INVESTIGATIONS INTO THE ORIGINS AND EVOLUTION OF ZEA MAYS (CORN)

by

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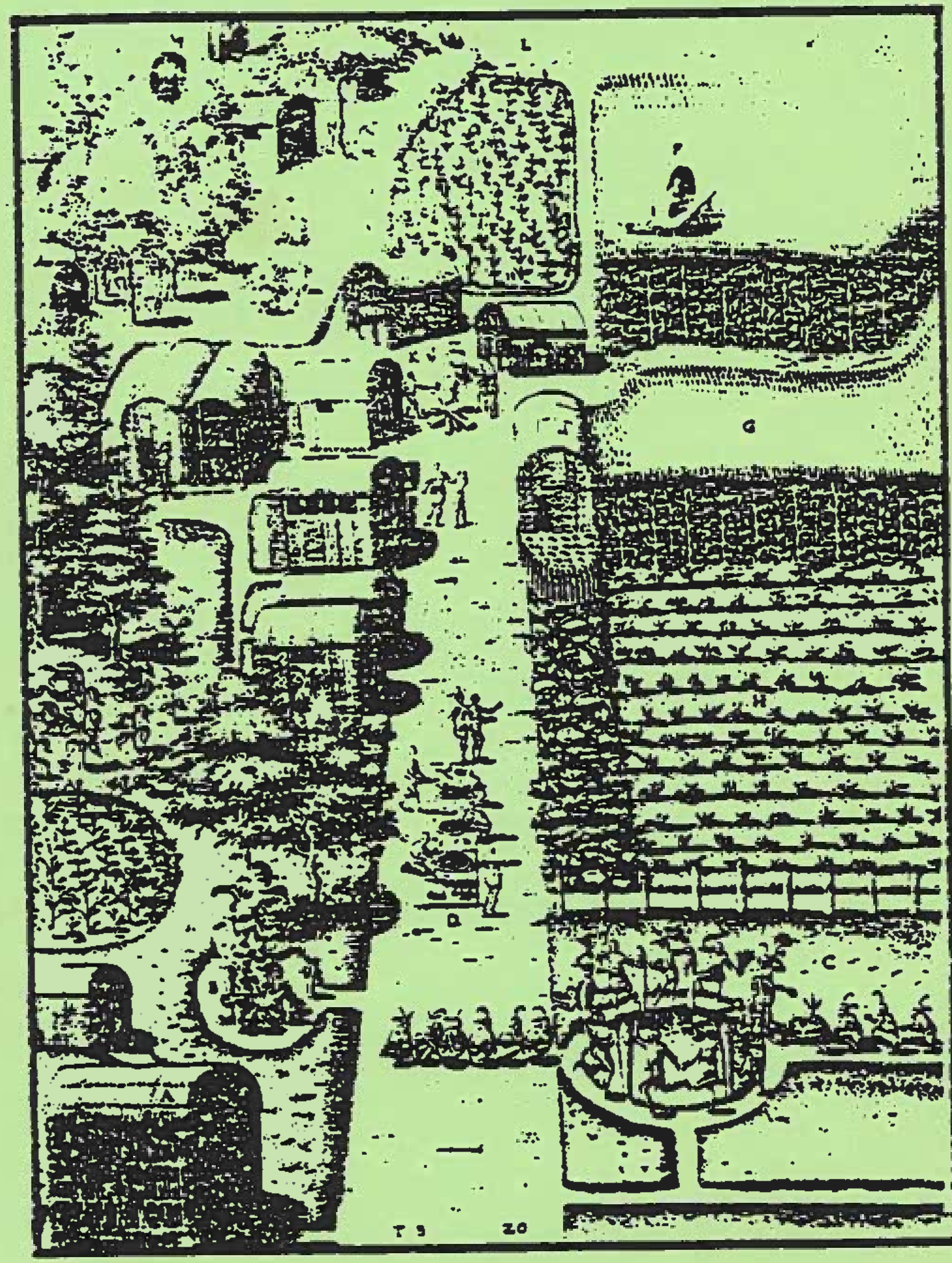

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INVESTIGATIONS INTO THE ORIGINS AND EVOLUTION OF CORN (*Zea mays*)

Draft Report

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Introduction

Many scholars have commented that perhaps the greatest single event in the history of the Old World was the discovery of the Americas. In all the strange and exciting things associated with this European discovery of the New World, the corn or maize plant today remains perhaps one of the greatest mysteries. The ancestral form of this magnificent genus has been lost or is misunderstood and much of its genetic evolution stands blurred by the passage of time. And yet today, a large portion of the world's population would be unable to exist if this plant were to disappear. For this reason, scientists are now, more than ever, interested in understanding the evolution and genetic development of the corn plant.

But why is this task so important? Afterall, corn is alive and growing today, so why concern ourselves with its past. We annually produce over 200 million tons of corn no matter what the past history of this agricultural crop was like. The need for embarking on research similar to this, however, is very important and maybe, in the long run, crucial for the survival of humankind on this planet. Try to visualize the situation from the following perspective.

In today's world there are almost ten million individual species of plants and animals on the face of the earth. These represent the culmination of at least three billion years of evolution and natural selection on our planet.

Beyond this, they also constitute the vast genetic reservoir upon which the continued evolution of planetary life depends. At the present time we know very little of the corn plant's past history. We hypothesize that, at best, corn's primitive ancestral form is still in existence although not conclusively recognized as yet, or, at worst, has become extinct and is lost forever.

Briefly, if the ancestral form of corn is extinct on this planet, its genetic heritage and wealth is also lost to us-- it is gone forever. Genes can only be stored or maintained in living systems. This loss of genetic material ancestral to today's modern corn, if true, could be devastating as our hybrid corn is made up of highly refined strains and hence is increasingly vulnerable to disease and pests. In other words, in the process of genetically engineering modern corn we have quite literally eroded away much of the natural vitality associated with the plant in the wild.[1] If a blight were to appear or develop upon which modern corn had no resistance there would be limited genetic material to breed back in or introduce into the plant in hopes of producing a resistant variety. You are probably fully aware that it would only take a few percentage points drop in world agricultural production to create a famine of catastrophic consequences (Berry 1977).

An alternative point of view exists in that the ancestral form of corn may still be present and just not fully recognized by scientists. From this perspective, with some diligent research science may someday hope to isolate, understand, and maybe even reproduce corn's evolutionary development. Plants representative of the genetic evolution of corn may then be preserved along with their genetic heritage in living plant, seed, and gene banks. Then, should the need ever arise, they will be available to plant breeders.

With these facts in mind, research on the corn plant at the National Colonial Farm, which is summarized in this paper, is initially geared toward assembling all available data concerning the evolution and genetic development of the plant. Many diverse opinions on this subject have been aired since the European discovery of corn but no single source is currently available to synopsize these findings. Based on the conclusions of this paper, we should also be able to suggest some implications of past and present research to the continued development of American agriculture.

The following format will be followed in the report. After this brief introduction, a section on the botanical nature of the corn plant will be presented. This should serve to refresh your memory about the modern corn plant so that you will have no problem following the discussion as we trace its evolutionary development. Next, a section on the differing views of corn's possible progenitors as well as prehistoric evolution will appear. This is then followed by a report of corn's development under European and American science and agriculture.

The Botanical Characteristics of the modern Corn Plant

Corn is one of the few major economic plants which is native to the New World. In the botanical classification system corn is a grass which belongs to the large and important family Gramineae which, in turn, sub-divides into the tribe Maydeae. This latter category contains eight genera including corn itself. Five of these are relatively unimportant, at least to this analysis, oriental genera:

1) Coix (Job's tears)
2) Schlerachne
3) Polytoca
4) Chinonachne
5) Trilobachne

These genera are native to an area extending from India to Burma, through the East Indies and into Australia (Jugenheimer 1976:25). The three New World genera, of great importance to this analysis, are:

6) Zea
7) Tripsacum (gamagrass)
8) Euchlaena (teosinte)

In this section of the report we will focus on Zea— the corn plant.

The genus Zea is represented by the single species Zea mays. This binomial classification is a product of Linneaus' system of plant classification based on the sexual similarities of plants (Kastner 1978:31). Zea, the genus name, is derived from the ancient Greek word for some sort of cereal (it is also remotely related to a word meaning to Live). The species denominator, mays, comes from the

Native American term for corn which has been anglicized to maize. Combining the genus and species classifications, one produces Zea mays which is simply the scientific name for the familiar corn plant.

As mentioned previously, like all of the cereals corn is technically a grass. It is a rather robust grass, but a grass just the same. Figure 1 represents a typical modern corn plant with most of its anatomical features labelled. Following T.A. Kiesselbach's (1949) classic work on The Structure and Reproduction of Corn we will proceed to review the functions of the various components which make up this plant in order to gain a detailed understanding of our subject. This review will serve as an important datum in assessing evidence on the evolution of corn under its Native American and American exploiters. Perhaps the best way to accomplish this goal is to start with a typical corn kernel and literally trace its growth into a full grown plant as well as its spectacular reproduction.

Basically, the corn kernel is not only a seed, but more properly a one-seeded fruit. This one-seeded fruit consists of an embryo and endosperm which is contained within a pericarp. The pericarp is actually a transformed ovary wall which forms a rugged outer covering for the protection of the delicate interior parts. It takes the place of the tough seed coats and husks which you commonly associate with other types of seeds.

When the pericarp is removed the endosperm and embryo are exposed. The endosperm, with the exception of some of the outer surface layer, consists of cells which are primarily filled with starch grains. At the base of this endosperm one finds modified cells which serve to conduct or transfer food from the parent plant to the growing endosperm and embryo. There are also some special cells at the surface which contain various oils and grains.

The embryo itself is embedded near the base of the corn kernel. Disecting this embryo reveals a central axis which is terminated at the basal end by the primary root structure and at the distal end by the stem tip itself. When the corn kernel containing the pericarp, endosperm, and embryo, which we have just discussed, is placed in an atmosphere of proper moisture content and temperature conditions the miracle of growth quickly commences.

In springtime, at the National Colonial Farm, the emergence of the seedling usually occurs in about 8-10 days. However, this will vary from location to location depending upon soil temperature and moisture content. Healthy corn seed usually has a high viability rate of between 95 and 100 percent. The chief cause of low germination can almost always be attributed to freezing. Kiesselbach (1949:14) has demomstrated that if corn seed has been stored properly it can be planted up to four years after harvesting.

When germination occurs, the organs of the embryo which had been formed during the development of the kernel and have remained dormant within the dry seed resume growth. The primary root and its enclosing protective sheath, the coleorhiza, begin to elongate and break through the pericarp. Soon after this the root itself will emerge from the end of this coleorhiza or sheath. At the same time, the plumule and its covering, the coleoptile, also begin to elongate and break through the pericarp of the corn kernel.

At first, the outer coleoptile grows at a more rapid pace than does the plumule but its growth is quickly arrested when the soil surface is reached and it becomes exposed to the sunlight. The plumule then breaks through its tip in short order. About this same time the first crown roots appear (to be discussed in more detail shortly). As the stem elongates leaf and branch initials are also formed.

The small plumule of the seedling which is now rapidly growing will, in most types of corn, give rise to tillers in the lower axils. In some corn types which are non-tillering, however, these will soon die and disappear. Other buds soon form ear shoots, most of which will also disappear with only the upper one or two developing ears capable of reproducing the plant. Generally speaking, the ultimate number of ears as well as presence of tillers will depend upon the specific variety of corn under examination as well as on the ever-important environmental conditions in which the plant is expected to grow.

Within four weeks of growth the process of tassel differentiation takes place. At this time, the plant is no longer considered a seedling as most external components have been initiated and further growth becomes more or less mainly a maturing process. So from this point on we will be referring to and discussing a full-grown corn plant.

The stem of a typical Nebraska corn plant consists of about 24 alternating nodes and internodes. Under favorable conditions a stem length of 254 centimeters (100 inches) will be attained. The greatest diameter of this stem will probably be about 3.8 centimeters (1.5 inches) near the base with a gradual taper evident as one moves up toward the tassel. Returning to the internodes one sees that eight are quite short and will remain below the ground surface forming what resembles an inverted cone shaped structure at the basal end of the stem. This structure is known as the crown and out of it arise the adventitious crown-root system. Brace roots (which literally serve to brace the plant) may also develop at the base depending on the particular variety of corn.

Leaf development, which originally started in the embryo, is also continuing to take place at this time. Basically, leaves are formed at each node and alternate between opposite sides of the plant. Eventually the mature plant will contain an average of 14-17 leaves but this will vary between varieties. On all plants some of the leaves are often torn loose and destroyed during the growth period. The leaves are of course the important center of photosynthesis which also produces free oxygen crucial to other life forms.

Returning to the subterranean portion on the mature corn plant one finds a root system which consists of two specific sets of roots. Again, this is a common feature shared with many grasses. One set of roots is known as the <u>seminal</u> or temporary root system. It was the initial development of these roots which was evident in the embryo. The other system is known as the <u>adventitious</u> or permanent roots. In some corn plants, however, seminal roots persist and function throughout the life of the plant so it is best to refer to the individual root systems by their proper designations.

Roy G. Wiggans (1916), as cited in Kiesselbach's monograph, found that the number of these seminal roots varies from between 1 to 13 per plant. The seminal roots consist of a primary or "radicle" root and a variable number of lateral roots which originate near the basal portion of the stem. When we get into a discussion of the prehistoric development of corn this root system will be central to the arguments presented by certain schools of thought. In general, however, the seminal roots form but a small part of the total root system and are of greatest importance during the early growth stage of the seedling.

The adventitious roots are located at the basal portion of the stem and after the seedling stage of the plant constitute the principal root system. These appendages are also known as the crown roots. Those crown roots on the lower portion of the stalk grow horizontally for some distance before turning deeper into the soil. Those which appear later in the growing cycle grow downward at once. Kiesselbach, following the investigations of W.M. Hays (1889), suggests that the peculiar phenomenon of growth direction, lateral in the early roots and vertical in the later roots, might be due to the low temperature of the deeper soil early in the growth season. It is hypothesized that at four weeks the deeper soil is warm and roots soon penetrate further down. The functional number of crown roots per stalk average about 85 in number and cover an area about 2.4 meters (8 feet) in diameter. Taking into account the branching and re-branching characteristic of the complete root system an estimated total length of these roots at 9.7 kilometers (6 miles) per plant is not unusual.

The development and structure of the reproductive organs of the corn plant involves examining tassels and the actual ear itself. Corn is thus termed monoecious because of the staminate flowers in the tassel and pistillate flowers on the ear. Staminate flowers refer to the part of the flower bearing the anther at its tip. Pistillate flowers are those which bear the ovary at their base. In corn these are the tassel and ear respectively. We will discuss each separately and then look at how fertilization takes place.

Intiation of the tassel, as mentioned earlier, begins very early after seedling emergence. At first both the central axis and branches of the tassel are smooth but outgrowths soon appear which become two lobed, each lobe giving rise to a spikelet with two flowers. Each of these flowers, in turn, bears three pollen sacs or what are properly termed anthers. Within these sacs the microspores or pollen grains are found. About 200 years ago this pollen or fertilizing dust was referred to as *farina fecundans*. (Wallace and Brown 1956:3). Symbolically, one may care to think of the pollen shedding tassel as the male organ of the corn plant.

As is the rule with most wind-pollenated plants, pollen grains are shed in enormous numbers. Each pollen sac, of which there are three on each flower, contains approximately 2,500 individual pollen grains with an estimated total pollen production per plant placed between 18 and 25 million tiny grains. That is about 25,000 grains for each of the approximately 1,000 kernels found on the average Nebraska corn plant or 42,500 pollen grains for each 2.5 square centimeters (1 square inch) of corn field under normal planting conditions.

The process of releasing this pollen begins when the anther or pollen sac breaks open near the tip and forms a release passage through which the pollen can escape. Generally, the complete pollenation process takes about three days although pollen is usually shed for a full week. Alot of this depends on environmental conditions as little pollen is shed unitl the anthers are shaken by wind or otherwise disturbed. In other words, little pollen is released until there is wind to carry it to the silks of a plant. Once the pollen is shed it sometimes will travel up to 8.1 kilometers (5 miles) from the original pollen producing organism. This feature serves as a natural mechanism assuring cross-pollenation as each plant is not necessarily fertilized by its own pollen.

For you avocational farmers, this is also why the one row of corn which is often seen in suburban garden plots will frequently not fertilize itself as the pollen is all carried away.

The ear of the corn plant is formed somewhat later than the tassel with many ears being formed initially and only the upper one or two reaching the fertilization stage. At first, when the ear is formed, its surface is smooth but protuberances soon form in rows. Each protuberance eventually becomes two lobed with each lobe developing into a spikelet with two flowers. However, only one of these flowers, usually the upper of the two, will fully develop. The exception where both flowers develop and are fertilized is seen in some sweet corns (e.g. Country Gentleman). The phenomena is immediately evident as so many kernels develop that the usually orderly arrangement of distinct rows is completely destroyed.

Returning to the flowers on the ear, one sees that each flower contains a single ovary terminated in a long style which is commonly referred to as the silks. These silks are covered with very fine "hairs" designed for capturing and holding the wind-blown pollen grains. Each silk represents a potential kernel and must be pollenated for that kernel to develop. Symbolically it may help to view the ear of corn as the female organ of the plant.

Given this, the male tassel sheds its pollen which is blown on to the silks and germinated. These pollen then thrust out pollen tubes which penetrate the tissue of the silk and travel toward the ovary on the actual ear itself. The pollen tubes, which are generally considered the fastest growing organs in the plant world, extend the entire length of the silk and reach the ovary within 15-25 hours. This time varies with silk length, temperature, and other factors. Nourishment for the pollen tube journey is provided by carbohydrates from the pollen grain.

Upon following the silk down to the ovary, one sees that the tube enters the embryo sac and ruptures thereby fertilizing the ovary. In reality, this is in fact a double fertilization as two sperms are released. Following Paul C. Mangelsdorf's description (1974), one of these fuses with a female egg nucleus to produce the embryo and the other fuses with a double nucleus to produce the endosperm. As you remember, the endosperm is the food storage organ which nourishes the embryo. This double fertilization phenomena was first described by L. Guignard (1901) in corn and has since been further substantiated by a number of scientists.

Genetically, all cells of the corn plant except those of the endosperm and gametes (male and female reproductive cells) have 20 chromosomes. The gametes, or sperm nuclei (carried by the pollen) and egg nuclei (ovary on the ear), each carry ten chromosomes or what is technically known as the haploid number. With the fusion of the egg and sperm at fertilization the full 20 chromosomes or diploid number is restored. The other exception to the 20 chromosome corn cell is found in the endosperm which contains 30 chromosomes or is triploid in constitution. This, as mentioned before, is because the endosperm is the product of the fusion of two female nuclei and one male nuclei.

Following fertilization the fused nuclei begin to divide and redivide. The kernels soon begin to swell as the endosperm and embryo develop side by side. In typical corn belt corn these kernels form rows which are always of an even number from 8 to 30 and sometimes even more (Wallace and Brown 1956:8). The average total number of kernels will vary between 800 and 1,000. Ear length usually does not exceed 20.3 centimeters (8 inches) but sometimes ears as long as 40.6 centimeters (16 inches) may be created.

The kernels are firmly attached to a rigid axis or "cob." Unlike most cereals where the individual grains or kernels are covered by glumes (what some people refer to as chaff) in corn the entire ear is instead enclosed by modified leaf sheaths. These are referred to as the husks or shucks. Thus, while other cereals protect their kernels individually, corn covers them en masse.

This en masse covering of the corn kernels results in corn being unable to reproduce itself without human intervention. If left to its fate with nature, the husks will eventually disintegrate dropping all of the kernels in one location. When conditions favorable to their germination are reached a group of seedlings so densely clustered that none are likely to survive will result. This feature of seed retention is a trait selected for by corn's first human exploiters as it allowed the harvesting of more kernels. In reality, the corn plant's ear structure is really an artifact of humankind. Fortunately, it is one of the few times that we have manipulated nature and come out ahead.

To end this introduction, in 6 to 8 weeks after fertilization, depending on the particular variety, the ear of corn is full grown. The cells of the endosperm at this point are packed with starch grains in ordinary field corn and filled with sugar, starch, and intermediate products in sweet corn. When picked, the sweet corn will become the succulent roasting ears which grace our tables and the field corn will become animal feed which also ultimately reaches our tables in many diverse forms.

With this, the introduction to the corn plant is complete. Drawing upon the knowledge gained in this short review of corn's botanical characteristics we are now free to examine its evolutionary development. Except where noted, this introduction has drawn upon the work of Kiesselbach (1949). Following Mangelsdorf's suggestion (1974:3), however, it will now be necessary to branch out and employ at least four different kinds of evidence in the search for corn's ancient progenitor and its subsequent development through the centuries.[2] This includes evidence from the fields of 1) history, 2) linguistics, 3) botany, and 4) archeology. All of these disciplines will be tapped in our research as the analysis moves toward an understanding of the evolution of corn from ancient to modern times.

Theories on the Origin and Prehistoric Evolution of Corn (*Zea mays*)

As mentioned before, the origin of corn is lost somewhere in antiquity. Nevertheless, speculation concerning its origin by students of the corn plant is rife in the corpus of literature. Within this section of the report we will examine the major theories of corn's origins and evolution during prehistoric times. Each theory and supporting data will be presented, as unbiased as possible, and after all are reviewed we will try and determine which, if any, is the most plausible. First, however, we need to quickly examine two of the corn plant's close botanical relatives.

Returning to the previous section, it was stated that three New World genera existed within the botanical tribe *Maydae*. These include *Zea* (corn), *Tripsacum* (gamagrass), and *Euchlaena* (teosinte). We have already discussed *Zea* or corn in some detail and it is now time to address the latter two genera. The reason for this is that *Tripsacum* and teosinte[3] figure prominently in many theories of corn's evolution.

Tripsacum or gamagrass is native to an area ranging from Florida and the Gulf Coast of Texas to South America (Wilkes 1972:1073). H.C. Culter and E. Anderson (1941) have also demonstrated that it can extend into northern portions of the United States. However, its greatest center of diversity and therefore probably its center or place of origin appears to be Mexico and Central America. Basically, the plant has some economic value as a forage crop but little as a grain crop.

Following Mangelsdorf's description of Tripsacum (1974:53) one sees that all of the species are perennial herbs that exhibit numerous tillers and shoots, some of which are short, sterile, and leafy, while others are long, fertile, and branching. Figure 2 represents a typical species of Tripsacum. As one can readily see, its relationship to corn is apparent.

Like corn, all species of Tripsacum are monoecious in that they have their male and female spikelets in separate positions. The male or staminate spikelets are borne on the upper part of the spike and the female or pistillate spikelets are borne below on the same spike. In both chromosome numbers and chromosome morphology Tripsacum differs from its cousins teosinte and corn. With the latter two genera the haploid number of chromosomes is 10. Of the nine recognized species of Tripsacum the haploid number of chromosomes in five is 18 and in the remaining four it is 36 (Mangelsdorf 1974:54). However, employing artificial techniques in the laboratory Tripsacum and corn can be "made" to hybridize. Mangelsdorf and R.G. Reeves (1939) first accomplished this feat although there is no evidence to suggest a natural crossing between the two genera has ever occurred or could ever occur in nature.

Teosinte (Euchlaena) is undoubtedly, at the very least, the closest relative of corn. Some believe that it actually represents something more than a relative (Beadle 1972 and 1977) but we will save our discussion of this point of view for later. At this time the leading authority on teosinte is H. Garrison Wilkes (1967, 1972) and it is his description which will be followed in this brief review.

Teosinte is very similar to corn in that it has staminate flowers borne in tassels and pistillate flowers enclosed in a system of husks. Figure 3 illustrates a typical teosinte plant. Like corn, the pistillate flowers are positioned in a lateral location on the plant. This pistillate fruit also reveals the chief difference between corn and teosinte. In corn the fruit is positioned on a polystichous structure (the ear) and in teosinte it is located on a distichous spike. Translating, on the former plant the kernels are arranged on several or more rows and in the latter they are disposed in two vertical rows. Teosinte is also further distinguished from corn in that it has the important ability to disperse its seeds by itself and thus can survive in the wild, while corn is an obligate genus dependent on human intervention for survival.

Today, the six recognized species of teosinte are geographically limited to the seasonally dry, subtropical zone with summer rain along the western escarpment of Mexico and Guatemala and the central Plateau of Mexico. The prehistoric distribution of the genus may have been much wider, however, more work will have to be accomplished before any definite statements can be made. At the present time, the plant is usually found in untilled areas but often enters cultivated fields of corn where it becomes virtually undetectable to the untrained eye.

Genetically, teosinte is also very similar to corn in that it has a diploid chromosome number of 20. It also rapidly hybridizes with corn in the wild (unlike _Tripsacum_) and the resulting first generation hybrid is both robust and fertile. In fact scientists are becoming increasingly alarmed by the eradication of teosinte evident in much of its natural habitat. It seems that much of the hybrid vigor of corn can be attributed to the constant introgressive hybridization with its closest relative teosinte. If the progenitor of corn is lost as some scientists believe it to be, it would surely be a shame if teosinte follows along the same path.

With this brief introduction to _Tripsacum_ and teosinte complete, we are now free to examine the various theories of corn's origin and prehistoric development. Evidence will be first presented from the various major schools of thought and we will then try to objectively arrive at some conclusions on the issue if possible.

Theories on the Origin of Maize

Based on a thorough review of the literature concerning the corn plant it seems that there are four principal or major theories relating to the origin of corn and its subsequent evolution during prehistoric times. These include 1) the theory that corn, teosinte, and _Tripsacum_ are descendant from a common ancestor via divergent evolution; 2) that pod corn is the progenitor from which corn arose; 3) the tripartite theory; and 4) the theory that teosinte was the progenitor of corn. This view of four principal theories follows closely with Mangelsdorf's (1974:11) treatment of the data. Our task now will be to go through each theory (actually they are technically hypotheses) and examine their respective foundations.

Theory of a Common Ancestry

Following Mangelsdorf review (1974:12), it appears that E.G. Montgomery (1906) was the first to outline a theory of common ancestry, although he did not include Tripsacum as one of the entities stemming from the common ancestor of corn and teosinte. Therefore, it was Paul Weatherwax (1918 who actually first hypothesized that corn, teosinte, and Tripsacum had a common ancestor. In subsequent publications Weatherwax (1919, 1950, 1954, and 1955) also further elaborated on this view. Logically, after examining the three plants in question this hypothesis appears to be a viable explanation.

Weatherwax thought that by divergent evolution (also known as cladogenesis) corn, teosinte, and Tripsacum after becoming isolated from their common ancestor evolved into their present forms. The forms of these organisms evident today is the result of mutations and differing selective pressures put on each genera in their individual evolutionary trajectories. Basically, this follows the classic thoughts expressed on evolution by Charles Darwin in the 19th century. If this point of view is true, the ancestor or progenitor of corn is now completely lost.

The Pod Corn Theory

Another hypothesis holds that corn was derived from a wild form of pod corn. Pod Corn is a peculiar type of corn in which the individual kernels are entirely enclosed in bracts, or what the common person would refer to a "chaff." This covering or envelope is a condition quite common to many wild plants and results in an organism which looks to be, quite frankly, very "primitive."

It was probably the French naturalist Saint-Hilaire (1829) who, in a letter to the French Academy of Sciences, first pointed out that pod corn could be a progenitor of corn. The presence of the kernels enclosed in bracts on a sample he obtained from Brazil no doubt led him to postulate that this was the condition of corn in antiquity and therefore pod corn could be linked as the ancestor of corn. It is evident from the literature that most serious students of corn have, at one time or another, stopped and speculated on the "primitive" characteristics of pod corn.

However, for numerous reasons pod corn can be dismissed as a direct ancestor of corn. This statement is based on studies of its breeding habits; the fact that it is frequently monstrous and sterile; and the fact that its genetic structure differs from that of corn (Mangelsdorf and Reeves 1939). Despite these objections, however, Mangelsdorf and Reeves (1959) have seen fit to include pod corn into their tripartite theory which will be discussed next.

The Tripartite Theory

In a paper written for the Accokeek Foundation by the eminent anthropologist Philleo Nash (the present writer was the junior author), the tripartite theory of Mangelsdorf and various subordinate authors was quickly labelled "the establishment view." This tripartite hypothesis, true to Nash's label, has for a third of a century been supported by its proposers and their students with the result being that it has thoroughly permeated the genetic, botanical, plant-breeding, anthropological, and who knows what other literature (Beadle 1977:620). It has also been repeated in encyclopedias, compendiums, and in texts; sometimes in the process it has seemingly even been transformed from hypothesis into fact!

Although this theory or hypothesis is very complicated and has, in fact, perceptively changed over the years (examine Mangelsdorf and Reeves 1939 versus Mangelsdorf 1974) a synopsis will be attempted. At any rate, as a result of extensive studies of the hybrids of corn with teosinte and <u>Tripsacum</u> Mangelsdorf and Reeves (1939) concluded that teosinte is actually the progeny of a hybrid between corn and <u>Tripsacum</u>. This does not explain the origin of corn itself, but with teosinte eliminated as an ancestor, they were free to examine other possible candidates. Like many, Mangelsdorf and Reeves (1939) then turned to pod corn as a possible progenitor of corn. It seems that they were impressed by the fact that pod corn's characteristic of covering its kernels was almost a universal feature of wild grasses.

The third part of the tripartite theory is the recognition that teosinte, since it is not the ancestor of corn, did, however, play an important role in corn's evolution under domestication. Teosinte's primary purpose was to provide a steady flow of genes back into corn and hence, many varieties of corn are a product of the hybridization of the two genera. Basically, it seems as if it was very hard for Mangelsdorf and Reeves (1939) to ignore the presence of teosinte in the corn fields of Mexico.

Before 1961, this tripartite theory was based on experimentation and the observation of living plants in their native habitats. However, between 1961 and 1964 Mangelsdorf associated himself with the Tehuacan Archeological and Botanical Project which searched for the origins of New World agriculture in the Tehuacan Valley of Mexico. This project, supported by the National Science Foundation and the Rockefeller Foundation, was the brain child of the archeologist Richard S. MacNeish. The implications of the excavations to corn's origin and prehistoric evolution according to Mangelsdorf, MacNeish, and Walter Galinat (1967) are summarized in the next few pages.

During excavations, corn was recovered by the project from five caves in the Tehuacan Valley: Coxcatlan, Purron, San Marcos, Tecorral, and El Riego. The significance of the recovered remains is as follows:

1) It includes the oldest well-preserved corn cobs

2) These cobs are those of wild corn according to Mangelsdorf

3) This corn appears to be the progenitor of two of the ancient indigenous races of Mexico, Chapalote and Nal-Tel

4) Specimens of all parts of the plants have been preserved and these also point to the ancestor of corn being wild corn as recovered in these caves

5) This collection portrays a well-defined evolutionary sequence of corn's development covering a period of 6,500 years

In actuality, the finding of prehistoric wild corn in the Tehuacan Valley was somewhat suprising. Corn is not noted for its drought resistance and in order to thrive it needs steady and adequate supplies of water. Mangelsdorf and Reeves (1938) originally postulated that wild corn, if still extant, would be found in the humid regions of the tropics and sub-tropics. At first glance, the Tehuacan Valley with its arid climate and xerophytic vegetation appears to provide an unsuitable habitat.

Upon closer examination, however, the authors feel that these conditions are offset by the fact that almost 90% of Tehuacan rain falls during a growing season stretching from April to October. This rain reaches its peak during corn's most critical growing period when it would be silking, shedding pollen, and the young kernels developing. The remaining months are quite dry and the seed of wild corn would probably lie dormant ready to sprout in the summer months. It is interesting to note that many wild plants have mechanisms for delaying germination, but corn has no such feature. Perhaps this is because it evolved in an environment where none was needed, i.e. the Tehuacan Valley.

Another reason why corn could have developed in the Tehuacan Valley, even with its generally arid environment, is that it is an annual plant. Annual vegetation which only grows in certain seasons need not be especially drought resistant. Wild corn would also not have to be subject to severe competition from drought-resistant perennial vegetation. The sites which are most suitable for corn, the alluvial terraces and fans, seem not to be well adapted to the growth of cacti and shrubs. Indeed the deeper the alluvial soil, the less likely one is to find cacti and shrubs. Instead, one finds grasses and other annuals among which corn would have been at home.

During the actual excavations, 24,186 specimens of what is postulated to have been corn was recovered from the five caves; 12,860 of these were whole or almost intact cobs. There are in addition to these intact cobs, 3,941 identified cob fragments and 3,878 possible unidentified cob fragments. Among the remaining specimens are found all parts of the plant; 46 roots, 506 pieces of stalk, 442 leaf sheaths, 282 leaves, 245 inner husks, 706 outer husks, 12 prophylls, 127 shanks, 384 tassel fragments, 47 husk systems, 5 midribs, and 797 kernels. There are also numerous quids representing 83 chewed stalks or leaves and 140 chewed husks.

The first excavation unit to be studied was San Marcos

Cave with a total of 1,248 specimens. The specimen size is not large but it does reveal a well-defined sequence illustrating corn's evolution over 6,500 years. This site was also analyzed first in hopes of developing a pattern useful in the study of Coxcatlan Cave's 15,000 specimens. As it turned out this was possible as all that the analysis of Coxcatlan Cave did was to corroborate the San Marcos Cave sequence.

The San Marcos botanical sequence is as follows: Zone E and F (the lowest and oldest stratigraphic levels) contained 26 cobs or cob fragments which were all remarkably uniform in size and botanical characteristics. Each cob had a length between 19-25 mm, eight rows of kernels, a mean number of spikelets of 55. The general characteristic was very similar to present-day pod corn. The majority of the cobs were originally bisexual, bearing their female pistillate spikelets below and male staminate spikelets above.

Mangelsdorf, et al. (1967) believe that in bearing both male and female spikelets in the same inflorescence the prehistoric wild corn resembles a genetically reconstructed ancestral form which they had previously produced as well as certain primitive races of corn found in Mexico, Columbia, and Peru. It is also similar to its wild relative Tripsacum.

The earliest cobs from this zone (dated at 5,000 B.C.) are regarded as those of wild corn for six reasons:

1) They are remarkably uniform in size and other characteristics and in this respect resemble most wild species.

2) The cobs have fragile rachises as do many wild grasses; these provide a means of dispersal which modern corn lacks.

3) The glumes are relatively long in relation to other structures and must have partially enclosed the kernels as they do in other wild grasses.

4) San Marcos Cave is located above an alluvial terrace which would provide a suitable habitat for wild corn.

5) There is no firm evidence that other plant species had as yet been domesticated at this time. Therefore, it is logical to assume that this corn is a wild form.

6) The predominating corn from the next archeological phase, in which agriculture was definitely established, is larger and more variable than the first corn.

This leads Mangelsdorf et al. (1967) to the conclusion that the earliest corn from the Tehuacan Valley is wild corn.

San Marcos Cave Zone D represents the earliest part of the Abejas archeological phase (3,500-2,300 B.C.) and contains 102 cobs or cob fragments. All but one are similar to, in their general characteristics, those cobs in Zone E and F but the majority are larger. Mean length is 43 mm (compared to 19-25 mm in Zone E and F. and mean number of spikelets is 113.

The larger size indicates that this corn was grown in a better environment. Also recovered were remains of two species of squashes (Cucurbita moschata and C. mixta), tepary and common beans (Phaseolus acutifolius and P. vulgaris), bottle gourds (Lagenaria siceraria), chilli peppers, avocados, and amaranths. It is assumed that these also represent the product of an improved environment resulting from the practice of agriculture.

If this corn in Zone D is indeed cultivated corn it is noteworthy that domestication had little effect except for the change in size. The botanical characteristics are virtually identical to the wild species from which it stemmed.

In Zone D husks were also recovered. They appear to be part of a two husk system with inner and outer husks. It is felt that the ears with these husks were usually borne in the upper part of the stalk sometimes immediately below the tassel. The husks protected the young ear before pollenation and in the early stages of development but then flare open at maturity allowing the ear to disperse its seeds. Ears with husks may also appear in lateral inflorescences.

San Marcos Cave Zone C represents the archeological Ajalpan phase (1500-900 B.C.) and includes new types of corn. This corn is designated "early tripsacoid" following a term introduced by Anderson and Erickson (1941) to describe any combination of characteristics which might have been introduced into corn by hybridizing with its relatives, teosinte and *Tripsacum*. Mangelsdorf et al. (1967) feel that this corn represents a product of the hybridization with teosinte or *Tripsacum*. However, they have no idea how this happened as there is no evidence of either teosinte or *Tripsacum* ever growing in the Tehuacan Valley.

The only possibility is that the early cultivated corn of Tehuacan was carried into other regions where it hybridized with teosinte or *Tripsacum* and then some hybrid progeny was later returned to the valley. However, due to the paucity of data there is no evidence to validate this hypothesis.

In Zone C roots of the corn plants were also recovered. The root development shows that the kernels were barely covered with soil when planted. Roots also show that the plants had a seminal root system. As mentioned before, in modern corn plants this is often temporary and only serves to maintain the seedling until the permanent root system develops at the lower nodes of the stalk. However, in certain drought resisting varieties grown by Native Americans in the southwestern United States the primary root system makes an early and rapid penetration into deeper moister soils and continues to function throughout the life of the plant. Tehuacan corn had a similar adaptation.

In summary, Mangelsdorf et al. (1967) feel that Zones E and F of San Marcos Cave contain specimens representing corn in its wild or natural state. This postulated wild corn is dated at 5,000 B.C. The next zone (Zone D) represents the first domesticated corn and is dated between 3,500 and 2,300 B.C. Corn from Zone D is virtually identical to that of the earlier zone except it is somewhat larger due to the better environment, as a result of agricultural practices, that it was raised within. Zone C remains, dated at 1,500 to 900 B.C., represents what is referred to as "early tripsacoid" corn. Mangelsdorf et al. (1967) feel that this represents corn that has hybridized with either teosinte or <u>Tripsacum</u>. However, neither of the latter two plants grew in the Tehuacan Valley so this particular corn must have originally developed elsewhere and then was brought into the valley. In upper zones, labelled C-1 and B (dated at 200 B.C. to 800 A.D) new types of corn begin to develop from the continued hybridization of corn and its relatives teosinte and *Tripsacum*. According to Mangelsdorf et al. (1967) this sequence substantiates the tripartite hypothesis.

However, at a conference held at Harvard University in June of 1972 Mangelsdorf, in front of his colleagues, conceded that there were "certain" problems with his original tripartite theory. For these reasons he has altered his thoughts. At the present time, Mangelsdorf (1974) still feels that the Tehuacan Valley sequence does, in fact, represent wild corn (Zones E and F). However, he now believes that teosinte was derived from wild corn by genetic mutation. In his original theory (return to page 22) teosinte was the product of hybridization between corn and *Tripsacum*. Before 1972 Mangelsdorf had been adamant that teosinte could not be ancestral to corn. Now teosinte comes from corn by way of mutation.

After reading this section on Mangelsdorf et al.'s research, one feels somewhat uneasy that the data does not exactly support the claims of the tripartite theory. Please be assured that a special effort was made to present Mangelsdorf's complex arguments and supporting data in as simple terms as possible while still retaining their original meaning. The Tehuacan Valley sequence is a very impressive array of data but it still seems that there is some question of the interpretations supplied for it. Could their be other explanations for this information? For now, however, we will move on to the last theory.

Teosinte: The Mother of Corn

As Mangelsdorf is the champion of what Nash labelled the "establishment view," the theory that wild teosinte was the direct ancestor of corn also has a noted scientist to further its cause. This time it is George W. Beadle, a Noble-Laureate and Past-President of the University of Chicago. In two convincing articles, Beadle (1972, 1977) has substantially rattled the "establishment" and advanced the theory that corn is a descendant of teosinte.

However, Beadle was not the first to express the thought that teosinte is the progenitor of corn. For example, Vinson in 1877 wrote that following the thinking of Darwin teosinte should be the ancestor of corn (Wilkes 1967:1072). Between 1920 and 1940 the Russian geneticist and plant breeder N.I. Vavilov also stated that he considered teosinte to be the ancestor of corn. Vavilov based this statement on the natural hybridization he observed between corn and teosinte as well as the two plant's overlapping natural habitats (Wilkes 1972:1072).

Beadle's interest began when he worked with R.A. Emerson as a graduate assistant at Cornell University. This work proved that the ten chromosomes of corn were highly compatible with the ten chromosomes of teosinte and that they paired normally during formation of sex cells in hybrids. It was also shown that in the nine chromosomes they could mark, the pairs exchanged segments in the hybrids essentially the same way as in pure corn. The conclusion, in so many words, was that cytologically and genetically corn and teosinte could reasonably be regarded as one species! Therefore, the hypothesis that teosinte in the progenitor of corn is entirely possible. Beadle believes that a relatively few gene changes could and probably did convert wild teosinte into a useful cultivated plant-- Corn.

In a nutshell, this is Beadle's argument. What must now be attempted is an explanation of the validity of the four theories which have been reviewed.

Review of Theories

What must now be undertaken is a process of elimination. Based on knowledge accumulated in this research we must decide which of the four theories seems plausible at this point in time. With this in mind, the following comments are offered on the matter.

First, the common ancestry theory of Weatherwax (1918, 1919, 1950, 1954, 1955) is a logical explanation and can not be discounted as a possible explanation. L.F. Randolph (1959) has also echoed this opinion. If you recall, this theory stated that corn, teosinte, and <u>Tripsacum</u> arose by divergent evolution from an ancestor common to all. In this view, the common ancestor is extinct. Mangelsdorf (1974:12) has stated in his typical narrow line of logic that as a theory this is fine, however, it is ultimately untenable because it is scientifically untestable.

Apparently Mangelsdorf does not see paleobotany as a science which could hold the key to the problem. It seems that the fossil record could contain evidence of such a plant necessary to validate the theory under question. Admittedly, it would be no small task to find this ancestor of corn and its relatives, however, this is no reason to reject a theory which quite possibly could be correct. Given this, the theory of common ancestry must not be ruled out.

Next, we come to the theory that points to a wild form of pod corn as being the ancestor of today's corn. From the literature, it seems as if pod corn has captured the imagination of many corn scientists because it encloses its kernels in bracts, a feature common to some wild grasses. However, let us stop and think about the logic of taking this characteristic of pod corn and constructing a grand theory for corn's origin.

For example, what is termed dog corn has been found to be a plant intermediate between teosinte and corn. This dog corn is so named because its kernels resemble dog's teeth and it also possesses the interesting characteristic of having each kernel set in an envelope of chaff almost like that of pod corn. However, the plant is easily reproduced and is, in fact, a natural hybrid of corn and teosinte. The point is, just because a certain plant has "primitive" characteristics does not mean that it is an ancient species. More evidence must be gathered to suggest that modern pod corn is a relic species ancestral to corn before this theory can be accepted.

At this point, we are left with two remaining theories. One, the tripartite theory, belongs to Mangelsdorf and various associates. The second, which sees wild teosinte as ancestral to corn, is championed by Beadle. To make matters clear from the start, it is firmly believed that the tripartite theory stands little chance of even being close to an adequate explanation. For much of the remainder of this section we will attempt to show why this tripartite theory is incorrect and at the same time illustrate the benefits of Beadle's theory of teosinte as being ancestral to corn.

A simple swipe of Occam's razor, the scientific and philosophical rule that states entities should not be multiplied unnecessarily (i.e. the simplest of competing theories always should be preferred to the more complex), would suffice to eliminate the tripartite point of view. Basically, the unduly complex tripartite theory will fall apart if any one of its three supporting assumptions can be declared invalid (see page 22-23). Beadle's view of corn's evolution, on the other hand, offers a logical explanation without unnecessary and complicated assumptions.

Another further advantage of Beadle's work is that it is based upon genetic research on corn and its relatives versus Mangelsdorf's theory which examines similarities of various plants to a hypothetical ancestor of corn. In some cases, Mangelsdorf even ignored genetic data which contradicted his assumptions. Perhaps we should look into the above statements in more detail.

First, in the tripartite theory Mangelsdorf originally viewed teosinte as a hybrid of corn and Tripsacum. However, as stated before, Tripsacum and corn can only be hybridized in the laboratory and there is no evidence to suggest that the two genera ever hybridized naturally in the wild. None of the 18 chromosomes of Tripsacum pairs normally with any of the 10 chromosomes of corn and even when hybrids are forced in the laboratory they are sterile. Galinat (1970) as well as Weatherwax and L.I. Randolf (1955) have clearly demonstrated that genetically there is no support for this aspect of Mangelsdorf and his various associate's theory.

DeWet and Harlan (1972) and de Wet et al. (1972) of the University of Illinois at Urbana, have also shown that in their extensive studies of hybrids between corn and Tripsacum they have never observed a segregant at all like teosinte. Further, contrary to the tripartite theory's assumption that teosinte is of relatively recent origin, the plant now has at least a 7,000 year antiquity as two teosinte seeds have recently been uncovered in an undisturbed pre-ceramic archeological horizon (Lorenzo and Gonzalez 1970). Needless to say, this portion of Mangelsdorf's theory can be laid to rest. Begrudgingly, even Mangelsdorf himself has acknowledged this fact.

Secondly, Mangelsdorf believes ancient wild corn, like that recovered in the Tehuacan Valley, was similar to a cross between pod corn and pop corn. In fact, he created such a pod-pop corn in his experimental fields which looked similar to the remains from archeological sites in the Tehuacan Valley. Again, however, does this pod-pop corn which Mangelsodrf has created in his laboratory mean anything?

If similarities can be taken at face value it is true that a cross between pod and pop corn does, in fact, look similar to what are assumed to be primitive forms of corn excavated from archeological sites. The question we must ask is whether this reconstructed form of pod-pop corn is "analogous" or "homologous" to the ancient samples from the Tehuacan Valley. Perhaps it would be best to illustrate the point with an example. The wings of a bird and an insect are analogous structures as they are both flapped in the air to contribute to flying. But the similarity is superficial. An insect's wing derives from an out-folding of the actual body wall, whereas a birds wing is derived from the same bone structures that give rise to a bat's wing or a human being's arm. These latter structures are homologous: They possess an underlying similarity based upon a common evolutionary descent. If pod and pop corn crosses are not evolutionary homologous to primitive corn it is like comparing insects and birds, i.e. the comparison is superficial only.

In other words, because Mangelsdorf was able to create a pod-pop corn which looked like primitive cobs assumed to be from wild corn does not mean that a cross between pod and pop corn was the progenitor of modern corn. It simply means that a cross between pod and pop corn resembles, maybe only superficially, what Mangelsdorf has passed judgement on as wild corn. Convincing proof of the genetic authenticity of the pod-pop corn cross must be presented before science can accept Mangelsdorf's arguments with a clear conscience.

Beyond this, one of the reasons which Mangelsdorf originally gave for eliminating teosinte as an ancestor to corn was fossil pollen recovered in samples from a construction core taken at the Belles Artes site in Mexico City at a depth of more then 50.8 meters (200 feet). Material at this depth should date to 40-80,000 years ago and the pollen recovered was assumed to be that of wild corn. Of course, if the interpretation was correct, the plant was growing long before any human, either Native American or European, had entered the New World.

However, palynology, the science of pollen analysis, is not always conclusive in its interpretations. At first the identification of these pollen grains was based on size, most modern corn pollen being larger then pollen from teosinte. As reported by Beadle, E.B. Kurtz et al. (1960) have now challenged the original identification of E.S. Barghoorn et al. (1954) on the grounds that maize pollen varies markedly in size depending upon environmental conditions and that, therefore size alone is not clearly diagnostic, nor is the ratio of the long axis of the grain to pore diameter which had been said to be a more reliable indicator. Galinat (1971) has gone on record as stating that he believes the fossil pollen in question is too large to be that of primitive maize.

As a result of the above controversy, a re-examination of the Belles Artes pollen was undertaken by H. Irwin and Barghoorn (1965) with the assumption that the pollen could now be reliably identified employing the exine characteristics of the grain as revealed by phase-contrast microscopy. Again, the pollen was judged to be that of wild corn. But, still more recently U.C. Banerjee has employed a superior method of electron microscopy which illustrates the futility of relying on pollen exines for identification (Banergee and Barghoorn 1972). Grant (1972) has echoed this conclusion. For these reasons, plus the distinct possibility of possible contamination in the engineer's original core, the data are inconclusive at best. Therefore, logically Mangelsdorf has no soild reason for ruling out teosinte as a possible progenitor of corn. As Nash has pointed out, it is unreasonable to assume that a plant existing almost 80,000 years ago lived until around 7,000 years ago so the aborigines of the Tehuacan Valley could convert it to domesticated corn and then disappeared leaving no trace (Nash and Dent 1978).

In conclusion, it is safe to state that two of the three assumptions serving as foundations for Mangelsdorf's tripartite theory are invalid or open to serious question. The last assumption, that teosinte has often hybridized with corn is not debated. Indeed, this fact has been recognized for years. One gets the distinct feeling that teosinte and corn hybridization was only included formally in the tripartite theory because there was nothing else to do with teosinte since it was denied any possible role as a progenitor of corn. Let us now turn to a more plausible explanation.

According to Beadle, teosinte may be the ancester of corn.

Beadle, as a graduate student, had the good fortune to be assigned to assist R.A. Emerson at Cornell University. In working together, they were among the first to confirm the fertility of hybrids between teosinte and corn thereby demonstrating that the ten chromosomes of corn are highly compatible with the ten chromosomes of teosinte. They also showed that the nine chromosomes of corn which they could mark, paired and exchanged segments in the hybrids essentially the same as in the pure parents. The conclusion was that, in so many words, corn and teosinte could reasonably be regarded as one species in genetic and cytological terms. Therefore, the hypothesis that wild teosinte was the direct ancestor of corn was possible. A relatively few minor gene changes could and did probably convert the wild plant into a more useful cultivated form.

Emerson had long pointed out that two mutations could easily make teosinte into an easily usable food plant (Beadle 1972:5). One mutation would involve creating a non-shattering rachis so that the fruit would not be scattered and lost as food and the other mutation would produce a soft fruitcase so that the kernels could be threshed free. Incidentally, these are the same two mutations which played a significant role in the evolution of cultivated wheat, rye, barley, and oats so they are entirely possible to select for.

The problem facing Beadle, however, was how to test his hypothesis or theory on the relationship of teosinte to corn. Beadle (1972, 1977) decided to supplement earlier small-scale studies indicating that near-equivalents to parental types could be recovered in second generation corn-teosinte hybrid populations. This would be accomplished by growing large-scale second generation and backcross populations in order to better understand and estimate the magnitude of genetic difference between corn and teosinte.

The first cross was undertaken with Chapalote corn, a primitive variety which is the most teosinte-like while still being clearly corn, and Chalcó teosinte, which is, in turn, the most corn-like teosinte while still being unmistakably teosinte. Gregor Mendel's laws were then called upon to interpret the results. These laws state that if the original parents differ from each other by only one gene, in the second generation of descendants each original parental type will reappear with a statistical frequency of one out of four. With a difference of two genes, each parental type will be reproduced with a frequency of one in sixteen times, and so on. For ten gene differences, the reappearance of the original parent types will be slightly less then one in a million. The point to be made is this, if teosinte and corn differ by a large number of genes, Beadle could never hope to grow and examine hybrid populations large enough to produce good offspring equivalent to the original corn and teosinte.

To this date, Beadle has grown up to 50,000 second generation plants which should give a reasonable chance of recovering parental types with as many as six or seven major independently segregating genetic units. Since teosinte plants will not mature at United States corn-belt latitudes there was a problem of where to grow the test populations. Fortunately this was solved by an agreement to grow the plants at the International Maize and Wheat Improvement Center near Texcoco, Mexico.

The results of the experiment were that good parental types appear with a frequency of about one of each type in every 500 plants (Beadle 1972:7). These frequencies are intermediate between those expected with four or five independently segregating genes. It seems clear enough that the genetic differences between corn and teosinte can not be so great as to render untenable the hypothesis of an ancestral relationship between the two plants. Beadle (1972:7) also feels that it is reasonable to assume that pre-Columbian human populations could have selected and preserved the relatively few mutants required to produce a useful plant from teosinte.

In response to doubts expressed by Mangelsdorf that the experiment conducted by Beadle was not conclusive as it depended on his ability to recognize the appearance of true parental types in the plants produced, a quiz was devised. What Beadle did was select cobs from the pure parental types employed in the experiment and also selected cobs from those reproduced in the hybrid populations. These were then sent to Mangelsdorf and also Galinat for classification. In both cases enough cobs of the hybrid variety were judged to be those of good corn to confirm that true corn types were indeed being recovered in reasonable frequencies to substantiate the experiment. This is of course contrary to Mangelsdorf's expectation, but still confirmed by his own expertise.

In response to the evidence excavated in the Tehuacan Valley and reported by Mangelsdorf et al. (1967) Beadle has the following comments. While agreeing that the material tells us a great deal about the evolution of corn, a different interpretation can be safely advanced. Because it is logically impossible at this time to prove that a true wild corn ever existed (the pollen evidence is not reliable; see page 37-38) one can seriously question whether the available evidence dictates that the earliest cobs from the Tehuacan Valley are really wild corn as Mangelsdorf suggests.

A more plausible explanation in Beadle's mind is that the oldest cobs from the Tehuacan Valley instead represent a transition between the ancestral teosinte and true corn selected for by human beings (1977:625). First, the earliest cobs are obviously much closer morphologically and genetically to teosinte than to corn. Furthermore, cobs closely matching the ancient material recovered in the archeological site are also readily recovered in second and later generations of corn and teosinte hybrids.

Secondly, Beadle states that if the earliest archeological types are indeed genetically closer to teosinte, as expected in his hypothesis, this should be evident in second and backcross generations of hybrids of those types similar to archeologically recovered specimens with teosinte (1977:626). Experiments now in progress indicate that genetic differences are indeed reduced in number this way.

Third, some of the earliest cobs recovered from archeological sites have their kernels in two distinct ranks or rows. This is another trait of teosinte.

Last, the earliest of what are assumed to be corn cobs by Mangelsdorf have longer glumes than those in modern corn. These long glumes suggest that teosinte could have been converted into a more useful food plant and logical precursor of corn. Emerson originally postulated that one of the first steps in the transformation of teosinte to corn would see the fruitcases of the teosinte kernels being reduced to shallow, less indurated cupules with enlarged and membranous outer glumes. The large glumes evident on the prehistoric cobs may be evidence of this process (Beadle 1977:626).

Beyond this, there is also linguistic evidence pointing to teosi as an ancestor of corn. As pointed out by Wilkes (1967), in the Nobogame area of Chihuahua in Mexico teosinte is known as _madre de maíz_ or the mother of corn. While many may scoff at what may be a form of "cultural memory," anthropologists will verify the significance of this data. Claude Levi-Strauss has long worked with the cosmologies of many groups of people and has demonstrated numerous cases of myths and legends revealing a great temporal dimension (e.g. see Levi-Strauss 1968)..

At this point, perhaps enough evidence has been presented to cause one to, at least, re-examine Mangelsdorf's tripartite theory and maybe also look a little closer at the work of Beadle. However, let us examine some other work on primitive corn which has recently been reported. This new evidence is not geared toward substantiating a particular theory or point of view but does raise some important questions about interpretations supplied with the Tehuacan data. This discussion is brought up only to further urge people to look again at the Tehuacan data-- data which has all too quickly become a scientific "sacred cow" in its permeation of the literature.

Based on the Theuacan data it has long been assumed that agriculture in the New World first achieved a high level of productivity in Mexico. Other data also points to the Central Andes of Peru as a second important area. Certain new evidence (Zevallos et al. 1977), however, does not fit comfortably with such general assumptions. In fact, it down right contradicts these two areas as being the only centers of agricultural development.

In relation to this, it has long been known that pottery of more then rudimentary competence was widespread throughout the moist tropical zones of northern South America before 2,000 B.C. This date is far earlier then when it appeared in either Mexico or Peru and the pottery also occurs in contexts that indicate large populations and stable settlements. The latter two factors are assumed only to be made possible by an agricultural subsistence base. In the past, it has been suggested that this earlier ceramic tradition and corresponding large populations were made possible by a rich maritime resource oriented society (see Willey 1966:221) or some archeologists even attributed the early pottery to contact with Japanese (see Meggers et al. 1965). It is in this context that the new data takes on significance.

The most important piece of evidence, from the San Pablo site in Ecuador, is a charred kernel of corn which was originally recovered in 1961 but ignored by archeologists. Presumably the ignorance of this new data is a reflection of sciences willingness to be "led on" by Mangelsdorf and his associates as well as the Harvard axis of archeology. At any rate, the new San Pablo data fits within the Valdivia and Early Cerro Narrio archeological cultures which existed from 4,000 B.C. and 2,000 B.C. in Ecuador. The great antiquity of these cultures is buttressed by a very large and unusually consistent series of radiocarbon dates. There can clearly be little controversy on this point.

Contrary to most published accounts, P. Norton (1971) in one of the more accurate accounts of the archeology of the area points out that Valdivia sites are not uniquely or even typically coastal as most authors stressing the postulated maritime orientation would lead you to believe. Instead, the sites are actually located with reference to land suitable for agriculture. The large size, deep midden accumulations, and temporal stability of a majority of the Valdivia sites strikes Zevallos et al. (1977:386) as prima facie evidence for a developed agricultural rather than maritime orientation. This is especially true in view of the rather minor contribution that aquatic resources make in the excavated middens. Of the investigated middens of any size, only that at the El Encanto site would be classified as a shell midden and on close inspection this appears to be mainly a preceramic site with a thin veneer of subsequent Valdivia occupation. So, it seems as if the Valdivia culture was not supported by maritime resources as many have thought.

The other possible "explanation" for the well-developed ceramic complex was the hypothesis that through trans-Pacific contact Japanese had introduced pottery to the area. However, Carlos Zevallos (1962) and Donald Lathrop (1970) have both independently pointed out that archeological evidence dictates the Guayas Basin as the ancestral home of the Valdivia culture and its associated artifacts. Their research illustrates that known Valdivia sites on the coast and in the coastal river valleys are relatively late and marginal with reference to the problems of Valdivia culture origins. Therefore, the hypothesis of Japanese ancestry forced upon the well-developed ceramic tradition common to the area deserves no further scientific consideration. In many ways the Japanese contact hypothesis arises out of a tradition determined to discredit the ingenuity of Native Americans.

The Early Cerro Narrio culture and other closely related cultural materials are widespread in the southern highlands of Ecuador and date to 2,500 B.C. (sometime after the Valdivia complex). If we have eliminated the postulated maritime economy of Valdivia and associated later cultures as well as the theory of Japanese ancestry, we are confronted with the question of what supported these large populations and sedentary way-of-life responsible for the ceramic tradition? The answer is an early well-developed agricultural complex in Ecuador.

During 1959 and 1960 Zevallos excavated the San Pablo site and while studying the materials he encountered a large pot sherd comprising about one-quarter of a shallow bowl. Embedded within the outer surface of the sherd is a piece of charcoal contained within a slightly larger space or negative cast. As Zevalos et al. (1977:386) point out, certainly few charred plant remains come to archeology with more secure chronological and cultural credentials.

At any rate, the nature of the piece of charcoal and the space which surrounds it are such that these can only be identified as Zea mays which had been included in the clay paste and consequently was then carbonized when the bowl was fired. Galinat in 1974 identified this kernel as having been shelled from near the butt or tip of an ear of corn and also as a kernel that had been in the process of germination for about three days. The embryo, endosperm, angular abscission layer, and primary root are all quite visible.

The San Pablo site has also yielded pottery with distinct representations of corn cobs still in their husks as well as ceramics with the actual impressions of corn kernels forming a decorative applique. Charred cobs have also been recovered at the highland Cerro Narrio site. The San Pablo data is dated to 2920 B.C. and there is no chance that the corn bearing ceramics represent intrusions of younger materials as there is no later material at the San Pablo site. The corn type is an eight-rowed, large kernel corn as well as a second type which appears to be a 14-22 row pop corn (Zevallos et al. 1977:387).

When the single charred corn kernel, corn effigies from the pots, sherds with kernel impressions, and charred corn cobs are juxtaposed together an interesting pattern emerges. As mentioned above, two corn types are evident. From this we can assume that two very distinct races of corn were maintained in the area from at least 2920 B.C. In addition to corn, a well-defined technology was also present in the form of manos and metates as well as a lime source to soften the hard, dry kernels before grinding. The latter is available from the shells of small snails that were locally available and which were also recovered in great numbers at the San Pablo site. A large number of carefully constructed bell-shaped subterranean pits also indicate an extensive storage capacity.

It is in this context that Zevallos et al. (1977) point out that well-developed forms of corn appear in Ecuador over 1,000 years before corn of comparable type and protein capacity occurs in either Mexico or Peru! Returning to Mangelsdorf and his data, the reader must decide if we should continue to accept the "establishment view" which has been expounded upon for so long? Through this section, we have seen

Mangelsdorf himself switch positions; we have seen important assumptions of his tripartite theory become severely erodded; we have seen his interpretations of the Tehuacan archeological specimens called into question; and finally we have seen that the whole notion of the Tehuacan Valley as the center, and therefore model, for New World agricultural development severely shaken. It seems blatantly clear that we are left with two alternatives for explaining corn's ancestry and evolutionary development.

First, Weatherwax and his theory of corn, Tripsacum, and teosinte as evolving out of a common, now extinct, ancestor seems to have emerged unscathed in the review. Secondly, Beadle's work examining teosinte as the progenitor of corn has been shown to be entirely feasible. The question is, in what direction does this point future research at the National Colonial Farm?

The theory spelled out by Weatherwax is a distinct possibility, but in terms of botanical research it offers few alternatives. The only recourse would be to search the fossil record for a plant which morphologically could be the "missing link" between corn, Tripsacum, and teosinte. Assuming this plant could be found it would mean little more than the ancestor of the corn plant had been finally located and the debate settled. In other words, the recovery of the hypothesized extinct plant would do little more than make a good museum specimen which would no doubt be reproduced for years in textbooks and compendiums on the subject. However, this is not too important to a "living" museum such as the National Colonial Farm. From the other point of view, if the

National Colonial Farm were to base its future research on Beadle's arguments, distinct possibilities become present. For you see, if we were to proceed on the assumption that teosinte was once the progenitor of corn, the fact that teosinte is still present affords many opportunities for future research and experimentation. In essence, Beadle has just opened the proverbial door, and it will be up to others to carry on.

For now, however, we must move on to the development of corn into a major food crop by the American farmer and the world's scientists.

The Historical Period

At the hands of Native Americans, corn or maize reached a high state of development before the white man ever set foot on the soils of the New World. Out of the prehistoric development of corn from a wild plant all of the prinicpal commercial types of corn recognized today: dent, flint, flour, pop, and sweet, were already in existence when the early European explorers appeared on the scene. Although details of the production of these corn varieties are largely unknown, and will probably remain so forever, it remains a fact that the aborigines or "First Americans" were excellent corn breeders. Take a moment and reflect on the unbelievable phenomena of taking a wild grass and converting it into the basis for a major food crop which is today one of the pillars of our civilization.

When European colonists came to the northeastern United States they found Native Americans planting an eight-row corn. Acreage with this corn type also stretched into the upper reaches of the Ohio Valley as well as into the Mississippi and Missouri River valleys. This particular variety of corn, usually referred to as flint corn, possesses a smooth kernel crown. Perhaps the "flint" comes from the fact that the kernels are so hard that they have to be soaked or ground before human consumption. Beginning in the National Colonial Farm region and strectching southward a 16 to 30 row corn borne on large stalks was usually grown. This soft corn probably filtered up from Mexico via the Mississippi and Ohio River Valleys (Galinat and Campbell 1967:14). To the colonists this corn became known as "gourdseed" corn as the fruit somewhat resembles certain forms of gourds. If you visit the National Colonial Farm today during the growing season you will be treated to viewing one of the few remaining crops of this type of corn grown today. Other areas of extensive corn production included what is now New Mexico and Arizona as well as Mexico and South America. In all, by 1492 the Native American inhabitants probably were planting and harvesting about 20,243 hectares (50,000 acres) of corn.

Laying aside the question of corn's origin and development at the hands of prehistoric Native Americans, we are now ready to examine the improvement of corn by Europeans and people of European descent. Again, the improvement of corn during the historic period becomes a form of evolution directed by humankind. In relation to this period, without a corn's evolution during historic times was produced by Henry A. Wallace and William L. Brown (1956). In this section of the report we will rely heavily on Wallace and Brown's interpretations for the simple fact that their research and writing is unsurpassed.

The question which arises next is when did Europeans actually first come face-to-face with the corn plant? To the best of our knowledge the befuddled Christopher Columbus, thinking that he had landed on an outpost of Asia (actually he was on the present-day island of Cuba), was the first person to observe and write about the corn plant. This information comes to us from a secondary source but is assumed to be accurate. Unfortunately Columbus' original journals are lost, however, an abridged copy written by a priest known as Las Casas is considered to be a near duplication. Even with this, it seems that Columbus was not very impressed by corn as he mentions it only briefly and therefore his accounts are of little importance except in terms of their chronological precedence. Beyond this, it is also now known that Norse explorers definitely reached the New World before Columbus although written accounts of their voyages are not available. Quite possibly, they also landed well to the north of corn's habitat at the time and may never have observed the plant.

With the domination of Europeans in the New World, we should examine the various names attributed to Zea mays. Columbus first mentions seeing it on a November day in 1492. Because it was similar to some grains familiar to him in the

Old World, he referred to it as panizo or panic grass in his journal (Weatherwax 1954:1). It came to his attention when several members of a reconnaisance party on the present-day island of Cuba returned with some collected specimens. Because most other English speaking countries use the word corn to refer only to the hard grain of cereal plants in general, the Native American term for the plant, maiz or mais, was anglicized to maize. The "corn" that Joseph hoarded for Pharoah in the Bible is not American corn, but really a form of wheat. Before European contact with the New World in 1492 corn (Zea mays) was unknown to the Old World. Therefore, we must remember that in the United States corn is corn, but to many others the word corn refers to any cereal plant and our corn is known as maize. In fact, the problem of what to call our corn so confused the early botanists that at least seven different spellings of maize appear in the early literature (Weatherwax 1954:3).

With this out of the way, Peter Martyr who was a young Italian scholar and counselor to the Spanish court, gives us our best early descriptions of corn. Martyr had the opportunity to interview Columbus personally, read the original journals of the first voyage, and talked with sailors and other members of the expedition. In the latter part of 1493 he wrote a series of letters which told of corn's discovery. The first pictures of corn were produced in 1554 in Ramusio's Italian translation of the accounts of the New World written by the Spaniard, Gonzalo Fernández de Oviedo y Valdéz. Las Casas, the re-writer of Columbus' journals, also wrote extensively on corn.

From early English explorers and colonists settling in the northeastern United States several reports of early corn are known. Captain John Smith of the Virginia Colony made several mentions of the plant and Governor William Bradford of Mayflower fame discusses, in his journal, the corn plant. In the latter case, corn was essential for the survival of the colony. Thomas Hariot, however, probably supplied the best accounts of corn in North America. In 1590 Hariot published a book titled, Narrative of the first English Planting of Virginia which also contained some of John White's famous illustrations of plants (including corn), animals, and the peoples of America.

Soon after this period, mentions and complete descriptions of the corn plant begin to appear in all of the great European herbals which were being steadily produced. For example, corn was described in detail in the famous Krautebuch of Tabernaemontanus published in the late 1500's. The author obviously yielded to his enthusiasm in devoting five and a half folio pages to corn and also included 13 illustrations in his treatment (Zirkle 1952:8). Mangelsdorf (1974) also cites an early, especially interesting description of the plant published in 1619. H. Lyte describes corn as follows:

> This corne is a marvellous strange plant, nothing resembling any other kind of grayne; for it bringeth forth his seede cleane contrarie from the place whereas the Floures grow, which is against the nature and kinds of other plants, which bring forth their fruit there, whereas they have borne their Floure ...at the highest of stalks, grow idle and

> barren eares, which bring forth nothing but the floures or blossomes (Lyte 1619).

If Columbus was not impressed by corn, the early botanists certainly made up for his lack of enthusiasm.

With this brief description of corn's introduction to the Old World complete, we will move ahead in years and examine the development of corn as a major subsistence crop in the Americas. As mentioned before, the Native Americans presented the colonists with all major types of corn recognized today.[4] With this gift, the American farmer and the world's scientists created what is now the world's third most important grain crop. As Wallace and Brown point out, decade by decade, beginning in 1718, the progress of American civilization was measured by the western expansion of the corn acreage and out of this resource came the vast quantities of animal protein which give the American people their unique vigor (1956:11).

Although the Native American corn was genetically equivalent to modern commercial varieties, improvements of yields and various other factors remained to be accomplished. In a sense, our ancestors undertook to create a process of evolution culminating in a much more productive corn. But where did this idea to produce a better corn come from? Wallace and Brown attribute this concept to stimulation arising through the scientific advances of this age (1956:44).

It seems that the scientific atmosphere after 1674 was rarefied when the Dutchman, Leevwenhoek first observed one-celled creatures through his microscope. Suddenly, thinkers were beginning to ask thousands of questions and also devise experiments to gain answers to those questions. The appreciation of the fact that plants of the New World differed greatly from those of the Old World also stimulated scientific interest. In reality, these two advancements were only steppingstones in the creation of scientific curiosity and probably not causational variables. There is no simple answer to the question of where the stimulation to produce a better corn came from. It is, however, evident that over the entire Western world people were beginning to think and observe in new ways. It will be our task to document this phenomena in relation to corn.

It seems that the 1700's were benchmark years in the improvement of corn. During this period we have the first scientific observers of sex in corn. All three of the American men responsible for these observations were somewhat nonconformists (Wallace and Brown 1956:44). Perhaps, however, when one reviews the history and nature of scientific innovation, this is always the case.

Chronologically, Cotton Mather was the first to observe, question, and write about the effect of corn pollen from one plant falling on the silks of another type of plant. This is the same Cotton Mather who was also a Puritan zealot condoning the prosecution of "witches" and the barbaric treatment of people of opposite faiths in colonial Massachusetts.

Mather had noticed in 1716 that in a neighbor's garden when one row of corn was planted with red and blue varieties and the remainder of the plot was planted in yellow corn, the yellow corn had its kernel color changed by the blue and red corn. The color change was also stronger on the portion of the garden which the wind usually blew toward and weaker on the side away from the wind. Therefore, Mather deduced that the wind must carry the fertilizing agent of corn from one plant to another. Information on his conclusions was made available in a letter written in 1716.

In 1724, eight years after Mather's contribution, Paul Dudley came out with a more precise account of sex in corn. It is interesting to note that Dudley was also a bitter enemy of the Mather famiy. However, like Mather he was a refined gentleman and scholar who belonged to the prestigious Royal Society of London. Through experimentation Dudley was able to eliminate one of the hypotheses which had been employed to explain the mixture of various corn varieties. It seemed many people had not read Mather's previous data on the subject.

Anyway, along the banks of a broad ditch he observed two different varieties of corn growing. Since the ditch of water was between the two corn types he could argue that the mixed colors evident on the kernels were not the result of the rootlets of different strains fusing underground. Although this should have been deduced from Mather's writing, the myth that corn was fertilized through its roots was common at the time of Dudley's report.

The last of the three innovators was an extraordinary

Irishman and Quaker named James Logan. If Logan had not suffered persecution for his faith in Ireland, he probably never would have come to America with William Penn as Penn's secretary, nor would Logan have conducted the first true scientific experiment planned and implemented to answer a specific question about corn. As Wallace and Brown report (1956:49), Logan in his own 10.2 by 20.4 meter (40 by 80 feet) backyard in Philadelphia, in 1727, performed an experiment with corn which was referred to for many decades afterward.

Through a series of four hills of corn which he planted, Logan set out to prove the role of silks and pollen in the fertilization process. Another noted gentleman of the time, M. Geoffroy, held that corn kernels were formed independent of silks on the ear. Logan, by detasseling, covering ears, and removing silks on various plants proved precisely the female functions of the silks and the ovules to which they led. Results of this experiment were then conveyed to Peter Collinson who was a Quaker exporter of textiles and importer of plants living in London. It was Collinson who put Logan's account of his 1727 experiment into the British publication, Philosophical Transactions, in 1736.

Based upon the knowledge gained in these experiments of the 18th century, scientific corn improvement was consciously initiated in the United States. In this report, we will go through the history of this process in chronological order. Many students of the corn plant like to examine the historic period from the perspective of different breeding methods.

However, this method sometimes becomes confusing as one is forced to shift back and forth between different time periods.

One of the first settlers to practice the mixing of corn varieties was Joseph Cooper who farmed in New Jersy, across the river from Philadelphia (Mangelsdorf 1974:209). In the first volume of the proceedings of the Philadelphia Agricultural Society published in 1808, Cooper described how he mixed a tropical flint variety of corn from Guinea and the larger and earlier corn typical to his region. By saving seeds from the plants which produced the greatest quantity of corn and which ripened first he found that his production capacity was greatly increased. According to Mangelsdorf (1974:209), this is the first recorded attempt at combining earliness and multiple ears. Cooper's accounts were also repeated in several publications and his work undoubtedly influenced many other scientists and farmers.

Another American, John Lorain, beginning in 1812, also began to mix different varieties of corn. A discussion of his work really serves to illustrate how the new country's people mixed the different varieties of corn gained from the prehistoric Native American populations. As Wallace and Brown point out, this mixture, made partly by design and partly by accident, in the states of Maryland, Pennsylvania, Virginia, and Ohio, eventually took over, at the very least, four-fifths of the Corn Belt (1956:54).

Lorain, as it turns out, lived on the southern border of Pennsylvania. This area of the United States is known as an "ecotone" or transitional region between the warmer southern climates and more harsh northern weather. The climate is such that it allows the growing of both gourdseed and flint corns. Lorain saw the results when the two varieties were mixed in their natural process of cross-pollenation. He was so impressed with the new corn that he deemed it possible to harvest 160 bushels of corn per acre where only 100 bushels of gourdseed or flint had grown before. In a book published in 1825, after his death by his widow, titled Nature and Reason Harmonized in the Practice of Husbandry, his observations on the corn of the region and how to improve it were laid out.

Here in the writings of Lorain from 1812 to 1823 we find set forth the objectives, materials, and methodology which were to govern, for the next century, the breeding of corn in the United States (Wallace and Brown 1956:56). In agreement with many other writers, no man before, and for a long time afterward, saw so clearly just how different varieties could be combined to produce beneficial new strains. As Wallace and Brown state (1956:56), Lorain almost seemed to have prophetic visions of how these combinations would create the dent corn which would completely replace the slender cobs of 8-12 row corn grown by the Native Americans in the Midwest with the 14-24 row new dent corn (called dent because of the indentations near the end of the cob).

One can not drop the interesting subject of Lorain without briefly discussing his life history. It seems he was brought to this country as a child from England and originally grew up and farmed on the eastern shore of Maryland. However, he found the climate in Maryland to be to his unliking so he later moved to the outskirts of Philadelphia where he also farmed as well as wrote on agricultural science and opened a store. When he left Kent County in Maryland for Pennsylvania he freed his slaves in light of his convictions against bondage. As he became well-known, Lorain also had the chance to make contacts with many influential people of the day, including Thomas Jefferson, George Washington, and John Bartram. As with many scientists of the time who have been overshadowed by the politicians and radicals, Lorain certainly deserves more credit then he has received in the histories of our country.

After Cooper and Lorain had made their respective cases for the mixing of corn types, the next person of significance to work with corn was Peter Browne. Browne, even though he was a professor of Geology and Mineralogy, made numerous observations on the corn of his home state, Pennsylvania. His statements were wide-ranging and touched on the probable origins of corn as well as descriptions of then-current methods of culture and types of corn extant in his state (Wallace and Brown 1956:61). Browne listed and described 35 different types of corn, mostly representing combinations of gourdseed and flint types, and also reported unique types such as Cooper's Guinea corn and a type of pod corn he had read about. Beyond the Appalachian Mountains, R.H. Hendrickson of Middletown, Ohio, was also beginning to mix corn types like the farmers and scientists of the eastern United States.

However, in Great Britian, perhaps the greatest scientist of our time, Charles Darwin, was laying the foundations for the even greater improvement of corn. Darwin, who is principally known for his work on evolution and natural selection, also came out with a book in 1876 titled, The Effects of Cross and Self Fertilization in the Vegetable Kingdom. This volume is of such great importance because Darwin worked carefully (for his day) and quantitatively with many genera, including *Zea mays*. In corn plants which were cross-pollenated Darwin noticed an interesting phenomena; crossed plants grew some 20 percent taller than the self-fertilized plants. This effect, later to be known as hybrid vigor, planted an idea which sprouted in Michigan, grew in Illinois, expanded in Connecticut and Long Island, and finally reached fruition to the amount of half a billion bushels of corn a year in the Corn Belt (Wallace and Brown 1956:64).

In essence, Darwin pointed out that cross-fertilization results, in many cases, in increased size, vigor, and production as compared to self-fertilization. Although he did not know this was due to differences between uniting gametes, Darwin's research and writing on the phenomena with corn made numerous improvements possible. In other words, Darwin was the first to establish or define a recognized pattern of behavior in corn which was then utilized by many other scientists (Shull 1952:13). Technically, heterosis is the term for the process of developmental stimulation from the union of different gametes in the plant, and hybrid vigor denotes the magnificent effects such as increased size and production that are evident (Jugenheimer 1976:56). By whatever name you wish to call it, hybrid vigor or heterosis, Darwin is responsible for defining a pattern which had been undoubtedly observed but not recognized by millions before him. Perhaps, this ability to recognize simple patterns in a complex universe lies at the heart of scientific epistemology and also serves to mark the great scientists of our time.

At any rate, the maturation of Darwin's statements were not long in coming. In terms of corn, a direct connection can be established between Darwin and William J. Beal. Maybe the link between the two was Asa Gray, the famous naturalist, who was Beal's professor at Harvard. Gray kept up a lively correspondence with Darwin and was, in fact, considered Darwin's main ally on the evolution issue in the United States. We do not know what influence Gray had on Beal's acceptance of Darwin's work, however, it must have been substantial. It is known that Beal obtained a copy of Darwin's book on cross and self-fertilization and immediately published an article that is little more than a paraphrase of what Darwin had originally published.

As a professor at Michigan Agricultural College, in 1877, Beal conducted experiments that undertook the first controlled crosses between varieties of corn for the sole purpose of increasing yields through hybrid vigor (Wallace and Brown 1956:69).

In 1876 Beal reported the conclusion of his first corn experiments and stressed the necessity of parental control in improving corn yields. This is in direct contrast to the other method of increasing yields which involved saving the best seed from the crop which was then planted the next season. With the encouragement of Darwin for his work, he and his co-workers then went on to try and sell the concept of hybrid vigor, what Beal referred to as "controlled parentage," to the American farmer. As with many innovations, however, the acceptance of this concept would take time.

Meanwhile, we have to leave the halls of academia and return to the corn fields to document what was happening next in corn's development. As it turns out, partly by accident and partly by design, most of the northern flint and southern gourdseed germ plasm found growing today in the United States passed through the hands of three men: Robert Reid, George Krug, and Isaac Hershey (Wallace and Brown 1956:80).It is this story which we now must review.

In 1864, Robert Reid who was the father of James Reid moved from Ohio to Delavan, Illinois. Like most pioneers the Reid family carried with them their seed for the first crop in their new location. The variety they carried was known as the Gordon Hopkins strain. Now the Reid family arrived in Illinois quite late in the season but still planted the seed anyway. This late planting, however, resulted in an immature crop of corn.

During the next growing season the Gordon Hopkins strain was again planted while missing hills were seeded with a local variety of corn known as Little Yellow. The resulting cross-pollenation of the two diverse strains produced a hybrid stock of germ plasm. In the years that followed the two Reids (James did the majority of the work) eliminated the reddishness in the Flint-Gordon Hopkins mixture and selected for a corn which was early and smooth. Out of this corn would come a strain which has served as a major source of material for present-day hybrids.

James Reid left the home fields and started farming for himself in 1867. Ten years later he grew a field of corn, employing his father's strain, which yielded 125 bushels an acre versus the average Illinois yield of only 27 bushels per acre (Jugenheimer 1976:76). The amazing fact is that this remarkable crop was produced without modern fertlizers or special cultural methods. This development of what became known as Reid Yellow Dent is an excellent example of the effective use of selection. Reid took the basic materials developed in his father's fields and fashioned a world famous corn.

Basically, Reid was convinced his father had already blended the essential elements necessary for a better type of corn. Perfection of the strain was now only a matter of selection. For example, to illustrate the care Reid exercised it was a fact that he never planted his crop in a field exposed to his neighbor's pollen even if it meant giving seed away. He was also so careful about his seed stock that it was kept between the two mattresses of his bed during the winter. All of this work paid off as Reid's corn was a consistent winner at corn shows (including the Chicago World's Fair). With this fame it quickly gained acceptance because of its field performance and fine feeding qualities.

Surveys indicate that Reid's corn and selected strains were grown on about three-quarters of the corn acreage in the Corn Belt over a 50 year period. In 1937, 27 years after Reid's death, the Reid Yellow Dent variety was still recommended by experimental stations in 21 different states (Jenkins 1936:455). Many inbred lines employed for future hybrids were developed from strains of Reid's corn. One of these inbred lines, WF9, was developed from the Wilson Farm strain of Reid Yellow Dent and is the parent of a substantial portion of all hybrid seed (Jugenheimer 1976: 76). Because of the country's debt to Reid, a bronze tablet was dedicated on the original Illinois farm of Robert and James Reid.

One man, however, did develop an improved strain of Reid corn. This quiet retiring farmer, George Krug, combined a Nebraska strain of Reid corn with Iowa Gold Mine to create the highest yielding strains of non-hybrid yellow corn ever grown (Wallace and Brown 1956:84). The Krug strain actually increased Reid's yields by ten bushels an acre.

Next, after Reid and Krug, the cornbreeder whose corn most affected modern hybrid strains was Isaac Hershey who was a Mennonite in Lancaster County, Pennsylvania (Wallace and Brown 1956:88). Into an original mixture of late, rough, large-eared corn and early flint corn Hershey added about six other varieties. After this, he stopped introducing new strains and began selecting for earliness and freedom of disease. Because of these qualities, his new corn was known as Sure Crop. F.D. Richey of the United States Department of Agriculture became impressed with the corn's performance and began inbreeding it for use in hybrid varieties.

An interesting phenomena of the early 1900's, before we move on to the hybrid period, was the corn show. Based on accepted standards which somehow grew out of these shows, uniformity of both ear and kernel type became the objective of almost every corn breeder during this period (Wallace and Brown 1956:102). Ironically, in striving for uniformity, yields were often sacrificed for the personal pride of winning a corn show. However, as Henry Wallace pointed out, 85 percent of the corn that was grown was fed to livestock which are not impressed in the least by the appearance of the ear.

With this, we may now move on to the story of hybrid corn. Although hybrid corn was a tremendous improvement over all the corn which had preceded it, a great debt is owed to the farmers and scientists who had participated in all of the advances up until the 20th century. Many people shared in the responsibility for improving corn as dictated by the new environment where it was expected to grow as well as in meeting the demands placed upon the American agricultural system for feeding the growing population of the country. The nation now streched to the Pacific Ocean, populations were steadily rising, and the nation's industrial growth was steadily sapping the rural populations as the factory work forces expanded.Now, more than ever, production yields needed to be increased to feed the growing country.

Wallace and Brown (1956:6) have reminded us of what corn was like before the hybrid era. They state in those days when one examined corn ears some ears were covered by many husks, and some ears only had a few short husks. Still other ears were borne at the ends of branches or shanks. By early fall, these ears on long branches would almost be lying on the ground and the ears on the short shanks would point straight into the air with water gathering at their bases causing mold and rot. Some shanks would be thick and hard to break at harvest and others would be so thin that the slightest touch would cause the ear to drop. Main stalks would also frequently blow down before the harvest because of the differential nature of the roots. Of course this corn was a great improvement over what the country had started with, however, a new corn was also on the horizon.

With this, the development of hybrid corn and the Corn Belt as one of the world's great agricultural regions is the result of the work of many individuals. One line of descent has to begin with Darwin and his work on hybrid vigor and follows in the work of Beal. However, as a device for increasing corn yields the method of crossing two open pollenated varieties of genetically heterogenous corn adovcated by these two gentlemen was not completely effective. Crosses were more productive than their parents but improvement was still possible.

George H. Schull of the Carnegie Institution made the needed contribution by way of an unexpected result from theoretical studies on inheritance he began in 1904. As with most scientific accomplishments many of the foundations of his work were laid down in the experiments of other scientists; this time Francis Galton and Wilhelm Johannsen. According to Mangelsdorf (1974:212), Galton realized that the progeny of parents above or below the average in any given character tend to regress toward the mean or average. This regression, however, is seldom complete and it was Johannsen who saw in those circumstances an opportunity for controlling heredity through the selection in successive generations of extreme variations from the average. In time, Johannsen's ideas became known as the pure line theory.

Shull's contribution was the application of the pure line theory to corn. He achieved spectacular results, though probably unpremeditated, when he experimented with the objective of analyzing quantitative or "blending" characteristics. To accomplish this goal Shull chose the number of kernel rows on an ear of corn as the object of study. In practicing artificial self-pollenation to produce line breeding true for various numbers of kernel rows he in effect isolated pure lines of corn. After this, as a first step in studying the inheritance of kernel row number, Shull then crossed two pure lines to produce hybrids which were quite uniform like their parents, but unlike their parents they were vigorous and productive.

Realizing his discovery, Shull published two papers in 1908 and 1909, proposing the isolation of inbred strains through self-pollenation and then crossing two of the selected inbred strains. The seed of this first generation cross, because of optimum hybrid vigor, would then be used in planting. Much like the original conceptual milestone of selecting for an improved corn, the idea of maintaining otherwise useless inbred strains of corn solely for the purpose of utilizing heterosis resulting from their hybridization is quite revolutionary and a creative achievement of the first order (Mangelsdorf 1974:212). Technically, this method of producing corn is known as a single cross.

It was Edward East, however, who did so much to point out the benefits of this new method. Without a doubt, the initial discovery of the importance of inbreeding belongs to Shull, but it was East who sold the benefits of this technique to the cornbreeders. At the Connecticut Experimental Station, East, in many ways paralleling the work of Shull, soon had also discovered the benefits of crossing inbred strains. It was East, however, who probably really recognized the significance of his work and developed interest among seed producers for hybrid corn (Wallace and Brown 1956:111).

However, even with this method of crossing inbred strains (the single cross), seed production was still rather expensive. As evidence of this, seed produced by this method was so expensive that it was sold by the thousand rather than by the bushel. A more inexpensive and practical method was needed. It remained for Donald F. Jones, working at the Connecticut Experimental Station (a student of East), to come to the aid of Agriculture in 1915 when he proposed a double cross which combined four inbred strains in a hybrid of two single crosses. As one can easily see, this is an ingenous way of making a small amount of single crossed seed go a long way, i.e. a few bushels of single cross seed can be converted to several thousand bushels of double cross seed. Ironically, soon after the use of double crosses established the production of hybrid corn, breeders found that by developing more vigorous inbred strains then originally isolated by early breeders and by employing cytoplasmic male sterility to avoid detasseling, single cross corn was once again feasible.

In all, by 1950, more then three-quarters of the total corn acreage in the United States contained hybrid corn. Today it is very hard to find a field which does not contain hybrid corn. As always, corn improvement is not standing still and resting on its past accomplishments. The quest for a better corn goes on today.

For example, astounding developments in agriculture today are again possible with research now being

sponsored by the Pioneer Hybrid Seed Company (see Doebley et al. 1979:186-187). Through the foresight of this company plant collecting trips have been sponsored to Mexico where a new teosinte (<u>Zea diploperennis</u>) which is described as a corn-like, robust, erect, and possessing a chromosome number of 20 (diploid); most important, it is also a perennial plant. The implications of this discovery, beyond giving clues to corn's origin, are very important. Because the plant has a like number of chromosomes and is fertile with corn it provides valuable germ plasm which may very well lead to the development of a perennial corn plant (Doebley 1979:187). Because this new plant would be a perennial instead of an annual, a great amount of time, money, and fuel, would be saved in the plowing under of old crops and sowing of new every year. This would be eliminated as a perennial corn would reappear every year. We truly may be on the verge of another revolutionary development in American Agriculture.

Concluding, we have briefly reviewed corn's origin and evolutionary development in this paper. Reflecting for a moment, the Native Americans who gave us this plant had, over thousands of years, entered into a special relationship with their life-supporting maize. The early pioneers of farming and science also embraced a similar view of corn. However, as corn passed out of prehistory and the historic period into modern industrial society, much of its former dignity has been lost. Perhaps if this report has accomplished nothing else, it will serve to remind us of the great heritage of this interesting and important crop. It is important that this tradition be maintained for the future.

Footnotes:

Number 1-When I say we have quite literally erodded away much of the genetic vitality associated with corn, I mean Native Americans, colonial farmers, and modern breeders. In the process of creating our modern corn plant much of the natural vigor associated with plants in the wild has been lost.

Number 2-Mangelsdorf suggestion (1974) follows a plan of research originally outlined by Alphonse De Candolle.

Number 3-Teosinte is the colloquial name for Euchlaena. As most of the literature refers to this plant as teosinte, we will also follow this practice.

Number 4-When I say that Native Americans presented us with all major known types of corn today, I mean this in the sense of genetic material. All genetic strains were developed by the Native American populations, however, an enormous amount of improvement in terms of the scientific manipulation of this stock has taken place since.

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