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RACES OF MAIZE IN SOUTH AMERICA

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SOUTH AMERICAN highland maize has long attracted attention because it differs so greatly from the maize commonly grown in North America and Europe. Following the discovery of teosinte, Mexico and Central America were considered of greater importance in the study of the origin and evolution of maize. Interest in South America as the original home of maize, however, has been renewed since Mangelsdorf and Reeves published their tripartite hypothesis (1939): that maize originated in South America; that Euchlaena is a recent hybrid of maize and Tripsacum produced in Central America by the crossing of cultivated maize with native Tripsacum; and that the addition of Tripsacum germplasm to maize produced the types of maize which are now most common in Central and North America. With their hypothesis as a basis it has been possible to carry on a program of study and experimentation which has led to a more complete knowledge of the composition and distribution of South American maize and related grasses, and to further evidence which has a bearing on the origin and dispersal of maize. Since 1939 a surprising

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amount of new information about maize has been obtained and, for the most part, it fits the Mangelsdorf and Reeves hypothesis better than any other. It is now possible at least to outline the characteristics of some of the major races of South American maize (Coroico, Guarani, Coastal Tropical Flint, Altiplano, Uchukilla, Valle, Cuzco) as a result of this study.

At various times in the past, scientific names have been proposed for certain groups of South American maize. Most numerous are the names based on collections made by the Russian expeditions of 1925–26 (Kuleshov 1930, Kozuhkov 1935). While these names may have been of some value in calling attention to certain peculiarities, they do not group the variations into practical working divisions or reflect natural relationships. As Anderson and Cutler pointed out (1942), it is too early to attempt an accurate classification of maize since good material is still lacking from critical areas, and some of the material now available is as yet incompletely studied. Also, many of the characters essential to a careful and conservative analysis of the relationships of races in Zea are imperfectly known and rarely utilized. To propose taxonomic categories and increase the confusion of synonymy which already clouds *Zea Mays* L. is unwise while critical studies are still in their primary stages.

Constancy and changeability of Maize varieties

Scarcely less amazing than the great diversity of maize which is familiar to all students of the plant is the fact that so many of the varieties cultivated today have remained constant over so long a period of time. Indian fields form plant populations where optimum conditions for the evolution of new races are present. Here are centers where plants grow isolated from their relatives cultivated by other Indian tribes or by other divisions of the same tribe, and where there is only occasional interchange of seeds as the result of war or commerce. That more races have not arisen is probably the result of rigid and constant selection toward definite standards. These standards vary in different districts and even today are often regulated by traditions and religious beliefs. Branched ears are preferred in some parts of Guatemala while in other areas different types are chosen. Ceremonial customs play a definite part. Large ears are often dressed in clothes and placed on an altar or carried about during a dance, then kept for planting the next season. Giving the best ears to the gods means that a standard of quality is maintained, but since many ears are planted, there is still room for considerable variation. Present day natives are not as careful as their fathers, for in addition to forgetting many customs which had a practical foundation, they have lost some of their hostility toward outsiders and frequently interchange products. They may even spend part of their time working in mines or in rubber or cattle areas, and when they return to their own land carry with them seeds of foreign origin. In most cases it is possible to determine which are the recently introduced varieties.

Prehistoric migrations of crop plants were probably slow, but new modes and routes of transportation and the destruction of many regional barriers have led to the rapid interchange of plants and weeds with the consequent introduction of new types. Many of the old cultivated plants have been discarded in favor of the new. Even where new plants have not appeared changes in customs may handicap the collector of old forms.

A case in point is sugar corn in Bolivia. Sugar corn was once highly prized in Bolivia for parching and especially for making *chicha*, an alcoholic drink. When the Incas ruled and thievery was punished severely, sugar corn was easily kept in a fairly pure condition simply by growing it in isolated fields. Now, in order to conceal it from thieves, it is planted amid the less desirable field corn, which has a similar appearance and which flowers about the same time. The crop is safeguarded by this practice since thieves are unable to distinguish the sugar corn in the field, but another result is that one now rarely sees ears of sweet corn which do not show contamination with other varieties. Similarly, sweet grains are of sporadic occurrence in nearly all the other races of maize in Bolivia and Peru.

Almost the same story can be told of *culli*, a deep reddish-purple type, which, like sweet corn, was once prized and maintained in a more or less pure state. Now it, too, is contaminated with other varieties and has left its mark upon them as well.

Methods of collecting and study

For reliable studies of the races of maize, their origin, spread and present distribution, it is necessary to have extensive data. Hasty trips through markets may serve to collect an impressive mass of ears and seeds which are useful for some studies but fail to tell the whole story. In spite of the selection of fairly uniform ears by native planters, the amount of variation in their fields is astonishing to one accustomed only to commercial maize plantings in the United States. An ideal collection would include some indication of the character of the plant and the amount of variation in a typical planting, the tassel, and some indication of the genotype of the plant for characters may be concealed by dominant alleles, dominant inhibitors or strong expressions of other genes which affect the same parts. Since some of these data can be secured only after long study in the field and by growing cultures under controlled conditions, ideal material for study is rarely seen. It must be recognized further that a collection of plants is rarely a random sample of the population. Botanists have more or less innocently practiced misrepresentation for many years by selecting specimens of a convenient size or those which were the most attractive, the most nearly perfect or the most unusual, even when these were unique in the population they were supposed to represent. Thus, in the case of maize, colored or freak ears frequently receive more attention than normal ones. For example, in a harvest of 8000 ears at Santiago de Chiquitos, Bolivia, only four ears differed from the predominating type, yet in a collection representing this lot three of the atypical ears were included and only four of the major type.

The present paper is based upon collections made and studied in South America and checked by growing plants in the same or similar localities; and upon collections at the Botanical Museum of Harvard University, the Escola Superior de Agricultura Luiz Queiroz in Piracicaba, Brazil, the Instituto Agronomico of Campinas, Brazil, the Missouri Botanical Garden, the Pioneer Hi-Bred Corn Company, and the Universidad Autonoma Simon Bolivar at Cochabamba, Bolivia. Through the kindness of the directors and staff of the Escola Superior de Agricultura and the Universidad Simon Bolivar, it was possible to grow and study native maize in their experimental fields.

The valleys of Peru and Bolivia have long been supposed to possess the greatest diversity of maize types and for this reason much emphasis has been laid upon this center, while little attention has been paid to the maize of the eastern Andean slopes and the adjacent lowlands. It is true that the highland areas do have a large number of visibly different types, but one must consider also the invisible variation, that which is recessive and masked by a few dominant characters, or is concealed by the action of inhibitors. From a few selected ears of lowland Bolivian corn nearly all the variations found in the valleys and highlands could be produced, as well as variations which are found in no other place but the lowlands.

Variations in the nature of the ear

The structure of the maize ear has, in the past, been poorly understood by many botanists, probably because it is difficult to study the mature and woody ear. Recently, the work of Weatherwax (1935), Anderson (1944) and Mangelsdorf (1945) has done much to demonstrate the true nature of its structure, but the general opinion persists that the origin of the ear must have been unique and nearly miraculous. That this is not the case is evidenced by the fact that ear-like structures may be found in grasses which normally do not bear them.

St. Augustine grass, *Stenotaphrum secundatum* (Walt.) O. Kuntze, a member of the Paniceae, usually has two rows of solitary fertile spikelets in alveoli on a flattened corky rachis. A variation occasionally found (although not as common as one with paired spikelets, one sessile and the other pedicellate) has four rows of alveoli on a much broadened and thickened rachis which has little tendency to disarticulate.

In the genus Trichachne, also in the Paniceae, there is an even more striking resemblance to the maize ear. This does not imply that this grass is concerned in the evolution of maize, but merely shows that the development of the ear and tassel as female and hermaphroditic or male inflorescences is not as difficult as might be thought. In this genus there may occur the usual normal plants with ordinary hermaphroditic inflorescences, plants with a lateral "ear" and a terminal hermaphroditic inflorescence or tassel, and plants with "ears" borne terminally and without a tassel. The internode pattern of normal plants of Trichachne follows that of ordinary grasses; the pattern of plants with the lateral "ear" and a terminal inflorescence follows that of the usual maize plant, and the pattern of plants with the terminal "ear" closely adheres to the pattern established by maize plants with terminal ears. The "ear" in Trichachne is a fasciation in which longitudinal growth is halted so that the inflorescence is enclosed by the leaves of the culm on which it is borne. It is significant that anthers do not develop in the "ears" although some of the seeds are nearly normal in size and apparently variable. Trichachne has been collected in both the fasciated and ordinary form in Jamaica, Surinam, Bolivia and the states of Ceara, Baia, Goiaz and Mato Groso in Brazil. Detailed information upon it will be presented in a later paper.

Maize in South America may be considered as influenced by three tendencies which may be termed Tripsacoid, Andropogonoid, and fasciated. Mangelsdorf and Reeves (1939) have postulated that there is some Tripsacum influence in North American maize, and suggested that some South American maize in the Andean region is also contaminated, but to a lesser degree. Further evidence supports this theory. The similarity of much lowland maize, especially that of Paraguay and Bolivia, to segregates from maize-teosinte crosses; the occurrence of *Tripsacum australe* Cutler and Anderson, a species without terminal chromosome knobs (Graner and Addison 1944); and morphological similarities between *T. australe* and some of the South American varieties of Zea suggest two possibilities. Either there is considerable Tripsacum contamination which cannot be correlated with chromosome knobs or some types of South American maize show resemblance to Tripsacum because they are not distantly removed from it. The great diversity in *T. australe* suggests that in South America, as in Central and North America, Zea contamination has probably increased the variability of Tripsacum. The most obvious effects of the Tripsacoid tendency are compression and condensation, with hardening of the parts, straightening of rows, reduction in row number, shortening of pedicels and sinking of parts into pits or alveoli on the rachis. Tripsacum, Zea and related grasses probably had some common ancestor and it is usually impossible to decide definitely how some particular variation might have been introduced.

The term "Andropogonoid" is not meant to suggest that this tendency is derived directly from the genus Andropogon or even from the family of this name, but the effect is so reminiscent of some Andropogons that it is well to keep the similarity in mind. The Andropogonoid tendency is toward freely branched parts, long pedicels and fibrous, as opposed to brittle parts.

A type of fasciation in which there is shortening of the longitudinal axis with continued development of the parts probably plays a much greater role in maize than is usually admitted. The origin of the ear as a fasciation was suggested long ago, but received little serious consideration. Recently, Anderson (1944) suggested that Mexican Pyramidal maize is fasciated. Fasciations occur frequently in other wild and cultivated plants (White 1945). A familiar example is cockscomb, which is rarely seen except as a fasciated plant. *Oca*, an oxalis cultivated in the Andes and parts of Mexico, produces its best edible rhizomes on plants with fasciated stems. The ear-like structure of Trichachne is probably a fasciation. Fasciations may be produced by the environment or be hereditary (although some of the hereditary ones appear only under certain conditions), and probably possess modifiers. If a primitive maize was a fasciation, it would have been in the homozygous condition when removed from its relatives and now would give little indication of being a fasciation. Besides this, the fasciation, if it acted like the one described in Trichachne, would hasten the divergence from its parent forms. Within the ear the anthers might become non-functional, although the seeds would continue to be produced. Tassel glumes, lemmas and paleas are loosely wrapped about large seeds so, if the size of seeds were increased, birds and insects would soon eliminate those plants which bore large seeds exposed on the tassel.

The general characteristics of South American maize

The Plant

Ordinarily the length of time to maturity is correlated with the number of leaves and the height of the plant, but when maize is grown under conditions differing from those of its natural habitat, this relationship is less exact. Maize from low altitudes requires more time to mature in high latitudes, while maize of temperate zones is precocious and dwarfed in the tropics. Plant height is directly related to length of season if allowance is made for the tillers. The races of maize described below vary in the length of time to maturity. Altiplano maize requires about 44 days from seed to first silk; Uchukilla, 56; Valle, 55 to 130; Guarani, 55 to 100 or more; Cuzco, 90 to 140. Coroico maize grown in Cochabamba was the latest and most tillered of all the races. While many of the plants had silks after 90 days, some required 140 before the main ear silked, and ears on the tillers were still far from this stage.

Tillers range from small basal shoots which never tassel or bear ears to stalks indistinguishable from the primary axis. Tillers are common in lowland maize. One plant of Coroico maize had twenty nearly equal tillers and many plants had five or more. Although all these tillers were basal, one may consider these plants as tending to branch from the stem, for the shanks of the ears were greatly elongated on many plants. Seedlings and very young plants of Coroico maize have laterally flattened culms, as compared with the terete ones of most other types. This resembles some grasses and probably is correlated with tillering.

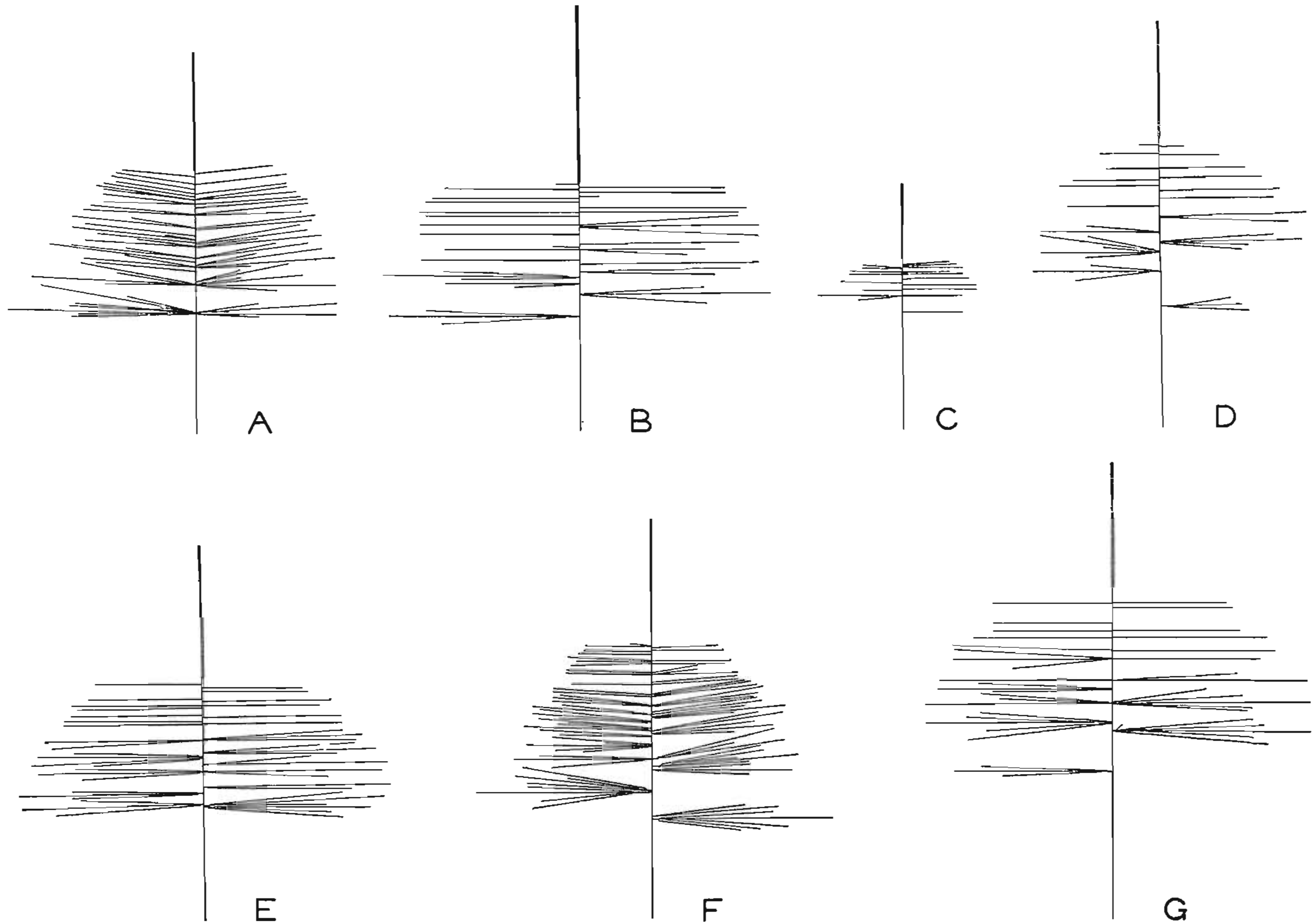
Leaves vary in shape, but it is difficult to measure them rapidly and to make comparison. Coroico leaves are more slender than those of the highland types, have a deeper channel over the midrib and the sheath is pubescent. Guarani maize has hairs along the edges and the upper part of the sheath, while highland maize usually has very little hair restricted to the edges near the auricles or may be practically glabrous.

The Tassel

Tassel branches are fairly constant in number for each race and, although unfavorable environmental conditions may reduce the number of branches, the reduction usually is within the range of the race. Fasciation may increase the number of branches just as it affects the number of spikelet pairs at a node and this has probably been the cause of the high number of branches in Bolivian sugar corn tassels (Figure 1 F), double that of other maize of the same race. The series of diagrams of typical tassels (Figure 1) shows that there is great difference in the number of branches, their length and points of origin.

Sterile Zone is a term employed for the distance meas-

FIGURE I (shown on opposite page). Tassel diagrams. A. Coroico maize. B. Guarani maize. C. Altiplano maize. D. Uchukilla maize. E. Valle maize (*morocho* or *huilcaparo*). F. Valle maize (*chuspillo* or sweet). G. Cuzco maize.


A
B
C
D
E
F
G

ured on the third secondary branch of the tassel, from the central axis to the base of the first spikelet. Tripsacoid influence greatly condenses this distance, although adverse conditions may also do this.

Glume shape is correlated with grain shape as Anderson suggested (1944). In Tripsacum and Tripsacoid maize the glumes are broad at the tip, not tapered to a point as in those plants considered as pure maize, just as grains of Tripsacoid maize are widest near the tip, often flattened across the top.

Anthers vary in shape and size, but no good correlation with any tendency or within any race could be discovered. This is also true of pollen. The maize which is considered most contaminated by other grass species has small pollen, just as one would expect because practically all other grass pollen is much smaller than that of maize. The pollen of other maize (sweet corn, for example) is occasionally small.

The arrangement of paired spikelets on the tassel branches is highly indicative of tendencies which are present in the plant. One of the spikelets is usually pedicellate while the other is sessile, a condition which is not only common in grasses but is found in the Palmaceae and many other plant families. The arrangement of these pairs on the branches is nearly always regular (Figure 2 A) and any variant follows certain forms. An index of the divergence from regularity of arrangement has been devised by Dr. Edgar Anderson (1944) and called *condensation index*. His definition, "The average number of spikelet pairs per apparent node in the most condensed central three quarters of the basal-most secondary branch," is applicable to most North American tassels, but when one studies the arrangement of spikelets of all maize, it is apparent that condensation index is increased in two distinct ways, by condensation and by multiplication. With condensation one internode or more may be so condensed that the spikelet pairs appear in whorls at one apparent node, as they do in much North American and in some Guarani maize (Figure 2 B), and the sessile and pedicellate spikelets retain the arrangement one

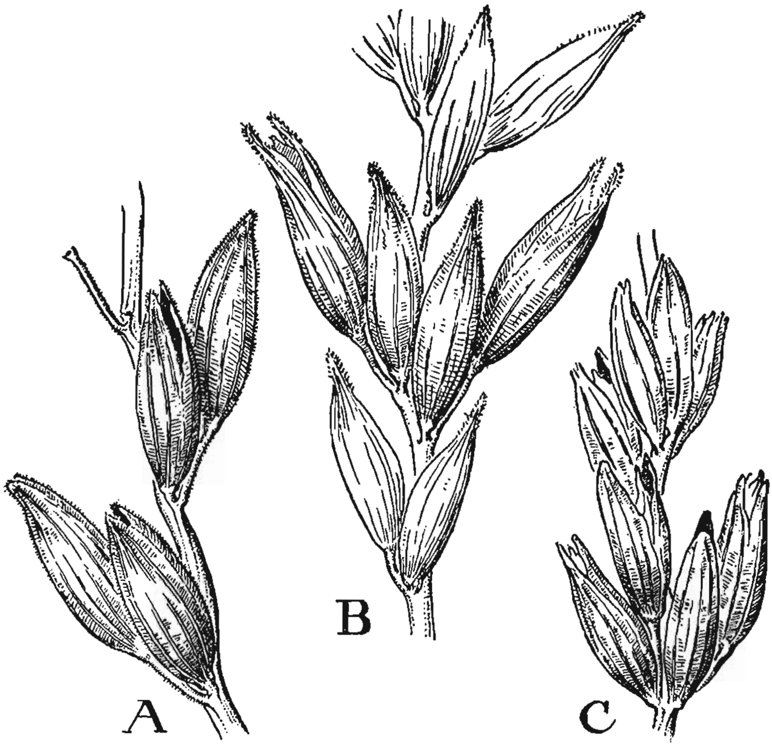


FIGURE 2. Spikelet arrangement on tassel.

would expect if a normal branch had been greatly shortened. With multiplication, however, the arrangement is different, with the sessile and pedicellate spikelets alternating at the nodes as if the primordia had branched to give rise to more pairs of spikelets (Figure 2 C). *Spikelet-node index* (Table I) may be defined as the average number of spikelet pairs per apparent node of the basalmost secondary branch in the three-quarters with the most spikelets. This includes multiplication and condensation, and if one recalls that in the races described here, only Guarani has a large amount of condensation and little multiplication, this index is a satisfactory measure of disturbance to the basic arrangement and still is simple to measure.

TABLE I. Median values of some ear and tassel characters of races of maize described in this paper.

	Coroico	Guarani	Altiplano	Uchukilla	Valle, excluding sweet	Valle, sweet only	Cuzco
Number of rows of grain	9	12	14	8	14	20	8
Mid-cob width in mm.	12	23	21	15	23	26	22
Kernal width divided by kernel thickness	1.5	1.8	1.3	1.9	2.0	1.65	2.3
Kernel length in mm.	9	9	11	11	14	12	15
Number of tassel branches	43	32	14	24	36	84	34
Sterile zone length, mm.	5	4	3	6	8	14	12
Spikelet-node index	1.1	1.3	1.1	1.1	1.1	1.2	1.1
Percent subsessile spikelets	4	6	10	6	4	36	8

The percent of sub-sessile spikelets is another measure of the amount of disturbance to the basic spikelet pair arrangement (Table I). It is taken from the same basalmost secondary branch as the spikelet-node index. Sub-sessile spikelets result from the Tripsacoid tendency to shorten pedicels or indicate irregularities in the order of the spikelets. In a series of spikelets with the pedicellate spikelet on the left, a sub-sessile pair of spikelets is often followed by several pairs with the pedicellate spikelet on the right.

The Ear

The shape of the ear varies greatly from one race to another, but is remarkably constant within the races (Plates XXXV–XXXVII). It has not been studied as well as it should have been because it is dependent upon numerous factors and measurements and comparisons are difficult to make. One of the peculiarities of Tripsacoid maize, which has high numbers of chromosome knobs in Central and North America, is the long naked cob-tip, which is also found in some Guarani maize of Paraguay. Andean maize and Guatemalan highland maize with few chromosome knobs have the tip of the ear completely covered by grains. Ears of Longfellow flint and some ears from the Iroquois tribes of New York also have this grain-covered tip.

Anderson (1944) has indicated a correlation between high condensation index and high row number in North American maize, and it is probable that the high row number in Bolivian sweet (Plate XXXVII, G, H) is brought about by the same fasciation which increased the number of tassel branches. Row number is dependent upon many factors and little is known about the manner in which it is regulated. It is, however, relatively constant within each race (Table I) and with the exception of the two lowland races, Coroico and Guarani, usually does not vary much within a race.

Mangelsdorf has shown that there probably are two types of arrangement for the ear and tassel (1945). His studies were made on tassels and tunicate ears of Guarani maize. More recently a method[1] of distinguishing between the paired spikelets of an ear has been developed and the ears examined support his contention that Tripsacoid types tend to have a systematic arrangement while

[1] Plate XXXIV shows an alicole of a maize ear after the lower glume has been cut away and the upper glume and the parts above it torn off. Note that one spikelet arose from a hair-fringed callus located in the bottom of the alveolus while the other was attached to the side of the alveolus at a point farther from the center of the cob.

purer maize types have a somewhat whorled or random arrangement, although there occasionally is a suggestion of spiralling.

Let us suppose that we slit a corn ear down one side and spread it flat upon this page. Then an ordinary ear with eight rows of grains could be shown as in Figure 3 A. Each pair of grains arises from a pair of spikelets and comprises, with the related parts of the cob, the alicole. The alicoles are arranged in vertical rows, the adjoining rows of alicoles shifted slightly (Figure 4 A). The arrangement may be interpreted as being derived from a spiral, from a whorled arrangement in which compression and the forcing of the alicoles into the most compact order results in the position shift of the vertical rows, or even from the fusion of vertical rows of paired spikelets. In ordinary maize, then, ears with eight rows of grains have four rows of alicoles, for each alicole bears two grains (diagrams Figure 3, and sketches Figure 4).

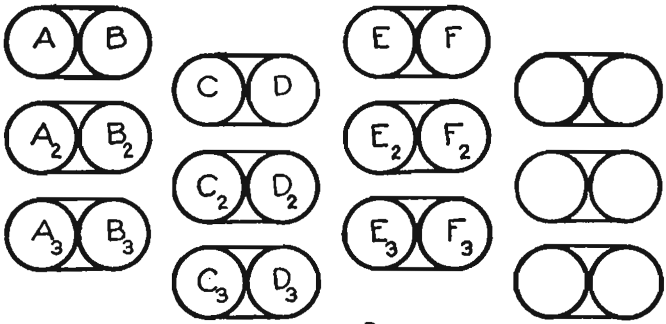
In the Coroico race, however, the arrangement differs in that, although an ear has eight rows of grains, it also has eight rows of alicoles as shown in Figure 4 B. The alicoles are placed like bricks, each alicole being covered by half of an alicole from the right and half of an alicole from the left so that in any row of grains, one-half of the row will come from one row of alicoles and the other half will come from an adjacent row of alicoles (Figure 4 B). The arrangement of the alicoles in Coroico maize and the location of the spikelet pairs upon a fibrous pedestal which is nearly twice as tall as wide, instead of upon the ligneous lower ridge of the alveolus as in nearly all

FIGURE 3 (shown on opposite page). Alicole and grain arrangements diagramed as though the ear was split open and spread out.

A. Normal arrangement of 8-rowed ear.

B. Coroico arrangement of 8-rowed ear.

C. Coroico arrangement of 9-rowed ear.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A2 B2
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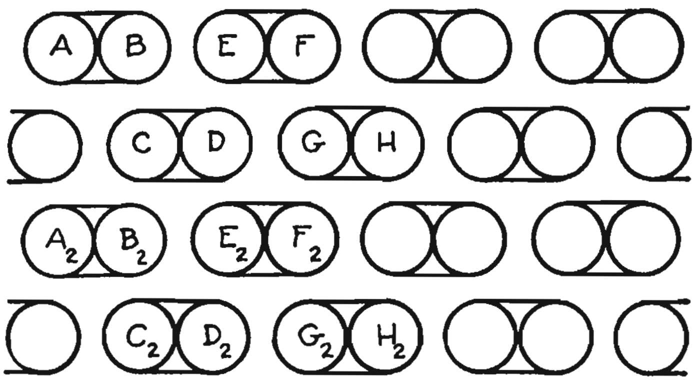
A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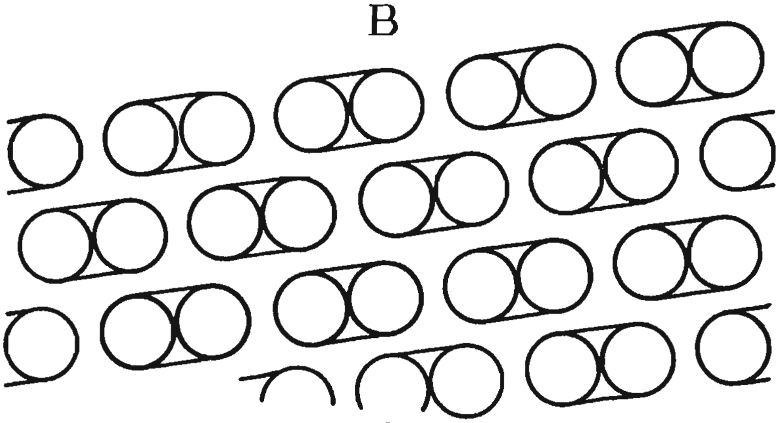

C

other races of maize, suggests an arrangement which could be derived from a shortened or condensed panicle. This arrangement leads to two curious situations in numbers of rows of grains.

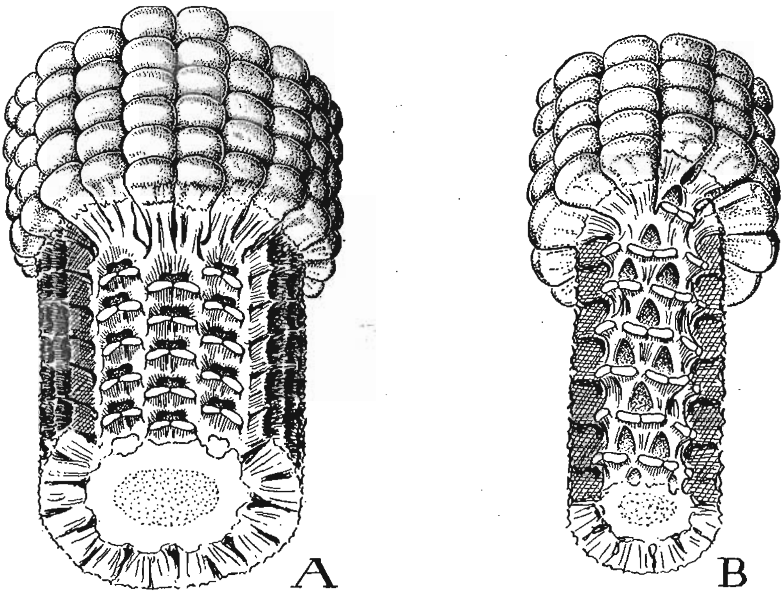

FIGURE 4. Arrangement of alicoles on the maize ear. The spikelets have been cut away in some of the alicoles and only the bases or pedestals left.
A. Normal arrangement of alicoles.
B. Coroico arrangement of alicoles.

Most unusual is the occurrence of ears with an odd number of rows of grains. It is true that ears are occasionally found in which part of the ear has an odd number of rows, but in the one case which was examined, an ear of the inbred R4 obtained from Dr. William L. Brown, this results from abortion of one of the paired grains in some of the alicoles, and an odd number of rows of grains is found only on a portion of the ear. On some of the Coroico ears there were 9 rows of grains

(Figure 3 C) over the entire ear except for a small portion at the base where there was a slightly irregular arrangement, based apparently on nine rows. Some of the progeny of these ears had 9 rows of grains and of alicoles.

A second novelty is the potential increase in number of rows of grains which is possessed by the Coroico race. If the ear is condensed longitudinally or spread out laterally, the grains and the alicoles assume the position of those in ordinary ears with the eight rows of alicoles arranged to form sixteen rows of grain. There is good evidence that this change occurs, for ears from localities near Coroico usually have row numbers near 16 or less (Plate XXXV, E, F, G), and have a high degree of tessellation or interlocking of the grains.

Is it possible that ears with row numbers less than 16 are affected by contamination or by selection for larger and softer grains which also reduced row number? The oldest South American prehistoric ears have 14–16 rows of small grains while later prehistoric ears have fewer rows of larger and softer grains or may have more rows and still have small hard seeds. This probably represents the development of maize for special uses from an original 16-rowed type, one type for boiling, parching or grinding, the other for popping. It is significant that much of the oldest maize in South America bears the paired female spikelets upon a pedestal similar to that in Coroico maize.

Prehistoric and pop corn are not included in this paper because they present special problems. Pop corn has primitive types as well as recent developments which owe much of their character to mixture with the races described here. In prehistoric maize there is much of the same problem, with some primitive types which persisted until quite recently and other types which may either represent developments in the region where their remains are now found or which may in prehistoric times have been introduced from another region. The study of prehistoric maize must be based largely upon the ears, for even where other material is found, it is practically never associated with an ear. For this reason a special set of characters must be utilized. The most useful ones are in the glumes and alveoles of the ear, but before valuable prehistoric material can be studied with maximum profit, a technique must be developed which will not destroy the specimens being studied.

Thickness of cob varies greatly and is quite independent of the number of rows of grains. The cob may be fibrous and flexible or lignified, hard and stiff. The paired female spikelets may be attached by a broad base to the lower margin of the alveolus so that a definite line of separation between glumes and cob is lacking, or the spikelets may be borne on a pedestal as much as 2 mm. tall. Glumes vary from horny, thickened and sculptured masses to delicate membranes, although the variation within each race is rarely very great. Lemmas and paleas vary much less.

Grains range from bird-shot sized spheres through pointed, beaked, polygonal, dented and other forms to the broad Cuzco grain. Most difficult to interpret is the occurrence of denting, and until some information on the cause and control of denting is available, it is impossible to discuss the distribution intelligently. Denting is found occasionally in all the races although it is often so slight as to be barely perceptible. It is strongly present in some Valle and Cuzco maize.

Isodiametrical polygonal grains which are widest at their tips are usually correlated with tesselation. This arrangement and shape of the grain is characteristic of Coroico and Guarani maize, which might lead one to suspect that they have been contaminated with Tripsacum, since a similar arrangement and shape occurs in ears from maize-teosinte crosses. Ears of Cuzco maize with more than the usual number of rows of grain often have isodiametrical grains in a tesselated arrangement. If this had been the result of Tripsacum contamination, one would expect to find it in the ears with lower row numbers instead of becoming more marked in the higher row numbers. *Salpor* of Guatemala and *Cacahuatzintle* of Mexico are similar to the many-rowed forms of Cuzco and occasionally have isodiametrical tesselate arranged grains.

Kernel width divided by thickness gives a positive number which is an index to the grain cross section (Table I). Variations in grain size are common in some of the races studied and when prehistoric specimens and pop corns are compared with races described here, it may be noticed that, although there are often vast differences in the sizes of grains, there are similarities in the shapes.

Colors have been used very little in this study for the examples found in most collections are the extremes. Colors are controlled by numerous factors which may interact, be modified or inhibited, be restricted in action to certain areas of the plant, or have a broad effect over nearly the entire plant. The most significant feature of colors in South American maize is the frequent occurrence of browns and reds or purples. These colors are common in grasses. Brown grains are not only colored by a combination such as yellow or orange endosperm plus blue or purple pericarp, but by true brown pigments.

The common maize of many districts is often divided into two types, a yellow and a white. This is true of the altiplano, where there is a flint with yellow endosperm and a white flour maize; of the valleys, where there are yellow and white forms of Cuzco; and of the Paraguay basin lowlands, where there is a flour maize with a yellow ("brown") aleurone and a white flint which belong to the Guarani race of maize.

Highland maize is susceptible to smut just as the varieties classified by Mangelsdorf and Cameron (1942) as Andean were susceptible. Perhaps there is some connection between the use of corn smut as food, a common practice in the highlands, and its occurrence. Lowland maize grown at an altitude of 2,500 meters in Cochabamba, Bolivia, was rarely attacked by smut. On the other hand, lowland maize grown in Cochabamba was badly damaged by rust. Coroico maize was most severely infested, then Guarani and least of all the Coastal Flints and the highland races. Several commercial yellow dent inbreds from the United States were so badly covered with rust that they died before tasseling.

Races of South American maize

Coroico maize

Coroico maize is the most unusual race known so far. Some of its characteristics are found in other races, especially in Guarani (Plate XXXV, C, D, E, F, G) but these are encountered less frequently in areas remote from Coroico, Bolivia, and no ears of this race have been discovered more than a short distance from Coroico. At present the race is restricted to those ears which have the alternate arrangement of alicoles or which approach this condition and have enough of the other characters (slender flexible ear, spikelet pairs on a pedestal, brown-orange aleurone and brownish cob) to distinguish them definitely from Guarani which is to the south and east, and from mixtures with the Coastal Tropical Flints, which are found in parts of eastern Ecuador, and in Brazil as far east as the states of Goias, Maranhao and Ceara. The town of Coroico is in a transition area close to the division between the highland and lowland Indian groups on the margin between the lowlands and the highlands, and not far from the separation of the Amazon and Paraguay River basins.

The most peculiar characteristic of Coroico maize (Plate XXXV, A, B) is the arrangement of the alicoles which has been described on page 272. The long, slender and flexible ears have a light brown cob with very little pith and the shallow alveoles and slender pedestals do not stiffen the ears like the trusswork system of deep alveoles with the horny attached glumes of North American and most South American cobs. The isodiametrical grains are nearly always brown-orange in color due to the presence either of the brown aleurone characteristic of Guarani maize or to a brown-orange aleurone hitherto unknown to students of maize. The presence of a dominant inhibitor for other aleurone colors makes grains of any color except brown-orange infrequent in this race.

The plant of Coroico maize is as distinct from the other races of South America as is the ear. When grown in Cochabamba it tillers abundantly and has narrow leaves with a distinct hairy channel over the midrib. All of the leaf sheaths have hairs which are stiffer and straighter than those found in the pubescent types of Central America.

Guarani maize

This is the maize grown throughout most of the lowlands and plains of the Paraguay River basin, an area inhabited mainly by the Guarani Indians and related groups. The ears (Plate XXXV, C, D) usually have 12 or 14 rows of grains, are of good size, nearly cylindrical, with the naked cob protruding beyond the grains as in Tripsacoid types. The number of chromosome knobs in the plants Mangelsdorf studied was extremely low and some plants had no knobs. Although the cobs are cream-colored, firm, quite stiff and possess moderate pith cavities and alveoles, some characters, especially in those ears from Santa Cruz Province on the southeastern Bolivian border, suggest Coroico maize. The grains in Santa Cruz Province are smaller, so strongly tesselated at times that the pairs almost overlap, and a dominant aleurone color inhibitor is found in most ears.

There are two types of Guarani maize, grown for separate purposes and planted separately: yellow soft flour, called *abati moroti*, and crystal-white flint, called *abati tupi*. The yellow color of the flour maize is formed by a brown aleurone, other colors being absent when the dominant color inhibitor is present. The flour types appear to be the older form. The ears of flint are stiffer, more ligneous, more cylindrical; the alveoli are deeply sunk into the cob, and the grains are rounded at the top, less flattened and less compressed by the husks.

The apparent uniformity of Guarani maize must not be interpreted as a lack of potential variation. Concealed within this race, in part by modifiers and inhibitors and by human selection of two definite varieties, is an amazing amount of potential variation. From selected Guarani ears it might be possible to develop many of the varieties of South American highland maize and still have some characters which are not found in other varieties.

Coastal Tropical Flint

The orange-yellow tropical flint which is the most common maize in Europe, Cuba and throughout the Caribbean area, is also found in eastern Ecuador, Brazil and Argentina. This variety belongs to the race of tropical flints described by Anderson and Cutler (1942) and probably has been spread by the Arawak, Carib and Tupi-Guarani groups which populated coastal areas from Cuba to Argentina. In Brazil, where it is called *Cateto*, it was previously limited to the coast, but is now spreading rapidly to the interior where Guarani maize was grown (Plate XXXV, H, I). The tight husks prevent much damage to the growing or stored ears and the hard flint grains resist weevils. There has been much active and intelligent work carried out in the selection of improved varieties of Cateto. Much of the seed grown by that name throughout Brazil originated in the State of São Paulo and may be contaminated with North American maize. The ears have 12 to 16 rows of flattened, not isodiametrical, grains, are slightly tapered and have an enlarged base, although this may not be evident in some ears.

Altiplano maize

Altiplano maize is widely distributed throughout the higher or less favorable parts of the Andes from Argentina and Chile to Ecuador and probably Colombia.

Altiplano maize plants are small and early, with few leaves and tassel branches, occasionally with one or two tillers, and nearly always with red or purple plant color on leaves and culms. The ears are small and nearly spherical, averaging about 14 rows of grains although often these rows cannot be distinguished until the grains are removed and the arrangement of the alicoles studied. The grains vary from hard pop to soft flour, with a wide assortment of endosperm, aleurone and pericarp colors, and grain shapes from nearly spherical through ovoid, pointed, beaked, imbricated and, very rarely, minutely dented.

When plants are grown under adverse conditions or near their growth limits, it is difficult to distinguish between the effects of environment and heredity. The small plants and nubbin-like ears of Altiplano maize (Plate XXXVI, A, B) resemble those produced under adverse conditions, yet when seeds are planted in a more favorable environment, as in material from Lake Titicaca planted under irrigation in Cochabamba, there is little or no change. The specimens of maize Anderson described from Río Loa, Chile (1943), as well as most of the prehistoric material discovered within the present range of the race, falls within the range of variation of Altiplano maize. Like most of the prehistoric material, Altiplano maize probably does not represent a primitive type but may be one of the early developments which could withstand the environment in which it is grown and may indicate the nature of the primitive type from which it was developed.

Uchukilla maize

The name, *Uchukilla*, is applied in Bolivia and Peru to a small crystal-white flint grown on the slopes of valleys at about 2600 meters altitude. The race includes, however, some flour and semi-flint varieties, usually yellow and often red, which are known locally by other names. The plants are small and mature earlier than other races in the same district, usually requiring 50 days from time of planting to the appearance of the silks. The ears (Plate XXXVI, C, D, E) are small, with 8 or 10 straight rows of grains. These grains are widest about two thirds of the distance from the base to the tip, and frequently very slightly beaked, pointed or dented. Ears of Altiplano maize which have low row numbers and a less spherical ear shape than usual approach Uchukilla in appearance. It is nearly always possible, however, to distinguish the few and distinct rows of nearly diamond-shaped flattened grains of Uchukilla from the larger number of somewhat irregular rows of rounded or slightly pointed and imbricated grains of Altiplano maize.

Valle maize

The favored places for human habitation in Bolivia and Peru are the highland valleys and it is in these valleys that agriculture is changing most rapidly. No longer are these valleys isolated centers where the people live shut off from their neighbors, and conserve their customs, habits and crop plants inviolate. No longer do feudal landowners and the state church, be they Incaic or modern, hold the workers to the soil, toiling on designated crops and laboring in a limited area. Now restrictions are few, travel is easy and rapid, and an influx of foreign materials and methods has changed the passive Indian to a confused citizen. With the loss of native customs, there has been less rigidity in selection of seed for planting; with the introduction of foreign customs and methods, such as drinking beer instead of chicha, or using animals instead of human labor, new varieties of plants are required. Maize in the valleys is in a volatile condition, with old types being lost and abandoned or modified to suit the newer concepts. An example of this has been given in the growing of two special types of Valle maize, sweet and Culli, or cherry pericarp, maize.

The four divisions of Valle maize, *hanka sara* or the mixture for toasting, *Culli* or the cherry pericarp *chicha* maize, *morocho* or the ordinary field and general use maize, and *chuspillo*, the sugar maize, differ greatly in length of growing season, size of plant and number of rows of grains. All, except *chuspillo*, have long grains which are widest slightly above their center, and usually dented and medium-sized strongly tapering or pyramidal ears with enlarged butts. As in all the races of maize discussed in this paper, with the exception of Guarani and Coastal Tropical Flint, the tip of the ear is rounded and covered with grains.

Heterogeneity in Valle maize is increased by the planting of a special corn for parching. The seed for this planting is obtained from ears which vary in color or grain shapes from the varieties normally planted, and which are floury or nearly so. This seed, known as *hanka sara* or *sechys* in Bolivia, thus contains the most varied assortment of grain shapes, colors and markings which can be found anywhere (Plate XXXVII, A, B). Dr. Martin Cardenas, rector of the Universidad Autonoma Simon Bolivar at Cochabamba, suggested that a critical study of this group would reveal many varieties no longer in cultivation in a pure form. Most of these varieties, however, would fall into the Valle race of maize and probably within the variation, except for color and some extremes in grain shape, of the other three divisions.

Culli or *morado* recalls the purple dye corn of the Hopi Indians. The plant is the earliest of the Valle maize, smaller, the grains shorter and thicker, and the row number usually lower (10 or 12) than others of this race. It suggests a close relationship with the very similar Uchukilla.

Morocho or *huilcaparo* is the most important maize of the Valley of Cochabamba and similar forms are the most common types of maize in other valleys of Bolivia, Peru and Ecuador. Although the present form usually has 14 or 16 rows of slightly dented flint grains and a brownish color, there is a tendency to select ears which are more variable in row number, softer and more dented and yellow-orange in color. The cob is nearly always a rust-red color.

Chuspillo or *chulpi* is the sweet corn, eaten only in the form of dried toasted grains or used by the wealthier natives in the preparation of a special *chicha*, but never eaten in the form of green fresh corn. The plant is very similar to that of *morocho*, but the leaves are a lighter green. The most curious feature of *chuspillo* is that the number of tassel branches and the number of rows of grain are approximately double those of *morocho*. The high spikelet-node index of *chuspillo* suggests that it differs not only because it is sweet, but because there has been some fasciation. There are frequent branched ears and some splayed tips or slight bear-pawing, but the flattened and bear-pawed ears which are associated with high row numbers and high spikelet-node indices in North American maize are not found in South American highland sweet corn, nor is condensation usually found in the tassel branches, though multiplication is common and characteristic (Table I).

The gene for sugary endosperm in Valle maize is probably the same as that involved in North American sweet corn, but there is some suggestion that there may be modifiers, for frequently the grains are not completely translucent, but are opaque for part of their length when crossed with North American sweet. It is also possible that there is more than one gene for sugar present.

Multiplication of row number has crowded the grains so that they are very slender, almost nail-like and the ear has become more rounded, with less tapering to a point and no visible enlargement of the butt. The grains are usually light yellow or nearly white, though occasionally red. In the purer forms the cob is white, but some cobs are red or rust-red, especially where there has been opportunity for crossing with *morocho*.

Two type of ears, one tunicate (called *paca sara* or hidden maize in Quechua) and the other with the double-grained spikelets such as are found in Country Gentleman (called *cuti sara* or turned maize in Quechua), are used as medicine in the Bolivian highlands. When planted these gave many ears which were of Valle type, but others had characters of Coroico or Guarani mingled with those of Valle maize. It is impossible to say where these peculiar and primitive types arose, but it is probable they will be found commonly in Valle maize because of the preservation of the heterogenous *hanka sara* or mixed toasting corn group.

Cuzco maize

This is the most famous South American maize for the grains are so much larger than any others that they have been collected more often and introduced in many places. It is likely that the extremes of Cuzco represent a comparatively modern development, for in the valleys near Cochabamba, Bolivia, with conditions as favorable as those in Cuzco, Peru, the two forms (Plate XXXVI, F, G, H, I) of this race are known by Spanish descriptive names, *mais amarillo* and *mais blanco* instead of the Quechua names by which they are known in Cuzco. The soft texture of the floury endosperm resembles that of *salpor* of Guatemala and *cacahuazintle* of Mexico. Like these two varieties, Cuzco maize may also be flinty, a form in which it can be transported or stored in areas where insects and mold would damage floury ears.

The ears are moderately long, tapered from a frequently enlarged and irregular butt to a round grain-covered tip. Typical ears of Cuzco maize have eight rows of grains with spikelets so strongly paired that the cob in cross section appears like a cross, with deep sulci between the rows of paired spikelets. Frequently the second and third ears on a plant or ears grown under difficult conditions are distichous, with a flattened cob bearing one row of paired spikelets on each edge, somewhat resembling, even to the turned up lower glumes, some of the progeny of teosinte-maize crosses. The grains on these ears, as on ears which have not been completely pollinated, are elongated spheres with a slightly pointed tip (the shape of the grains in teosinte and Tripsacum). Cuzco grains are usually wide, flattened, slightly dented and with a small beak or overhang on the upper edge similar to that found in much Valle maize, in Mexican pyramidal dents, and some North American dents.

Just as in Guarani maize, planters made two main divisions of Cuzco maize, white and yellow, but unlike Guarani, there usually is no difference in the endosperm and both are floury. The large haciendas of Bolivia are selecting ears with 10 or 12 rows for their plantings and most of these show clearly by their shape and color that they have been crossed with *morocho,* the most common Valle maize. The yellow ears show most contamination with other races. Both white and yellow Cuzco may have calico pericarp, but most of the ears which exhibit other colors are contaminated by other races of maize.

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EXPLANATION OF THE ILLUSTRATIONS

PLATE XXXIV. Three alicoles of a maize ear with the lower glumes cut away and the upper glumes and parts of the spikelets above the upper glumes torn off to show the attachment of the pairs of spikelets. One spikelet of each pair arose from a hair-fringed *callus* in the depths of the alveolus while the other spikelet was attached to the side of the alveolus further from the center of the cob.

PLATE XXXV. Representative ears of South American maize. A. Coroico maize, Coroico, Bolivia. B. Coroico maize, Coroico, Bolivia. C. Guarani maize, yellow flour, Concepcion, Paraguay. D. Guarani maize, white flint, Concepcion, Paraguay. E. Guarani maize, with characters approaching Coroico, near Robore, Bolivia. F. Guarani maize, with characters approaching Coroico, near Robore, Bolivia. G. Guarani maize, with characters approaching Coroico, near Magdalena de Itenez, Bolivia. H. Coastal Flint maize, State of Maranhào, Brazil. I. Coastal Flint maize with Guarani influence, State of Ceará, Brazil.

PLATE XXXVI. Representative ears of South American maize. A. Altiplano maize from shores of Lake Titicaca, Bolivia. B. Altiplano maize from shores of Lake Titicaca, Bolivia. C. Uchukilla maize, Cochabamba, Bolivia. D. Uchukilla maize, Cochabamba, Bolivia. E. Uchukilla maize, Tarija, Bolivia. F. Cuzco maize, white, Cliza, Bolivia. G. Cuzco maize, white, Cochabamba, Bolivia. H. Cuzco maize, yellow, Cochabamba, Bolivia. I. Cuzco maize, yellow, Sacaba, Bolivia.

PLATE XXXVII. Representative ears of South American maize. All the ears shown in this plate are Valle maize. A. Toasting maize, a speckled ear in the mixed group of Valle maize, Sucre, Bolivia. B. Toasting maize, a white-capped red ear in the mixed group of Valle maize, Cochabamba, Bolivia. C. *Culli*, Cliza, Bolivia. D. *Culli*, Cliza, Bolivia. E. *Morocho* or *huilcaparo*, the common field corn, Cliza, Bolivia. F. *Morocho* or *huilcaparo*, the common field corn, Sacaba, Bolivia. G. *Chuspillo*, sweet corn, grown among *morocho* at Cochabamba, Bolivia. H. *Chuspillo*, sweet corn, Cochabamba, Bolivia.

PLATE XXXIV

PLATE XXXV

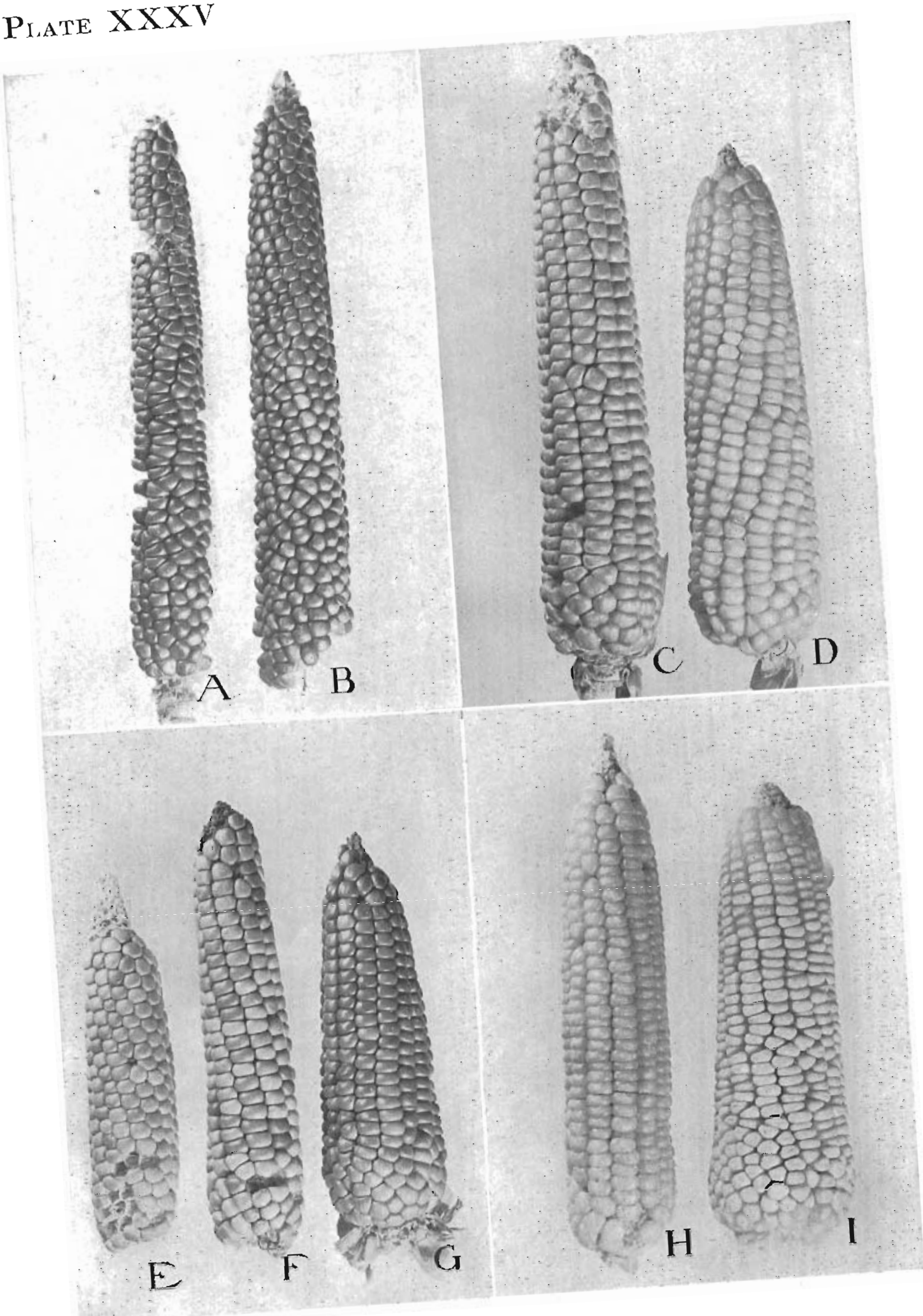

PLATE XXXVI

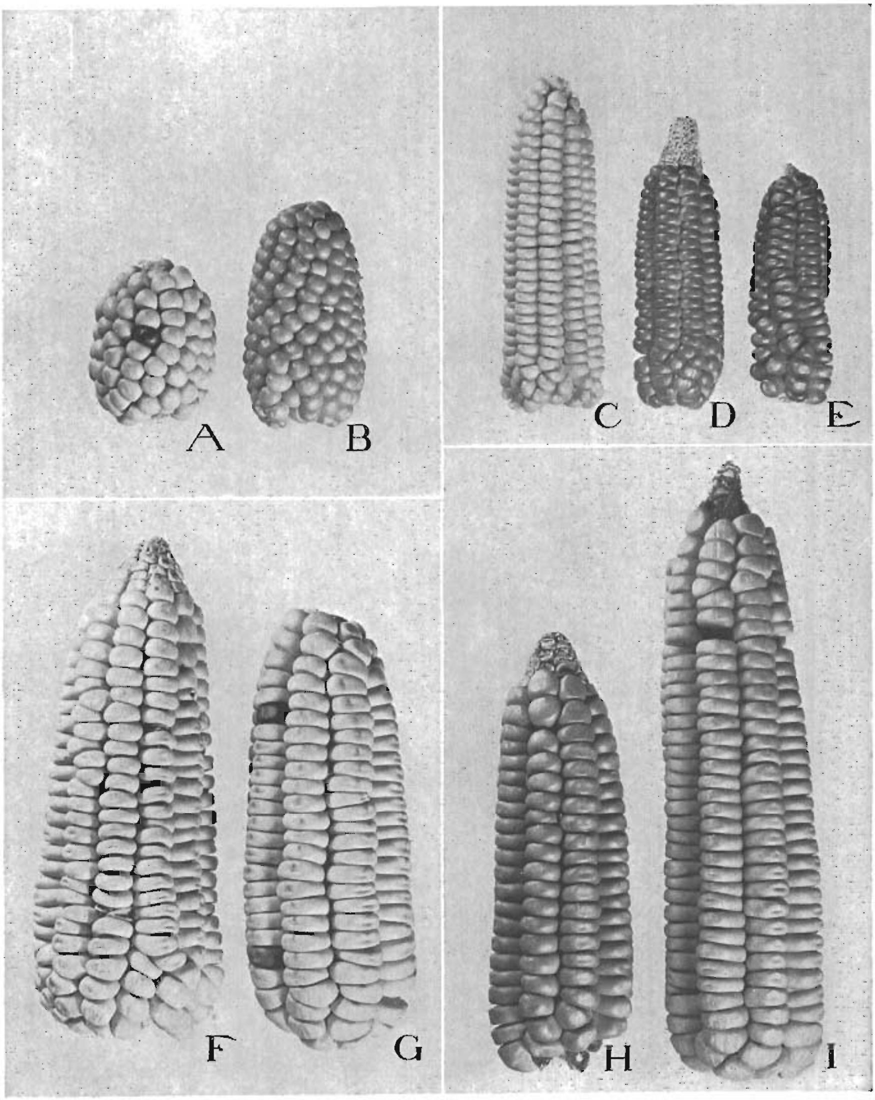

PLATE XXXVII