



Corn and Culture in the Prehistoric New World

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14

Variation in Modern Andean Maize and Its Implications for Prehistoric Patterns

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Introduction

In the past, the study of the origin and evolution of maize has been a matter of basic research and academic exercise. Now, as we face recent trends in reduction in per capita food production, population growth, erosion of plant variability, extinction of the rain forest, land degradation, climatic change, the energy crisis, and the failure of technology to solve world poverty, the study of maize evolution must have other objectives. These alarming trends point to imperative reasons for studying the evolution of the species into the highly developed and efficient crop that is now in our hands as well as for studying the creation and maintenance of the genetic variation that the evolution produced.

Some statistics can help us visualize the present situation. In Latin America 150 million people, about 35 percent of the population, are living in poverty (Durming 1989). Year after year the poverty increases, mainly due to population growth, which pushes people into marginal lands and from there to the city slums. This situation is very dramatic in some countries. Table 14.1 compares the economic production and population growth of Latin America to that of the industrial countries and the world as a whole. To give some specific examples, in Peru, the rate of population growth is 2.5 percent yearly, while the annual grain production is declining at a rate of -2.1 percent,

Table 14.1. Economic production and population growth.

	<i>Economic Production Annual Variation</i>	<i>Population Growth Annual Change</i>
World	3.8	1.7%
Industrial Countries	3.9	0.7%
Latin America	1.4	2.2%

and the cumulative change in per capita income is -11 percent. In comparison, Japan, West Germany, and the United States have a population growth of 0.7 percent, -0.2 percent, and 0.7 percent and a cumulative increase in per capita income of 21 percent, 10 percent, and 10 percent, respectively (Brown 1987).

Due to population growth in the Andean countries, food production per person is declining even though total production is increasing, as shown in Table 14.2. In the present circumstances, it is almost impossible to increase food productivity in Andean countries by using more irrigation, fertilizers, and energy. If we compare France, which uses 309 kg/ha of fertilizers and has 80 tractors per 1000 hectares, to Bolivia, Colombia, Ecuador, and Peru, which use 2, 77, 41, and 31 kg/ha respectively and have less than 10 tractors per 1000 hectares (FAO 1989), it might appear that the Andean productivity could be increased with these inputs. But at present this is an illusion, because the costs of adding irrigation capacity, fertilizers, and energy to agriculture have risen very drastically in the last decade.

The increase in per capita productivity in the developed countries and its decrease in Latin America is changing the pattern of world grain trade. In 1950, North America had a net export of 25 million metric tons, and Latin America had one million. In 1988, North America exported 119 million metric tons, and Latin America had to import 11 million tons (Brown 1989).

Many ecological problems are associated with the decline in Latin American agricultural production. In the delicate ecosystems of most Andean zone farming regions, farmers overexploit their own resource base as productivity declines. The Latin American rain forest, with an original extent estimated at 693 million hectares, will be reduced to 366 million at the end of this century. The increase in world temper-

Table 14.2. Food production given as a percentage of the 1979-1981 average.

Country	Total		Per Person	
	1985	1988	1985	1988
Bolivia	117%	120%	102%	97%
Colombia	106%	120%	96%	101%
Ecuador	119%	111%	103%	89%
Peru	111%	117%	98%	95%
Venezuela	103%	115%	90%	92%

ature resulting from carbon emission from fossil fuels will decrease summer moisture in the countries that export cereals. Also, Latin America is not exempt from the erosion of genetic diversity that plant breeding, change in ecology, and cultural practices are producing worldwide. As evolution is increasing diversity, modern agricultural practices are producing uniformity. There are many documented cases; see Plucknett *et al.* (1987) for a convincing summary.

The crop plants of the Andean zone still exhibit considerable genetic diversity, and many individual crops originated there. However, current food production is insufficient and genetic erosion is endangering future availability. The forces that sustained the admirable evolution of maize, for example, can no longer operate unless humans bring about a reversal of the situation. Can we breed maize in such a way as to assure a sustainable evolution of the crop? To answer that question, we need to review maize use and maize evolution in the Andean zone.

Maize in the Andean Zone Today

Maize is a major crop in the Andean zone of South America. More than 50 percent of the population depends largely on maize as a staple food. The total areas under maize production and production and yield figures for each country and region are presented in Table 14.3. The internal demand for corn has grown steadily in the last years. In 1971, the Andean countries produced all the corn needed, except Venezuela that produced 87 percent of its necessities. In 1985, Colombia pro-

Table 14.3. Maize area (in 1,000 hectares), production (in 1,000 tons), and yield (tons/hectare) in lowlands and highlands of Andean countries.

Country	Region	Area	Production	Yield
Bolivia	lowlands	171	334	2.0
	highlands	178	222	1.2
Colombia	lowlands	320	534	1.7
	highlands	300	390	1.3
Ecuador	lowlands	126	209	1.7
	highlands	109	97	0.9
Peru	lowlands	175	496	2.8
	highlands	184	206	1.1
Venezuela	lowlands	313	547	1.8
	highlands	-	-	-
Total	lowlands	1,105	2,120	1.9
	highlands	771	915	1.2
	TOTAL	1,876	3,035	1.6

duced 94 percent of its required grain, Peru 75 percent, and Venezuela 60 percent.

The lowlands and the highlands, two completely different ecosystems, are characterized by different patterns of maize production and use. Maize produced in the lowlands of Bolivia, Ecuador, and Peru is mainly for animal consumption. This is also true in Colombia and Venezuela, where yellow flint or semi-dent corn is used mainly for poultry food, but the people of these countries also use a white semi-dent corn as a mill product to make *arepas*, a popular bread and a main source of energy and carbohydrates. Until recently, many people in the eastern Andean region produced their own *arepas*, but now it is a very important industry in Venezuela, using pre-cooked maize flour in massive amounts. In Colombia maize production and consumption is more traditional, and about 80 percent of the total production (about one million tons) is for human food, mainly as *arepas*, while 15 percent is for animals, and 5 percent for industrial uses. Productivity in the lowlands varies greatly, depending on technological inputs. Average yield on the coast of Peru is 4.1 tons/ha while in eastern Ecuador it is only 1.0 tons/ha. In the highlands, maize is mainly for

human consumption. Productivity in the highlands is uniformly low in all countries, averaging 1.2 tons/ha. Maize productivity in the highlands is very traditional and variable, every region having different varieties, ways of cropping, and forms of preparation.

Variety in Patterns of Human Consumption

In Colombia, Ecuador, Peru, Venezuela, Bolivia, and surrounding areas of Chile, Argentina, and Paraguay, maize is used in a thousand ways. As one example, I give a very brief description of the variation in *chicha* making in the Quebrada de Humahuaca in northwestern Argentina (Camara-Hernandez and Arancibia 1976). *Chicha* is a form of beer, made by fermenting an aqueous extract of pre-germinated corn grain. There are many ways to make *chicha*, and many ways to consume its sub-products. The main source of variation is the maize variety used; it should be of the *morocho* type (floury corn with a thick external flint layer of endosperm tissue). To produce a condensed, heavy, or clear *chicha*, other varieties could be used. The flour could be mixed with saliva, producing *mukeado* (salivated corn flour), or *chicha postiza* (false *chicha*) can be made without the salivation process. *Bollos*, a form of bread, is made by mixing the flour with hot water. The fermented flour is boiled with water to produce porridge-like *apuña*, which becomes sweeter the longer it's boiled, producing variation in the resultant *chichas*. The boiled mixture is transferred to a large pot. After decanting, the layers of the mixture are used in different ways; the first layer is for aromatic purposes and for making bread, the second for making *chicha* for carnival, and so on. The Quebrada de Humahuaca is one very small place in the northwestern Argentine highlands. To the amazing variation in *chicha* in this one valley must be added regional variation; every *marca* or region in the Andean zone has a different way of making *chicha*.

The same variation characterizes other methods of corn preparation in the highlands of South America. Puga (1984) describes, for example, many different ways of making *mazamorra* (thick corn soup) in the Ecuadorian highlands for particular occasions; e.g., *aya-api* is the *mazamorra para los muertos* (for the dead); *cuyapi* is a *mazamorra* eaten a day after a funeral. Valdez (personal communication) describes

thirteen generic ways to use green corn, five for dry whole grain, eight to use corn flour, as well as three types of *mazamorra*, three of bread, and five of *chicha*. Each of these can vary with the maize variety, the region, and the culture. Local customs affect the way corn is used not only for food, but for fodder, medicine, and crafts.

Given this diversity in custom and consumption, one can understand the enormous variability of the species, and visualize the length of time the whole complex of maize use must have been in South America in order to develop complexity. Further, factors contributing to the variability can be seen in methods still used to plant maize in, for example, the Cuzco area. There, planting corn is almost a religious ceremony. Selection of seed is carefully done, but mixtures are tolerated and even encouraged. Many of the small farmers mix seed intentionally, increasing the possibility of varietal hybridization and consequently genetic variation.

In summary, human cultures as well as biological factors have created and maintained the great maize variability in the South American highlands. Artificial selection by farmers for specific purposes has played a major role in maize evolution.

Maize Evolution in Peru

Archaeological Evidence

Although it is difficult, given very limited evidence, to trace an evolutionary route from Mesoamerica to South America, the trends of the spread and evolution of maize within South America can be followed with more precision. To that end, I review the archaeological evidence for maize.

The first reported evidence of maize in highland Peru is from the Guitarrero cave in the Callejon de Huaylas, an intermontane valley in the Andes of north-central Peru. Thomas Lynch of Cornell University excavated the cave (Lynch and Kennedy 1970) and Earle Smith identified and interpreted the archaeological plant remains. He identifies some of the maize races present as Ancashino and Huayleño. These he thinks originated from a Mesoamerican maize, probably Palomero Toluqueño. He also notes the similarity of some ears to the

Colombian races Pira and Pollo. Walton Galinat also examined some ears from Guitarrero cave and states that they are similar in shape to the primitive Peruvian pops, Confite Morocho and Confite Puneño.

Smith points out some variation in the Complejo III at Guitarrero cave, which belongs to the last part of the preceramic period, about 4000 to 2000 B.C. Some ears look like the most ancient cobs from Bat Cave and Tehuacan, and are also similar to Pira and Pollo. Smith also finds some relationships of the thicker cobs to Confite Punteagudo, and the thinner cobs to Confite Morocho.

In the thicker cobs Smith finds only one cob typical of Confite Chavinense; the rest he classes as Ancashino. In contrast, Grobman (Bonavia 1982:176) thinks these thicker ears are Huayleño, and based on the morphological data in Smith's report, he thinks that most of the cobs are nearer to Confite Chavinense.

MacNeish excavated caves in Ayacucho in the southern Andes of Peru (see Bonavia 1982:263, 264). The maize cobs from Ayacucho have been analyzed by Galinat and also by Grobman. Galinat (1972) assigns these cobs to the Confite Puneño and Confite Morocho races and also to a hybrid between these races that he called Ayacucho, which no longer exists. According to Grobman (1974), all samples belong to two races: Confite Morocho and Confite Chavinense. The date of the Ayacucho cobs is difficult to determine. Bonavia (1982) states that two cobs that MacNeish found in the Chihua face date to between 4300 and 2800 B.C., while Galinat's report deals with later archaeological material (2500-1750 B.C.)

The Guitarrero Cave maize and the Ayacucho maize are only partially described and there are many gaps in the chronological data. The facts described above are from Bonavia (1982). His excellent criticism of the validity of archaeological data is of enormous value in any discussion of maize evolution.

The best-described preceramic maize in Peru is in Huarney from a site called Los Gavilanes, excavated by Kelley in 1957 and 1958, and by Bonavia in 1960 (Kelley and Bonavia 1963). Maize was found without ceramic association. This maize has been described by Alexander Grobman (Grobman 1982). Based on cob morphology, he concludes that the cob samples ($n=103$) belong to three races: proto-Confite Morocho (42 percent), Confite Chavinense (45 percent), and proto-Kculli (1 percent). Twelve percent of the cobs are difficult to

classify and he describes them as hybrids between the three races. Other ear, kernel, and plant characteristics indicate that the sample represents a very ancient maize, assigned by Grobman *et al.* (1977) to a preceramic context 5,000 to 4,000 years old.

The length and width of the ears and the row numbers of the archaeological specimens are typical of the assigned races. The kernels were pops or flint with some floury starch in the center; they were very small with dark brown or red pericarps. The plants had single, colored stalks. Internal ear characteristics are good evidence of the racial assignment. The Gavilan maize classified as proto-Confite Morocho has a cupule length to width ratio of 1.14. This fits very well with that of the modern Confite Morocho (1.07); this is the only known race that has a ratio of more than 1.0. The modern races that have evolved from Confite Chavinense, in contrast, have a very low ratio, from 0.2 to 0.4.

The maize of Los Gavilanes is one of the very few reported instances of preceramic maize from the coast of Peru. Lately, maize remains have been found by Uceda in the Casma Valley that have radiocarbon dates of 6070 ± 70 B.P. (Bonavia and Grobman 1989b).

Several very ancient sites other than those reported from Peru deserve some comment. Material from Argentina and Chile has been discussed by Bonavia (1982:377-380). In a context in Huachichocana, Jujuy (northwestern Argentina) about 5,000 years old, Fernandez-Distel found four cobs that Camara-Hernandez classifies as Pisincho, an Argentinian popcorn. The radiocarbon date for that sample is 9,000 B.P., greater than any other archaeological maize, but there are some doubts as to its antiquity. In northern Chile, archaeologists have been very active recently and have reported several very ancient samples of maize. A sample of coprolites and maize pollen from Tarapaca has yielded a radiocarbon date of 6480 B.P. At the site of Pichasca in the province of Coquimbo, ears analyzed by Galinat as similar to the races Capio Chico, Negrito Chileno, and Curagua have been recovered, but the specimens appear too developed to be considered as ancient the 5,400 years suggested by radiocarbon dating. At the Tilinche site in Pisagua, which has radiocarbon dates ranging from 6,950 to 6,700 years B.P., some ears classified by Galinat as Coriocos have been recovered. Although there are some doubts about the antiquity of the Argentinian and Chilean material (see Bonavia 1982; Pearsall, this

volume), these data at least suggest that maize may have been present in South America very much earlier than was previously thought.

In Ecuador there have also been interesting developments in the last fifteen years. Zevallos *et al.* (1977) concluded from finding a charred corn kernel embedded in a sherd at the San Pablo site that intensive maize agriculture may have characterized the Early Formative period of Ecuador. According to these researchers, the kernel belonged to a highly developed 8-row flint race of maize which existed in Ecuador 1,000 years before a comparably developed maize occurred in Mexico or Peru.

Pearsall (1980) reported on an analysis of an archaeological maize cache of carbonized kernels from Manabí, Ecuador. The kernels were recovered from a vessel of the Chorrera ceramic tradition, dating from 1,000 to 300 B.C. She recognized the difficulty of the racial identification of maize:

The results of the test of the accuracy of the angle determination of row number and the degree of increase in size of kernels during carbonization illustrate the difficulty of attempting racial identification of maize from grain alone (Pearsall 1980:347).

This problem, as well as others, make the racial identification of the Valdivia charred kernel somewhat uncertain. The photograph of kernels from the Manabí cache (Pearsall 1980:Figure 3) is very eloquent; the large kernel size indicates a race with a long history of evolution. However, Pearsall emphasizes that the width to length and width to thickness ratios of the kernels are ratios which depend on the position of the kernel on the ear, with the ratio being larger for kernels from the shank end. Some of the kernels in the photograph appear to have come from near the shank, throwing some doubt on the racial identification of this sample of maize kernels. Nevertheless, the Chorrera maize is good evidence of how dynamic maize evolution was in western South America. Pearsall concluded that a yellow flint 8-row maize of the southern highlands of Ecuador may have evolved from a lineage of low row-numbered, round-kernelled popcorn, thus linking the small popcorn of Mesoamerica and northern South America (proto-Nal-Tel, Chapalote, Pollo group) to those of central Andean South America (Confite Morocho group).

Overall, there is little evidence concerning the migration of maize to South America before 1,000 B.C. (but see Pearsall, this volume). The only evidence based on morphological similarities linking Mesoamerican and South American races are some characteristics of the Andean race Confite Punteagudo, which is unique in two morphological characteristics: large number of tillers and high degree of pilosity. These characteristics are also characteristic of Mesoamerican races. But it is difficult to conclude that this race came from Mesoamerica since it has long been exposed to influence from the amazing variability of the pop races in the southern South American countries (Sevilla *et al.* 1984).

Morphological Evidence

Since cobs are frequently found in archaeological sites, the morphology of the cob has been extensively used in tracing evolutionary and racial relationships. The length and width of the ear are helpful characteristics in determining its antiquity as long as only one race was present in an area. However, after racial differentiation begins, the linear regression between length and width and antiquity is disturbed.

Depictions of maize on pottery have been shown to be helpful in tracing evolutionary relationships. The pioneer work of Grobman *et al.* (1961) placed races in cultures and sites on this basis. However, the clearest ceramic depictions in Peru come from the Mochica and Chimu cultures, giving evidence for only a short and relatively late period. I will return to this topic in the section discussing the races of maize in Peru.

Dunn (1975, 1979) described ceramics from Mexico and Peru as evidence for the prehistoric distribution and relationship of maize races. On the basis of ear morphology, she identified on Peruvian pottery dating to about A.D. 800 the Andean races Kcello, Karapampa, Pira, and Clavo, and also Pollo, which is "quite close to metric data for Nal-Tel and Chapalote" (Dunn 1979:769).

Due to the fact that many features such as a flexible rachis, shape, wide butts, and row number are common to several races that could never have been in contact, maize samples can look similar without having any genetic relationship. The identification of the maize races

depicted on the archaeological ceramics must be based mainly on ear morphology, but, as Grobman *et al.* (1961) has pointed out, the context in which these races evolved must also be taken into account.

The internal characteristics of the maize ear have been found to be a useful tool in evaluating relationships among races as well as also between maize and its relatives. These characteristics are very consistent and relatively free of environmental bias (Goodman and Paterniani 1969; Ortiz 1985; Vega 1972).

Galinat (1970a) has used cupule morphology as evidence for the relationship between maize and its relatives. The length of the cupule in teosinte and in some primitive races of maize is greater than its width. In teosinte the length to width ratio of the cupule is about 2; in the primitive maize *Confite Morocho* it is about 1; and in modern maize is less than 0.5.

"Condensation" or compaction of the pistillate rachis is another characteristic used by Galinat (1970a) as an indication of the antiquity of the maize race. In modern maize the barren side of the internode is so reduced that the cob is stiffly clad in vertical rows of successive cupules.

In contrast, the cob of South American maize is generally lax and the interspace between the lip of the cupule and the divergence point of the next pair of spikelets above is apparent as it is in some of the most primitive archaeological maize of Mexico and in the relatives of maize (Galinat 1970a:7).

Alexander Grobman has made the most complete morphological description of the archaeological maize of Peru (Grobman *et al.* 1961). Morphological trends for coastal Peruvian maize are summarized as follows.

In an evolutionary sequence comprising perhaps 300 to 500 years for Los Cerillos (early Paracas, 2300-2500 B.P.), from the lowest to the upper level, the average cob length increased from 4.9 to 8.0 cm, and the ear diameter from 1.8 to 2.6 cm.

From the early Paracas to the late Nazca period (500 B.C. to A.D. 800) was a trend toward a) increase in ear length and diameter; b) changes in kernel arrangement from irregular to rowed; c) increase in duration in the cob tissues; d) increased variability in several morphological

traits; and e) appearance of new races and evidence of hybridization (Grobman *et al.* 1961:85).

In the Viru Valley sequence from Tomaval (300 B.C.) and Huaca de la Cruz (A.D. 500) very little change took place in the general morphology or the dimensions of the maize from the Guañapo to early Mochica periods. A slight increase of several millimeters in the length and diameter of the cob represent the only definite change occurring over a span of 1,000 to 1,500 years (Grobman *et al.* 1961:88).

At the Tiahuanaco level the continuous and consistent trend of increasing cob dimensions is abruptly stopped, and shorter ear maize is introduced. The new ear type found at this level exhibits in all its characteristics a definite similarity to the floury Chullpi-like maize from the La Molina site (Grobman *et al.* 1961:89).

The introduction of floury maize to the Peruvian Coast preceded the Tiahuanaco Period. It was a slow diffusive process into the original popcorn races, as it is evidenced by the Paracas and Nazca archaeological material. The great predominance of floury maize in the Coastal Tiahuanaco period following the era of slow diffusion was brought about by a sudden massive introduction of new maize from the highlands to the Coast, as the Ancon sequence and comparisons between other pre- and post-Tiahuanaco collections indicate (Grobman *et al.* 1961:91).

When stratigraphy permits chronological classification of ancient materials, it is possible to study in more detail the evolution of maize based on ear morphology. Bonavia (1962) has described the Teatino style from a site in Ancon on the Peruvian central coast. The cobs found by Bonavia were studied preliminarily and reported by Grobman *et al.* (1961). A more detailed report is presented here to show how dynamic the evolution of maize was on the coast of Peru. To study the cob morphology we used the internal ear characteristics as defined by Grobman *et al.* (1961). The data are presented in Table 14.4. Levels 1-8 at Ancón represent a span of about 300 years, from A.D. 800-1100, with level 8 being the earliest. The average ear length increases from level 8 (earlier) to level 5, and then decreases sharply. It should be recognized that, even though the measurements were taken very carefully, the short mean ear length in the later levels (2 and 1) could be

Table 14.4. Averages of external and internal ear characteristics for eight stratigraphic levels at Pozo Miramar, Ancón, Peru. Measurements are in centimeters.

Level	N	Cob Length	Cob Width	Cob/Rachis	Glume Texture ^a	Glume Pubescence ^b	Cupule Length/Width
Level 1	7	4.97	1.94	1.42	2.71	1.28	0.40
Level 2	7	4.40	1.71	1.42	2.50	1.21	0.52
Level 3	5	broken tips	1.60	1.43	2.25	1.25	0.45
Level 4	16	8.43	1.74	1.39	2.27	1.50	0.51
Level 5	13	10.60	1.74	1.46	2.35	1.45	0.44
Level 6	10	7.30	1.60	1.44	2.30	1.75	0.42
Level 7	14	7.80	1.78	1.39	2.00	1.66	0.48
Level 8	8	6.10	1.54	1.49	1.92	1.83	0.52

^aOn a scale of 1 = soft to 4 = hard.

^bOn a scale of 1 = no pubescence to 3 = very pubescent.

due to some broken ears that were erroneously measured as unbroken ears, but we are convinced that the trend is real. The cob diameter increases from level 8 steadily to reach an average of 1.94 cm in the upper level. Apparently there is no change in the cob/rachis index or in the cupule length to width ratio. Although Table 14.4 shows some decrease in both characteristics from the lower to the upper levels, the trend is not clear enough to permit definite conclusions.

The more interesting trends are in the glume texture and pubescence; the glume becomes harder and losing its pubescence from the lower to the upper levels. According to Wellhausen *et al.* (1952), these tendencies are due to the incorporation of teosinte genes. These data from Ancón may reflect the incorporation of teosinte genes through Mexican introduced races of maize.

The maize from the lower levels apparently is related to Confite Morocho. The increase in ear length and diameter levels in 8 to 7 could partially be due to the heterosis of two sympatric races, possible Confite Morocho and Confite Iqueño. Beginning in level 6, the maize cobs are similar to proto-Pagaladroga. This is evident in the increase

in length and the reduction in rachis diameter that is seen in level 5. Chullpi intromission took place between levels 4 and 3. This produced more variability eventually producing a new population that may be called proto-Chaparreño. In the uppermost level, level 1, the cobs show a increase in length but none in diameter, so there is no evidence of the presence of more evolved races such as Alazan or Chancayano.

The diversity and relatively rapid change seen in this maize collection is characteristic of the maize found abundantly in archaeological sites on the coast of Peru starting from early Paracas, 2,500 years ago. In contrast, preceramic maize is scarce. Bird (1990) finds several difficulties with the early maize chronology. It is difficult to imagine that maize could have been grown in the central and southern highlands in the sixth to the fourth millennia B.C. without spreading to the coast before 2000 B.C. Also problematic is that the preceramic maize from Los Gavilanes and Aspero dated to before 1750 B.C. does not appear elsewhere in the region until after 1000 B.C. Bird (1990) also argues that the morphology of the cobs found in supposedly preceramic contexts is too developed to be as ancient as is claimed.

Obviously more archaeological work needs to be done with detailed stratigraphic associations. It is necessary to fill the gaps between the early material from Los Gavilanes, which the quality of the archaeological and botanical work makes convincingly preceramic, and the massive presence of maize in sites of the first millennium B.C.

Other classes of evidence are also needed to relate the early races of maize in the Andean zone to modern races and to Mesoamerican maize.

Karyological Evidence

Because morphological traits are subject to visual selection, humans can produce in a relatively few years morphological changes that disturb the picture of the evolutionary pathway. Unlike morphological traits, chromosomal characteristics have not been directly influenced by human selection. This permitted McClintock (1978) to trace the origin and migration of races of maize in the Americas. Based on the information obtained by Kato from the teosintes of Mexico and Guatemala, she concluded that the Mexican teosinte is the

source of all the basic germplasm of maize. However, the so-called Andean complex, characterized by a small knob on the third position of the long arm of chromosome 6 and a small knob on the long arm of chromosome 7, is so unique that apparently there is no close relationship between Andean and Mesoamerican maize. McClintock concluded that the initial introduction of maize into the Andes came from the highlands of Guatemala. More recently, Bretting and Goodman (1989) have discussed the postulated origin of several races based on the karyotypic evidence, isozyme analysis, and the interaction of morphology and genotype with environmental factors, finding some inconsistencies with the maize relationships proposed by Wellhausen *et al.* (1952). The systematic studies of Bretting and Goodman (1989) reveal a strong difference in karyotype between lowland and highland races. However, the known association between karyotypic variation and altitude has a notable exception at the chromosome 6 knob position, which means that these differences are due to the racial origin rather than an environmental effect. Bretting's work supports McClintock's (1978) and Kato's (1984) hypothesis that Andean races are derived from Guatemalan races.

In the following section, descriptions of the Andean races will be accompanied with a brief description of each karyotype in order to evaluate differences and relationships among races.

Races of Maize in the Andean Zone

In the Andean region the differentiation of races is notable. Goodman and Brown (1988) described a total of 252 races of maize, of which 132 races belong to the Andean regions. A brief description of the more important races follows. These races have been described by Brieger *et al.* (1958), Grant *et al.* (1963), Grobman *et al.* (1961), Roberts *et al.* (1957), Rodriguez *et al.* (1968), and Timothy *et al.* (1963).

Primitive Races and Their Derivatives

All the evidence points to Confite Morocho as the most ancient maize race in South America. It is still cultivated in Ayacucho in small

farmers' fields, associated but not crossing with other more recent races. Its morphology indicates that it is a primitive maize. Its few pop grains are inserted into a very thin cob with unusual, superficial, long cupules.

There is evidence of a very early presence of Confite Morocho on the coast of Peru. The already-cited maize from Los Gavilanes is about 50 percent proto-Confite Morocho. It has also been found at Los Cerillos in Ica, with an antiquity of 2,300 to 2,500 years; in Paracas (1700-2500 B.P.); in Viru, Huaca de la Cruz (1500 B.P.); and in the Moche Valley in the post-classic Chimu period (A.D. 1000-1400) (Grobman *et al.* 1961). Its derived races proto-Alazan, proto-Rienda, and proto-Pagaladroga were found in the same sites.

Two other races apparently cultivated as early as Confite Morocho were Confite Chavinense and Confite Iqueño, neither of which survive. Confite Chavinense has played a major role in the origin of several Peruvian races. It originated in the northern Peruvian highlands and spread to the west coast very early, as is evident in Los Gavilanes (Grobman 1982). Confite Iqueño is another primitive race with major influence in the evolution of the lowland early floury races. It appears at Los Cerrillos in the Ica Valley (2300-2500 B.P.). It was also found in the Nazca valley (A.D. 1-800) and at Huaca Prieta on the north coast, associated with a very elementary pottery and with squash, peanuts, and beans. Here was also evidence of hybridization between Confite Morocho and Confite Iqueño (Grobman *et al.* 1961).

From Confite Iqueño the two modern races Mochero and Chaparreo have originated. Mochero is the early floury kernel race of the northern Peruvian coast, and Chaparreo is the early floury race of the southern coast. Huachano is another coastal race whose morphology relates it to Mochero.

Kculli is another very ancient race. According to Mangelsdorf (1974), it is one of the six lineages from which all modern races have originated. It was present at Los Gavilanes. Mochica and Chimu pottery include molded ears unmistakably of Kculli. The most distinctive characteristic of this race is the dark color of the pericarp, glumes, and cob due to the high frequency of genes that produce antocyanic pigment. The frequency of this gene is very high in Peru and clearly decreases both north and southward. In Ecuador, a more developed race is called Racimo de Uva. In Argentina and Bolivia,

this race is known by its Quechua name Culli or Kulli. Besides the Andean karyotypic pattern, this race has a knob on the 4L chromosome and B chromosomes.

Chullpi is another of Mangelsdorf's ancient lineages. This race originated from Confite Chavinense. It has a unique rounded ear, a very high kernel row number (up to thirty), and kernels with sugary endosperm. One important trait is the ratio between grain weight and cob weight, which is the highest known. There is convincing archaeological evidence for the presence of Chullpi on the coast of Peru. I have already demonstrated how Chullpi influenced the ear morphology of the Peruvian coastal races. A site in La Molina, 800 years old, had many ears similar to Chullpi, some intermediate between Chullpi and Chaparreo, and some like an early Chaparreo, showing an evolution of Chullpi in the direction of modern Chaparreo. Chullpi is now grown in Ecuador, Bolivia, and southern Argentina.

According to Mangelsdorf (1974), the Mexican race Palomero Toluqueo was the father of all the pop races. If this is true, it produced Confite Punteagudo and all similar races in South America. Canguil, a popular Ecuadorian race, belongs to this group. As in Confite Punteagudo and Pisankalla from Bolivia and Argentina, it lacks the typical Andean chromosome knob pattern. Besides 6L and 7L, they have knobs on 4L, 8L, and 9L, and Pisankalla of Bolivia has additional knobs on chromosomes 1, 2, and 5. Knobs on 4L, 8L, and 9L are typical of some early races of northwestern Mexico, as well as some races with small ears related to the Mexican dents.

Goodman and Brown (1988) grouped all races with conical ears and pointed kernels, growing mostly at medium or high elevations in central Mexico, into one category including Palomero Toluqueo, Cónico, Chalqueo, and Arrocillo Amarillo. Confite Punteagudo has some characteristics resembling these Mexican races, including pubescent leaves and stalks, many tillers, and sparsely branched tassels. Quechua names for Confite Punteagudo such as *chilisara* (old maize) are evidence of its antiquity in the Andes. Its long history in South America is also evident in its amazing variability in Argentina, Chile, Paraguay, Uruguay, Brazil, and Bolivia.

Anciently Derived Races and Their Derivatives

Ancashino has played a major role in the formation of races on the coast of Peru. Ancashino belongs to the same group as the highland races Huayleño, Shajatu, Maraño, and Huanuqueño. They vary as a cline, Huayleño being the most ancient, and the coastal races Jora, Pagaladroga, and Alazan being on the periphery of the cline. The ears from the Guitarrero Cave that Smith defined as Ancashino are probably Huayleño or Confite Chavinense (Grobman 1982), which is the parent of Huayleño as well as of many broad-eared Andean races.

In Mochica pottery there are molded ears that Grobman *et al.* (1961) identified as proto-Ancashino, proto-Pagaladroga, and proto-Alazan, indicating that these races co-existed on the coast. Today Ancashino grows in the highlands while Alazan and Pagaladroga are limited to the north coast. Ancashino and Huayleño have a limited distribution in the north-central highlands in the Callejon de Huaylas, where Guitarrero Cave is found. The variation in pericarp color in Ancashino is the largest known for any race.

Related to Ancashino but adapted to lower elevations are the races Shajatu, Maraño, and Huanuqueño. They have larger ears characteristically found in Ecuador and Colombia, overlapping the Sabanero area of diffusion. Ancashino and Shajatu have the Andean knob pattern, as does Huayleño with an additional knob on 9L. Pagaladroga has only one knob on 7L, but its related races Alazan and Jora have from four to fourteen, indicating their foreign origin.

In the central Andes of Peru, the common races belong to the San Geronimo Huancavelicano complex. Apparently they have derived directly from Confite Morocho, but they also have the typical round ear that characterizes the Confite Chavinense lineage. They have peculiar soft kernels that are appreciated for eating directly as *choclo* (green corn), *cancha* (dry and toasted corn), and *mote* (boiled corn). White grain color is typical in the San Geronimo and Huancavelicano races, and purple mottled or speckled aleurone is typical of Piscorunto of Peru, Checchi in Bolivia, and Oke in northern Argentina. Huillcaparu is a related Bolivian race with a high frequency of brown pericarp and purple aleurone. Granada of Peru has a round ear and a very high frequency of red coloring in the pericarp and glumes.

These races are closely related to the Paro-Capio racial complex, members of which also have very soft floury kernels. They tend to have a high row number, a trait relating them to the Chullpi race. Capio from Argentina and Bolivia belongs to this group as well as Capio Chileno and Harinoso Tarapaqueño from Chile. Harinoso Tarapaqueño has ears very similar to the Peruvian San Geronimo, but has not adapted to the central highlands of Peru because of an extreme susceptibility to rust. Diseases, mainly the stalk and ear rot produced by *Fusarium moniliform*, limit the diffusion of this race.

Almost all races in the San Geronimo-Huancavelicano and Paro-Capio complexes have the Andean knob pattern; Paro has only one knob on 7L. The homogeneity seen in the chromosomes can also be seen in the isozyme variation, which, according to Goodman and Stuber (1983) and Doebley *et al.* (1985), is very limited in the Andean highlands compared to that found in Mexico, further evidence that the Andean races are closely related to each other. However, for Mexican germplasm, the isozyme variation within races in many cases is greater than the variation between races, so the relationship between isozyme variation and real genetic variation still cannot be determined.

Cuzco Racial Complex

The Cuzco maize race has had much influence in the Andean highlands. Many races of the lowlands and highlands show its influence in large grain size and a low number of straight kernel rows. In contrast to the early floury races of the coast, which probably derived from Confite Iqueño, the late floury coastal races used as *choclo* probably originated from Cuzco. The presence of Cuzco on the coast of Peru is demonstrated by its depiction in Mochica and Chimu pottery. The Spanish chroniclers made frequent references to this race. The spread of Cuzco, as with many other highland races, probably followed the influence of the Inca empire.

The popular *choclo* coastal races Chancayano and Pardo are related to Cuzco. Chancayano has some influence from foreign races as is evident from the karyotypic analysis. Pardo has the Andean knob pattern. Another *choclo* race, Huachano, is also related, but its internal cob structure is very similar to Mochero, and it also has the knob in 9S that

is typical of the Guatemalan big grain complex (Bretting and Goodman 1989).

A related race, Cuzco Cristalino Amarillo, is one of the highest elevation maize races in the world. Its plant is very short for efficient life and reproduction in severe environments. Its influence is mostly southward from Cuzco to Bolivia and northeastern Argentina.

Goodman and Brown (1988) included the following races in a group with Cuzco: Uchuquilla, Amarillo de Ocho, Chake-sara, and others such as Niñueño, Aysuma, Kcello from Bolivia, Marron, and Patillo Grande. All of these share with Cuzco Cristalino the trait of eight very straight rows of kernels, a pattern that shows low variability. They all also have broad, flat, *morocho* kernels embedded in a very narrow cob.

Another Bolivian race, Carapampa, is more ancient than the others and may be the parent of Uchuquilla and related races. Many features of this race resemble Confite Morocho, from which it originated.

Chillos, a yellow, floury, large-kerneled race from Ecuador is closely related to Cuzco, from which it inherited the large kernel size. Chillos is also related to the soft floury kernel group of races of northeastern Peru, where there is another clinal variation having Ancashino as the central core.

The most productive race in the Andean region, Cuzco Gigante, is derived from Cuzco. It is a late-maturing race, generally with white kernels, whose exceptional size is much appreciated. A sub-race with yellow *morocho* kernels can produce as much as ten tons per hectare in the Cuzco area. Even though this race has a very specific adaptation, it can be found in other countries; in Bolivia a very similar race called Hualtaco is commonly used for *choclo*.

The race Cuzco has produced other races with special local adaptations such as Arequipeño and Coruca, adapted to the southern Peruvian and northern Chilean coast. The pattern of evolution that goes from smaller to larger has an exception in the Ariquepeño race, which has a Cuzco origin but smaller ears. Another case is Confite Puneño and possibly Altiplano from Bolivia, which derived from the Cuzco variability to occupy a very limited and narrow environment on the islands and shores of Lake Titicaca. In this case adaptation to extremely high elevations has resulted in reduced ear and plant size.

Flexible Cob Derivatives

A less obvious pattern of evolution is the case of the flexible cob. The flexibility of the cob results from a lower degree of condensation, suggesting that this trait may be earlier on the evolutionary pathway. However, a strong selection for ear length may produce flexible cobs in some races; this could be tested experimentally.

Two flexible cob races that have almost disappeared in Peru are Rabo de Zorro and Rienda. Grobman *et al.* (1961) consider Rabo de Zorro directly derived from Confite Morocho and give it a major role in the evolution of maize in Peru. Based on internal cob characteristics, Rabo de Zorro looks very ancient, but since the flexible cob is found in other races, the role of this race is questionable and deserves more study. The same can be said of Rienda, which has a flexible cob due to the long internodes between cupules in the rachis. The value of the cupule length to width ratio is one of the largest, indicating the presence of Confite Morocho in its genealogy. Rienda is sympatric with the race Perla, the most productive race on the coast of Peru, and it is sometimes mistaken for a variant of Perla. Like Perla, it has many chromosome knobs.

The race Morocho is widespread in the Andean zone. The term *morocho* is applied to a type of kernel that has a floury core and a thick external layer of flint endosperm tissue. This type was often mentioned by the early Spanish chroniclers as having been used by the Inca army to feed its soldiers.

Analysis of the ear based on internal characteristics shows an evolutionary pathway starting with Confite Morocho, going through Morocho, and spreading in its most recent form, Morocho Cajabambino, into the northern Andean countries Ecuador and Colombia.

Sabanero Race Complex

In the northern countries the tendency is to grow late varieties in the warmer valleys of the highlands. The Sabanero race originated in these regions. According to Goodman and Brown (1988), Sabanero is central to a number of clines of variation throughout the north Andean region. The group of races related to Sabanero diverges from it in few

characteristics. Pollo from Venezuela and Colombia and Patillo from Ecuador have smaller ears than Sabanero but retain the relatively large, rounded kernels. Cabuya from Colombia and Huandango from Ecuador are similar races; they have a lower row number than Sabanero. They share a common aleurone color with Cacao, another race of this group from Colombia and Venezuela with a brown or bronze aleurone, and with Cariaco, a lowland Colombian and Venezuelan race. Brieger *et al.* (1958) detected many similarities between Cariaco and some of the races of the Avatzz group from Paraguay, but as they pointed out, the resemblance of races based on morphological characteristics is not sufficient evidence of their relationship, since similar mutations could occur in different races, be maintained by selection, or evolve in a similar way giving the impression of a common origin.

Montaña and Amagaceño from Colombia, and Morochon from Ecuador have longer ears than Sabanero. This group of races resemble the Quicheño-Oloton group of highland Guatemala. Capiro, a Colombian race that is a floury form of Montaña (Goodman and Brown 1988), also resembles another Guatemalan floury-kerneled race, Salpor.

Some of the Colombian races such as Montaña, Amagaceño, Capiro, and Cacao do not have the Andean chromosome knob pattern.

Races from the Amazon Region

The race Piricinco of the eastern lowlands of Peru, also called Coroico or Entrelazado (Brieger *et al.* 1958), is a very peculiar race with long narrow ears, expanding shank ends, interlocked rows of kernels, several layers of aleurone, and strongly attached shanks. Another interesting feature of this race is the very low condensation between cupules; the cupules have a length to width ratio close to 1, similar to that of Confite Morochò.

Piricinco is still found as pure stands in isolated places, but as it is now sympatric with some introduced races, there are many crosses which maintain the typical Piricinco ear. It may be that karyological analysis has been made on these contaminated Piricinco samples, because besides the knob on 7L that is part of the Andean pattern, they

also have knobs on 4S, 2S, and 8L similar to Caribbean and Mexican dent races.

Enano is a race that used to be grown in the southeastern jungle of Peru but has now almost disappeared. It shares similar characteristics with its sympatric race Piricincó, but Enano has a very small ear. This may be a case in which Piricincó was developed by direct selection for ear length from the earlier Enano race. However, such an evolutionary pattern requires a large genetic variation whose origin is difficult to explain.

Introduced Tropical Races

The trend of extinction for races such as Piricincó and Enano is due to the planting of a group of races recently introduced into South America that have been used intensively in breeding. Brown (1960) has documented the introduction of such races as Coastal Tropical Flint, Cuban Yellow Flint, and Tuzón from the West Indies.

There is a controversy about the origin of Coastal Tropical Flint and the Catetos of eastern South America. Based on karyotypic analysis, Blumenschein (1973) thinks that the Catetos were formed by the combination of genetic material from three sources: Tuxpeño, a maize from south Guatemala, and the small knob complex that evolved in the highlands of Guatemala. He placed the origin of Cateto in Las Antillas. Bretting *et al.* (1987) used karyologic and isozyme studies to suggest that Cuban Flint is an indigenous Cuban race rather than a South American Cateto recently introduced into Cuba, as the more accepted hypothesis proposes.

In any event, flint and dent races related to the West Indian maize have been in eastern South America for a considerable length of time, as evidenced by their great variability (Sevilla *et al.* 1984). We can expect sufficient divergences of the eastern South American races from the Mexican, Central American, and Caribbean maize as they take advantage of hybrid vigor.

Implications of the Past for Future Breeding of Corn

Goodman and Brown (1988) have pointed out that understanding the variability of corn is important (1) to shed light on the history and relationships of the people whose lives are closely related with maize and (2) to point to the most efficient and effective ways to minimize the genetic vulnerability of commercial corn. In addition, corn breeding can benefit from a better understanding of the evolutionary history and genetic variability within the genus. The first and second reason are so important and self-explanatory that nothing more need be said. The third reason is of major interest for Latin America because through sustainable plant breeding it is possible partly to solve the problems discussed in the introduction to this chapter without losing the genetic variability that evolution has created over thousands of years.

At present there are two trends for maize breeding in Latin America: (1) more extensive use of heterosis and testing different heterotic patterns, and (2) selection in limited environments to create varieties adapted to the marginal lands of Latin America. It is well known that heterosis, or the excess of yield of a hybrid compared to the parental yield, depends on the level of diversity or divergence between the parents. However, heterosis cannot be predicted — the combined ability of the parents has to be tested experimentally. Knowledge of the origin of the races can help in planning and reducing the extensive work required to know the ability of every parent to combine efficiently with all other possible parents. Knowledge of maize evolution will be necessary for broadening the genetic base of the maize breeding population. Creating varieties resistant to disease and insect attack and adapted to the stresses imposed by soil and weather conditions requires the use of germplasm that has evolved under those limiting conditions. For example, Galinat (1967) described two special mechanisms by which southwestern corn has adapted to an arid environment: a greatly elongated mesocotyl that permits deep planting, and a single thick radicle that rapidly descends to the moist subsoil and supplies water during the critical seedling stage.

Complete and precise records of the morphological variation among the races of maize at various times in antiquity in areas with a limiting environment would be very helpful to modern maize breeding.

Studying the evolution of these races can shed light on the avoidance mechanisms that the plants produced through adaptation to those environments.

In studying the evolution of corn in the Andean zone, we come to the conclusion that many of the adaptive mechanisms allowing maize to be grown in a variety of severe environments were fixed very early in the evolutionary process. Greenblatt (1985) and Sevilla (1987) have detected some avoidance mechanisms that permit some races to adapt to very cold weather in Peru. To neglect these mechanisms in the process of breeding or to lose them by genetic erosion would cause irreparable damage. Nature will never again create such variability. The task for maize breeders in the near future must be to create methodologies for a sustainable and conservative breeding.

Discussion

The great variability of maize has to be used for the benefit of humankind. To use the whole diversity of maize properly, it is necessary to know it and to understand how that diversity has been created.

Archaeologists and paleoethnobotanists have an enormous task tracing the evolutionary pathways of maize. Every single cob must be analyzed. Racial assignment of the archaeological sample is a necessary step in the understanding of maize evolution. Comparative morphology is a good start in racial classification, but it is insufficient. Due to selection by humans, the main force of evolution in the Andean region, different races became similar in characteristics such as shape and color.

Size and shape are very important features and decisive when there is only one variety from an archaeological site. In that case it may be possible to use the dimensions of the cob as chronological markers. The correlation between morphology and chronology becomes more difficult when more than one race is present. In that case a detailed racial analysis must be done.

Small samples present real problems (see Goodman, this volume), since with only a few ears it is almost impossible to get a good racial assignment. Methodology for cob morphological analysis is well developed (see Bird, this volume), and it is encouraging to see a

growing interest in studying the causes of physical changes in archaeological maize material. Corn grains are easily analyzed, but conclusions must be drawn carefully since variation in kernel size and shape within a single ear can be very large.

To draw conclusions from archaeological maize remains one must have an extensive knowledge of the modern races of maize. Comparing measurements is not enough; erroneous conclusions can be produced since many races that have similar morphologies are phylogenetically distinct. One needs to know the area of diffusion of the race, its scope of adaptation, the context in which the race evolved, and its eco-geographical and phylogenetic relationships.

Now that molecular techniques for the characterization of ancient maize are being applied (see Doebley, Goloubinoff *et al.*, this volume), the evolutionary relationships between archaeological maize and modern races will be defined more accurately. The modern races can be used as probes to search for similarities at the molecular level. Thus knowledge of modern racial variation is of paramount importance if archaeological maize is going to play a role in the study of past human culture.

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