of a true-breeding pod corn. The shortening of the internodes of the upper part of the stalk causes or is accompanied by a tassel which bears both male and female flowers. The withered silks immediately below the tassel are from female flowers on the tassel branches which bloomed several weeks before this photograph was taken. Several seeds, resulting from pollination of these flowers, are visible. Such seeds are easily dispersed when mature by the breaking of the fragile tassel branches. The fresh silks to the left of the tassel are from a subtassel ear which is enclosed in husks when young but can emerge from them and disperse its seeds when mature. The silks of this ear can be pollinated by pollen from the anthers in the tassel of the same plant, but the female flowers in the tassel can receive pollen only from another plant. Thus, the reconstructed primitive corn plant has devices for both self- and cross-pollination.

Asiatic. The plants are shorter than ordinary corn because one of the numerous effects of the pod-corn gene is to shorten and thicken the upper internodes of the stalk. This is well illustrated in Fig. 7, which shows three plants of popcorn in one family: one lacking the pod-corn gene, one having the gene on one member of its fourth chromosome pair, and one having the gene on both members of the pair. There is a progressive decrease in height through this series of three genotypes resulting from a shortening of the upper internodes. This shortening causes, or at least is accompanied by, the development of a terminal inflorescence which bears both male and female flowers, the male flowers at the tips and the female flowers at the bases of the same tassel branches (Fig. 8). These branches are quite brittle when mature and break apart easily when disturbed by the wind or by birds. They thus provide one of the most important primitive characteristics which cultivated corn lacks: a mechanism for the dispersal of seeds.

Position of the Ear

Plants of homozygous pod corn frequently do not have ears—most of their energy is apparently concentrated in the terminal inflorescences—but when they do have ears these are usually borne high upon the stalk (Fig. 8), often at the joint of the stem immediately below the tassel. This elevation of the position of the ear has profound effects which are illustrated by the diagram in Fig. 9. The diagram, which is based on data from several many-eared plants, shows how a number of the characteristics of the ears are determined by their position on the stalk: (i) The higher the position, the smaller the ear, partly for the simple mechanical reason that the stalk at this position is slender and is incapable of bearing a heavy load. It would be mechanically impossible for the large modern ear of corn to be borne near the slender tip of the stalk. (ii) The higher the position, the more likely is the ear to have both male and female flowers. (iii) The higher the position, the shorter the lateral branch or "shank" upon which the ear is borne. The shorter the branch, the fewer the joints from which the husks arise, the fewer the husks and the less completely the ear is enclosed. Thus an ear borne immediately below the tassel is enclosed while the young seeds are developing, but as these mature the husks flare open, allowing the ear to disperse its seeds. In short, a simple change in position determined by a single gene change can provide a mechanism for dispersal of the seeds borne on the ear as well as those borne on the fragile branches of the tassel.

These facts seem to answer several of the most puzzling questions involved in previous attempts to explain corn's evolution: How could wild corn have survived the handicap of an ear incapable of dispersing its seeds? And if wild corn had no ears, how could the ear of modern corn, its most important organ, have come into existence?

The position of the ear has an effect on still another characteristic illustrated in Fig. 9, the length of the streamers or leaf blades which in many varieties terminate the outer husks. The higher the ear, the more likely are the leaf blades to be short or absent. This may explain the absence of leaf blades in prehistoric husks found both in Bat Cave (*6*) and in La Perra Cave (*9*).

Fig. 9. Diagrammatic longitudinal section based on data from several plants of a many-eared corn stalk, showing how the position of the ear on the stalk affects its characteristics. The higher the ear, the smaller its size, the fewer its husks, and the more likely it is to bear both male and female flowers. [W. C. Galinat]

Modern and Primitive Corn Compared

The most primitive ear we have so far obtained by combining popcorn and pod corn is shown in Fig. 10 in comparison with an ear of modern dent corn and with the most primitive cob, dated at 4445 ± 180 years, from La Perra Cave, which was excavated by Richard MacNeish of the National Museum of Canada.

In weight and number of kernels our reconstruction is much closer to the prehistoric La Perra specimen than to the ear of modern dent corn. The modern ear weighs 317 grams. The ear of pod-popcorn weighs 1.99 grams. However, only 24 of its 38 female flowers developed kernels. Had all done so, it would weigh 2.47 grams, assuming the additional kernels to have the same average weight, 0.034 gram, as those which are present. The La Perra specimen weighs only 0.52 gram, but it lacks both the 48 kernels, which it once bore, and a male spike. Without its kernels and its male spike, the reconstructed ancestral form weighs 0.87 gram, only slightly more than the prehistoric specimen.

Although we have not yet completely reconstructed wild corn, nor duplicated exactly the most primitive specimens from either Bat Cave or La Perra Cave —the glumes of the pod-popcorns are

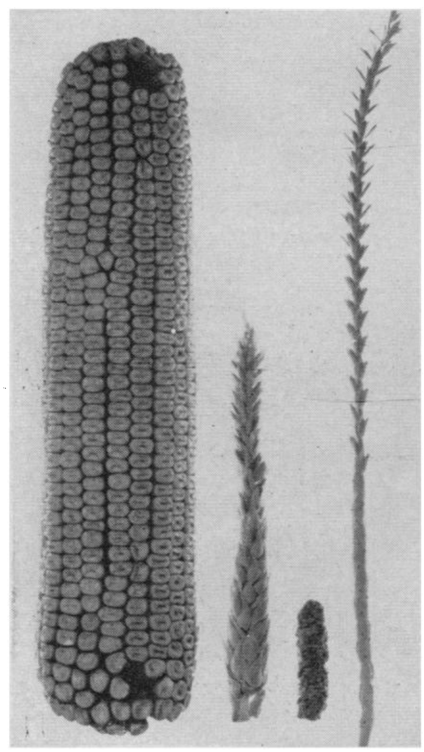

Fig. 10. The reconstructed ancestor of corn, an ear of pod-popcorn (second from left) compared with a modern ear of dent corn (far left) and a prehistoric cob of La Perra Cave corn (second from right). The dent corn weighs 317 grams; the reconstructed ear 1.99 grams. The reconstructed ear has female flowers below and male flowers above and in this respect resembles a spike of *Tripsacum* (far right), a wild relative of corn. The La Perra cob also once had a male portion, which has been lost; only the stump of its stem still remains. Without its kernels and male spike, the reconstructed ear would weigh 0.87 gram—only slightly more than the La Perra cob, which weighs 0.52 gram.

Fig. 11. A prehistoric Zapotec funerary urn from Mexico with two representations of primitive corn ears in the headdress and one in the hands of the maize god.

Fig. 12. Details of one of the ears shown in Fig. 11. It is probable that the slender column above the small ear was intended to represent the male spike of a prehistoric ear similar in some of its characteristics to the reconstructed ancestral form illustrated in Fig. 10.

still too prominent to match those of the prehistoric specimens—we have succeeded in developing what is probably the world's most unproductive corn. This is useful in suggesting that we are on the right track in attempting to retrace corn's evolutionary paths.

The reconstructed ear illustrated in Fig. 10 has female flowers on its lower half and male flowers on the remainder. This, as Fig. 9 shows, is a characteristic of ears borne in a high position on the stalk. If our reconstruction is valid, should not prehistoric ears also bear male flowers? A reexamination under the microscope shows that at least some of them once did and that these have since been lost in handling. Some of the ancient cobs, including the one illustrated in Fig. 10, have stumps, previously unnoticed, of a slender stem on which male flowers were undoubtedly borne. Thus our genetically reconstructed ancestral form has taught us to look for a characteristic in prehistoric ears which we had previously overlooked. It has also shown us the significance of ears bearing terminal male spikes which are still found in certain races of corn in the countries of Latin America: the races Nal-Tel and Chapalote of Mexico (*10*), Pollo of Colombia (*11*), and Confite of Peru. Finally it may explain some curious ears, which had previously puzzled us, moulded in bas relief on a prehistoric Zapotec funerary urn from Mexico. The urn is shown in Fig. 11, and the details of one of the ears in Fig. 12.

In bearing both male and female flowers these ears of pod-popcorn also resemble the lateral inflorescences of *Tripsacum*, a perennial grass and a wild relative of corn (Fig. 10). This resemblance has in turn called attention to additional characteristics in which the reconstructed corn resembles *Tripsacum*: (i) the flowering of the female spikelets before the male in both lateral and terminal inflorescences; (ii) the many-stalked condition; (iii) the small, hard, pointed seeds.

Fig. 13. Environmentally induced and genetically controlled variation in the corn plant. Plants (from left): (i) a plant of pod-popcorn as it might have grown in nature in a poor site in competition with other natural vegetation; (ii) the same, grown under primitive agricultural conditions; (iii) the same, grown in a fertile site free of competition with weeds (this plant is essentially the same as the plant at right in Fig. 7); (iv) a popcorn plant which has lost the pod-corn gene (this is the counterpart of the plant at left in Fig. 7); (v) New England flint corn, in which human selection for larger ears has tended to eliminate the secondary stalks, reducing them to "suckers"; (vi) Cornbelt dent corn, in which the trend noted for (v) has been carried still further; Cornbelt dent corn is usually single-stalked, commonly bearing a single large ear in the middle region of the stalk. The middle position of the ear has both mechanical and physiological advantages over a terminal position and probably accounts for corn's superiority over other cereals in its capacity to produce grain. [W. C. Galinat]

Actually this reconstructed corn might easily be classified an an annual form of *Tripsacum,* or conversely, since corn was the first of the two to be given a Latin name, *Tripsacum* could be classified as a perennial form of the genus *Zea,* to which corn belongs and which, until recently, has been represented by the single species *Zea mays.*

These unexpected results of combining popcorn and pod corn—the production of a counterpart of corn's wild relative, *Tripsacum*—we regard as additional evidence that our reconstruction has validity.

Evolution under Domestication

Figure 13 illustrates some of the principal environmentally induced and genetically controlled changes which are believed to have occurred during domestication. The first three plants illustrate the genetically reconstructed ancestral form as it would be expected to develop in three different environments. The first plant, a short, single-stalked plant with a slender, unbranched tassel bearing both male and female flowers and no ears, is intended to represent the wild corn plant growing in nature in a site of low fertility and in severe competition with other natural vegetation. Such a plant would barely reproduce itself.

The second plant represents this same genotype grown under primitive agricultural conditions. Here it it still single-stalked but under these somewhat better conditions is capable of producing a branched tassel and a single small ear borne high upon the stalk. The third plant (a counterpart of the third plant in Fig. 7) represents the genetically reconstructed ancestral form grown under modern agricultural conditions with an abundance of fertilizer and in freedom from competition with weeds. Under these conditions it has several stalks as well as several small ears on each stalk. Plants like these might also have occurred sporadically in the wild under unusually favorable natural conditions.

The ability of the wild corn plant to respond in a spectacular fashion to freedom from competition with weeds and to high levels of fertility is undoubtedly one factor which led to its domestication. This ability to take full advantage of the improved environment usually afforded by an agricultural system is one of the characteristics found in almost all highly successful domesticated species. There are many wild species which do not have this trait; they cannot stand prosperity.

Since the corn plant is genetically plastic as well as responsive to an improved environment, domestication may soon have brought other changes, which are illustrated in the last four plants in Fig. 13. One of the most important of these was a mutation at the pod-corn locus on the fourth chromosome. This single genetic change had numerous effects. It reduced the glumes which in wild corn completely surrounded the kernels, and the energy released from chaff production now went into the development of a larger cob, which in turn bore more and larger kernels. The mutation also lowered the position of the lateral inflorescences, and this had profound effects of several kinds which can be understood by referring again to Fig. 9. This shows that: (i) the lower the ear, the stronger the stalk at the position at which the ear is borne and the greater its capacity for supporting large ears. (ii) The lower the ear, the more likely it is to bear only female flowers which develop kernels when pollinated. (iii) The lower the ear, the longer the shank, the branch on which it is borne, and this in turn has a number of important secondary effects: the longer the shank, the more numerous its nodes or joints and the husks which arise from them; the greater the number of husks, the more completely the ear is enclosed and the less capable it is of dispersing its seeds.

In short, a rather simple change but a very important one, the lowering of the position of the ear (comparable, perhaps, to moving the engine of a primitive airplane from a position behind the wings to one in front of them), has separated the sexes, and made for a larger, strictly grain-bearing ear which is completely protected by the husks and is no longer capable of dispersing its seeds. In short, a mutation at a single locus on chromosome 4 has made the corn plant less able to survive in nature but much more useful to man.

The last two plants in Fig. 13 show some of the changes which human selection has subsequently effected. Selection for large ears has tended to eliminate the secondary stalks and to reduce the number of ears per stalk. The fifth plant in Fig. 13 represents a typical New England flint corn in which the secondary stalks have been reduced to low tillers, known to the farmer as "suckers," which in days of cheaper labor were often removed under the erroneous impression that their removal was a kind of beneficial pruning operation. The last plant represents a typical Cornbelt dent corn which is predominantly single-stalked and often bears only one ear, in approximately the middle region of the stalk.

The corn plant has a distinct advantage over other cereals in bearing its ears in the middle region of the stalk, which, being thicker and stronger than the tip, is capable of supporting a larger ear. This is a simple and obvious mechanical advantage. There may also be a less obvious but even more important physiological advantage. We have evidence (*12*) that, under otherwise constant conditions with respect to the genotype and the environment, a decrease in the weight of the tassels may be accompanied by an increase five times as great in the weight of the ears. There is at least little doubt that corn, by virtue of its botanical characteristics, is potentially more productive than the other cereals. For example, record yields of wheat seldom exceed 100 bushels per acre; the maximum yields of corn recently reported are more than 300 bushels per acre.

There have, of course, been other factors, not discussed here, in corn's evolution under domestication: mutations at many loci in addition to that governing the characteristics of pod corn; extensive hybridization among distinct races (*10, 11*); repeated hybridization with teosinte (*9, 13*) and perhaps also with *Tripsacum* (*7*); and human selection for many different characteristics. But it was this one mutation at the pod-corn locus—this single change in a molecule of the hereditary material—which more than any other factor has determined the botanical characteristics of modern corn and which set the plant upon new evolutionary paths that have made it more useful to man and more dependent upon him for survival.

References and Notes

1. The research reported in this article was supported in part by a grant from the National Science Foundation. I am indebted also to Dr. Walton C. Galinat for his assistance in some aspects of these studies as well as for the drawings reproduced in Figs. 5, 9, and 13.
2. O. T. Bonnett, "The inflorescences of maize," *Science* 120, 77 (1954); P. Weatherwax, "Structure and development of reproductive organs [of corn]," in *Corn and Corn Improvement* (Academic Press, New York, 1955).
3. P. C. Mangelsdorf, "Corn," in *Encyclopaedia Britannica* (1958).
4. E. S. Barghoorn, M. K. Wolfe, K. H. Clisby, "Fossil maize from the Valley of Mexico," in *Botan. Museum Leaflet Harvard Univ. No. 16* (1954), pp. 229–240.
5. P. C. Mangelsdorf, "New evidence on the origin and ancestry of maize," *Am. Antiquity* 19, 409 (1954).
6. ——— and C. E. Smith, Jr., "New archaeo-

logical evidence on evolution in maize," in *Botan. Museum Leaflet Harvard Univ. No. 13* (1949), pp. 213–247.
7. P. C. Mangelsdorf and R. G. Reeves, "The Origin of Indian Corn and its Relatives," *Texas Agr. Expt. Sta. Bull. No. 574* (1939).
8. P. Weatherwax, *Indian Corn in Old America* (Macmillan, New York, 1954); ——— and L. F. Randolph, "History and origin of corn," in *Corn and Corn Improvement* (Academic Press, New York, 1955).
9. P. C. Mangelsdorf, R. S. MacNeish, W. C. Galinat, "Archaeological evidence on the diffusion and evolution of maize in northeastern Mexico," in *Botan. Museum Leaflet Harvard Univ. No. 17* (1956), pp. 125–150.
10. E. J. Wellhausen, L. M. Roberts, E. Hernandez, in collaboration with P. C. Mangelsdorf, *Races of Maize in Mexico* (Bussey Institution, Harvard Univ., Cambridge, Mass., 1952).
11. L. M. Roberts, U. J. Grant, R. Ramirez, W. H. Hatheway, D. L. Smith, in collaboration with P. C. Mangelsdorf, "Races of Maize in Colombia," *Natl. Acad. Sci. Natl. Research Council Publ. No. 510* (1957).
12. A report on this evidence is in preparation.
13. W. C. Galinat, P. C. Mangelsdorf, L. Pierson, "Estimates of teosinte introgression in archaeological maize," in *Botan. Museum Leaflet Harvard Univ. No. 17* (1956), pp. 101–124; P. C. Mangelsdorf and R. H. Lister, "Archaeological evidence on the evolution of maize in northwestern Mexico," in *Botan. Museum Leaflet Harvard Univ. No. 17* (1956), pp. 151–177.

Can There Be Too Much Research?

With competing demands on scarce resources, more applied research may curtail education and progress.

Fritz Machlup

This article deals with an important question arising from the recent growth of research and development and the loud cheers that have accompanied this growth. Several kinds of research will be touched upon, but my chief subject will be industrial research and development. This four-word phrase will be referred to often, and the use of "IRAD" as a code word for it will save space.

Phenomenal Growth of IRAD

It has been estimated that the expenditures for IRAD in 1930 were less than $120 million; in 1953 they were $3700 million, and in 1956 they were $6500 million. One might make two reservations concerning the legitimacy of measuring the growth of IRAD by dollar outlays: that the data for the earlier years are not reliable and that the value of the dollar has diminished over the period. Yet neither of these considerations can throw any doubt on the order of magnitude of the figures in question.

The figures for recent years include large amounts of public funds spent by industry under government contracts; in 1956 no less than 49 percent came from the Federal Government. In addition there were direct expenditures of the Government for research and development performed by its own agencies ($1400 million) and expenditures for research, basic and applied, in universities and other nonprofit institutions. Some expenditures for *basic* scientific research are included in the figures for IRAD, but this is only a small portion—about 5 percent in 1953—of the activities of industrial organizations. Hence, when we speak of IRAD we mean primarily *applied* research and development, designed to produce new or improved technology—some of it in the form of inventions, patentable or unpatentable; some of it concerned with the application or adaptation of inventions and the acquisition of know-how; but all of it useful in industrial production involving new products, new devices, new processes.

Much of the phenomenal growth of IRAD has been connected with the war and defense effort of the nation, either directly, as in the execution of "crash programs" for the development of weapons and other defense materiel, or indirectly through the transfer of the "research-mindedness" of defense production to industry in general. Some of the increase in IRAD expenditures has probably been connected with the tax laws, especially the combination of high corporate income tax rates (and still higher excess-profits tax rates after the war) with the deductibility of IRAD payrolls from taxable income. In any case, industrial research has become very popular, not only among industrialists but also with the consuming public, as one can infer from the public-relations emphasis upon industrial research. In the main, the new research-mindedness of industry has probably proved profitable as well as productive, and everybody is satisfied that the increase in industrial research has been a splendid thing all around.

The More the Better?

If this past increase has been such a desirable development, should we be content with the level attained or should we press for more? Should we devote an ever-increasing portion of our resources (chiefly human resources) to industrial research, or is there perhaps some limit beyond which we should not go? It is easy to see that an economy might fail to allocate enough of its resources to IRAD. But can there ever be too much? Is not more research and development always better than less?

For most noneconomists the answer looks simple: More IRAD will produce more invention of better products and of better production techniques; this, in turn, will raise our standard of living; hence, we should always encourage industrial research, by allotting more government funds, by further liberalizing the tax laws, by strengthening the patent system, by employing whatever methods seem appropriate. "Let us have more IRAD, the more the better."

This view fails to recognize the existence of an economic problem—that is, a problem of choosing among alternatives. Economics comes in where more of one thing means less of another. To be sure, it would be nice to have more of a good thing, but if this implies that there will be less of something else, one should compare and choose. It is the

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