



# The origin and diversity of maize in the american continent

José Antonio Serratos Hernández  
Universidad Autónoma  
de la Ciudad de México

**GREENPEACE**

[www.greenpeace.org.mx](http://www.greenpeace.org.mx)

This document was written for Greenpeace Mexico  
by Dr. José Antonio Serratos Hernández,  
researcher and maize project coordinator at the  
Universidad Autónoma de la Ciudad de México

January 2009

# Index

<b>Introduction</b>	<b>2</b>
<hr/>	
<b>The center of origin of maize</b>	<b>4</b>
History of research on the origin of maize. 1700 - 1990	5
History of research on the origin of maize.1990 to the present	10
Status of the knowledge on the center of origin and domestication of maize	12
<hr/>	
<b>The diversity of maize in the American Continent</b>	
Studies on maize diversity from 1940 to 1980	14
Studies on maize diversity from 1990 to the present	18
<hr/>	
<b>Maize migration and diversification in America</b>	<b>22</b>
<hr/>	
<b>The peoples and cultures in America and maize diversity</b>	<b>24</b>
<hr/>	
<b>Analysis and perspectives of maize diversity in the American Continent</b>	<b>29</b>
<hr/>	
<b>References</b>	<b>31</b>

# Introduction

Maize is the cereal of the peoples and cultures in the American continent. The most ancient civilizations in America –from the Olmecs and Teotihuacans in Mesoamerica to the Incas and Quechuans in the Andean region of South America- flourished accompanied with this plant. This link between culture and agriculture had motivated the humanists and scientists to ask: which is the origin of this cereal? How was the evolution of maize once the different human groups adopted and cultivated it for their own profit? These questions had led them to explore the past, and nowadays -thanks to the technological and scientific development- led them to unravel several enigmas which surround the domestication of this crop.

Although not all the details that allow us to explain its origin and domestication had been found, the scientists reached a consensus: the direct ancestor of maize is the teosinte. Nevertheless, during more than 70 years and before reaching such conclusion, there was a deep debate which contributed to the advancement of knowledge in several areas of the scientific endeavor. So is it that some of the greatest scientists of the 20th century studied maize, its origins and diversification. For example, in 1983 the American researcher Barbara McClintock was awarded the Nobel Prize in Physiology due to her discovery of the mobile genetic elements<sup>1</sup> in the chromosomes of maize.

Maize is the cereal which has had more importance in the economy sector worldwide during all the 20th century and the beginning of the 21st. In the industrialized countries, maize is mainly used as forage, raw material for the production of processed foods and, recently, for ethanol production. On the other hand, in some Latin American countries and increasingly more in Africa, a great percentage of maize produced or imported is used for human consumption. In this sense, maize had been and still is a key factor for the survival of farmers and indigenous people who live in most of the countries of the American continent. It is paradoxical that, even with each time less and less economic resources allocated for the inhabitants of the poorest communities, they are the stewards of maize diversity. Such situation is putting at risk valuable seeds: the researches and studies conducted through out several years from the point of view of scientific and humanistic disciplines, have proved that the role of the farmer is of uttermost importance for the preservation and diversification of maize. However, the research and development programs for in situ conservation of maize are very restricted and had not been generalized to important regions with great concentration of ethnic and farming groups.

Nowadays, keeping maize germplasm banks, or ex situ conservation, is the dominant

strategy because it is linked to the technological path of the developed countries and also because the in situ conservation in several less developed countries is not supported due to financial restrictions. It is foreseen that within a few years, the lack of care and attention to these rural communities where the mayor percentage of native germplasm is, will have a negative impact on maize diversity. It is also foreseen that the public policies that promote the intensive capital technologies which move the jobs towards urban areas or towards foreign countries, will determine the rate of extinction of genetic resources of maize.

The risk of losing the genetic diversity of maize is very high. The economic conditions of poverty and marginalization faced by the farmers, as is already evident in several regions of America, will lead to a generalized extinction of maize diversity. One way to alleviate this situation is to re-value the crop through the knowledge of its origin and diversification in the American Continent. This document aims to recover the history of the scientific research and socio-cultural aspects related to the origin and diversity of native maize, in order to allow the peoples of America rescue the plant which is a symbol of the American continent and its culture.

<sup>1</sup> These genetic elements are also known as "jumping genes", due to its ability to "jump" from one part to another in the chromosomes.

Image: Maize from Noregachi, Chihuahua / © David Lauer



## The center of origin of maize

One of the greatest geneticists and researcher of cultivated plants of the 20th century, Nikolai Vavilov (1887-1943, <http://www.vir.nw.ru>), contributed to the concept of center of origin.

Thanks to his research we know about and were explored the eight regions in the world where the cultivated plants have their origin. More than theory, it is the field work and the biogeographic exploration which constitutes the legacy of Vavilov to the human race. This legacy is kept in one of the first germplasm banks of cultivated species in the world, and which was built at the beginning of the 20th century in Leningrad.

The "Center of origin" of cultivated plants had been defined

as a geographical zone where the major part of the crop diversity is located and where its wild relatives coexist or coexisted (Figure 1). Particularly, Vavilov takes into account several aspects to define the centers of origin of agricultural crops: 1) they are geographical areas where such crops are still sown; 2) they are linked to large land extensions; and 3) "the primary centers of origin of crops are located in mountain ranges". According to Vavilov's findings, the origin of maize and approximately 49 species more are located in the Primary Center VII (Figure 1), which is in southern Mexico and Central America. Since its first exploration in Mexico, it was evident for Vavilov that *Euchlaena*, the genus in which

teosinte was classified, was the maize's closest wild relative.

Along with maize, teosinte was described during Colonial times in Mexico, and Francisco Hernandez Boncalo (1515/1517-1578) was the first one to report the existence of this plant in 1570. The Spanish botanist and physician Hernandez Boncalo carried out expeditions in order to study Mexico's flora and wrote several documents regarding the plants of the New World and its medicinal herbs. Many of his writings were lost in the fire at El Escorial, in 1671, but these were recovered thanks to the copies Boncalo kept in several different writings about botany and medicine.

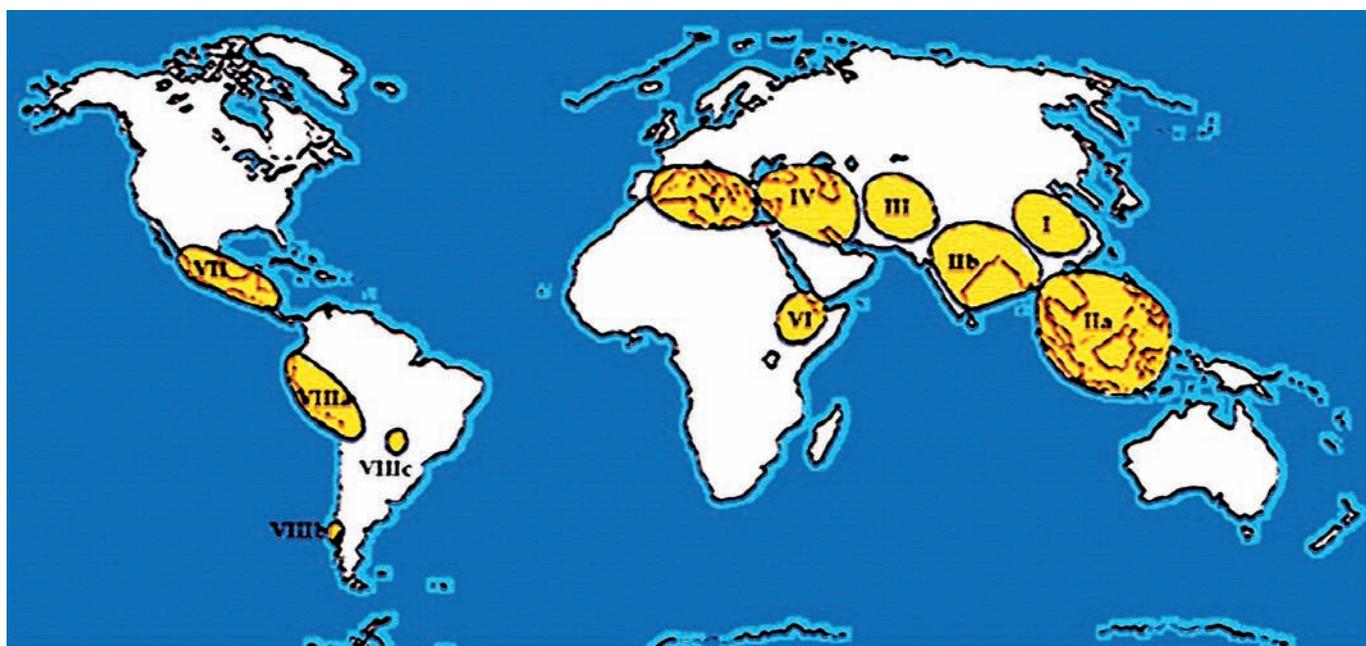


Figure 1. Location of the centers of origin / domestication of cultivated plants, according to Vavilov. Adapted by Antonio Serratos from: <http://dataservice.eea.europa.eu/atlas/viewdata/viewpub.asp?id=2718>

# History of research on the origin of maize

## 1700 – 1990

After those first references from Francisco Hernandez during the rule of Felipe II in Spain, and the first dispersion of maize through out Europe during the 16th century, the research on maize and teosinte stopped until few centuries later.

Maize, from the Natural System of Linnaeus (1748), was classified in the genus *Zea* and since then it did not suffer any major modifications until the 20th century, when teosinte was included in that genus. Other taxonomical and botanical studies carried out at the end of the 19th century and the beginning of the 20th; summarize the relationship between teosinte and maize and their possible evolution. The pioneer studies of teosinte taxonomy were done by Schrader (1833), who classified it as *Euchlaena mexicana*. According to George Beadle<sup>2</sup>, in 1875 the botanist Ascherson already considered that *Euchlaena* truly belonged to the genus *Zea*; but he found really difficult to explain how

“a simple ear of teosinte evolved into and gave origin to the huge maize cob, even with the influence of human selection”. Other studies regarding the origin of maize were carried out by Hershberger (1893). These studies suggested that maize is the result of hybridization between teosinte and other kind of grass, maybe an extinct one.

The origin of maize has not been easy to track down. The ear is unique among cereals; therefore, its evolution has been a great scientific challenge. On the other hand, the fossil record of ancient remains of maize, found in several parts in Mexico, show a great morphological change from the small female inflorescence (“mazorquita” or “small ear”) of teosinte –which only has a few kernels that are easy to thresh, and the female inflorescence (ear) of maize which has a great amount of kernels strongly attached to the “olote” (cob or raquis). Although there is a notorious discontinuity

in morphology from the female inflorescence of teosinte to the ear of maize, the analysis of intermediate structures (Figure 2) produced by their progeny suggested different interpretations of the origin of maize.

During the first quarter of the 20th century, before the first archeological explorations related to maize took place, the studies on the cell-genetics of teosinte and maize started. Between 1930 and 1932 Barbara McClintock<sup>3</sup> laid the foundations of the research which would grant her the Nobel Prize, 50 years later, due to her findings on the genetics of maize and to the methodology for chromosomal analysis.

<sup>2</sup>G.W. Beadle, 1978. “Teosinte and the origin of maize”. *Maize breeding and genetics*; D.B. Walden (Ed.), Wiley Interscience; Pages 113-128.

<sup>3</sup>McClintock B. 1929. “Chromosome morphology in *Zea mays*”. *Science*, Volume 69, Number 1798, Page 629; McClintock B. 1930. A Cytological Demonstration of the Location of an Interchange between two Non-Homologous Chromosomes of *Zea Mays* PNAS Vol. 16, Number 12; Pages 791-796; Creighton HB, McClintock B. 1931. A correlation of cytological and genetical crossing-over in *Zea mays*. PNAS Volume 17, Number 8, Pages 492-497.



Figure 2. Morphological sequence of the possible evolution of the ear from teosinte to maize. Elaborated by Antonio Serratos from several sources: The pictures 1 and 2, from left to right, are from the web page of the Koshland museum ([www.koshland-science-museum.org/exhibitdna/crop02.jsp](http://www.koshland-science-museum.org/exhibitdna/crop02.jsp)), pictures 3 and 7 were obtained from the webpage of the John Doebley's laboratory ([teosinte.wisc.edu/taxonomy.html](http://teosinte.wisc.edu/taxonomy.html)), and figures 4 to 6 from Iltis (footnote No. 12). Pictures 8 and 9 are of the race Conico from the Altiplano (Antonio Serratos personal files).

At the same time, the study of the cytogenetics of maize and teosinte progeny, as well as the morphological analyses, shed some light on the origin of maize by reproducing morphological series which suggested a possible path in the evolution of maize from teosinte. The studies of differences and similarities in the chromosomes of maize and teosinte hybrids, and the morphology of its progeny, gave researchers such as Collins (1921), Emerson (1924), Beadle (1932, 1939), Emerson and Beadle (1932) and Arnason (1936) elements to set possible steps in the evolutionary path of both species.

Nevertheless, for many researchers the weakness of the fossil record and the differences between the ear of both plants were facts that prevented them to give a satisfactory explanation on the origin of maize from teosinte. In 1938, Paul Mangelsdorf and R. Reeves<sup>4</sup> proposed the foundations for one of the most influential hypothesis on

the origin of maize; this hypothesis explicitly ruled out teosinte as the ancestor of maize.

Particularly, a research of Mangelsdorf (1959) put forward some of the events that could have happened during the evolution of domesticated maize.

This research was based on the morphological analysis of the remains of maize found in the Bat Cave (New Mexico, United States of America) in comparison to the more recent maize considered to have primitive traits (the tunicate maize and the popcorn maize) and its wild relatives: teosinte and tripsacum. With the information derived from his experiments with the hybrids of tripsacum and modern maize, Mangelsdorf (1959) established that an extinct wild maize of the tunicate kind and a species of tripsacum gave origin to maize (Figure 3). During the 70s, in the 20th century, with the discovery of the perennial teosinte (*Zea diploperennis*), Mangelsdorf modified his theory and proposed

that the maize originated from a cross between perennial teosinte and an ancient tunicate-popcorn maize. Based on this theory, he postulated that the existing teosinte sprung up from the hybridization between these two species.

For decades, the theory of the origin of maize from a wild type of maize -supposedly nowadays extinct- had several different "versions". At the same time, the hypothesis of teosinte as the ancestor of maize remained as antagonist to the hypothesis of a wild extinct maize. George Beadle, who since 1939 had carried out researches regarding the origin of maize<sup>5</sup>, shaped the theory of teosinte evolution and the human intervention in the process of maize domestication.

<sup>4</sup>Mangelsdorf, P.C. and R.G. Reeves. 1938. *The origin of maize*. PNAS 24(8). Pages 303-312.  
<sup>5</sup>Beadle G.W. 1939. "Teosinte and the origin of maize"; J. Heredity 30; Pages 245-247.

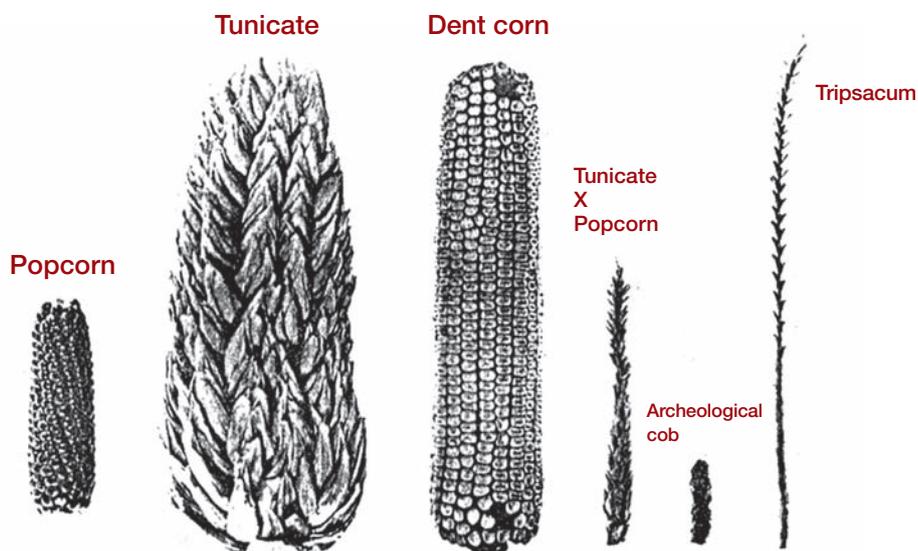


Figura 3. Analysis of tunicate maize, popcorn and tripsacum in the theory on the origin of maize, according to Mangelsdorf (1959). Adapted by Antonio Serratos from the illustration of Mangelsdorf (1959).

In two papers – the first one written at the beginning of the 70s and published in 1978 and a second one, its sequel, published in 1980<sup>6</sup> - Beadle summarizes the evidences he had gathered so far and develops its hypothesis of teosinte as the ancestor of maize. First, in spite of its morphological differences, maize and teosinte can have fertile progeny and can cross in a natural way in the fields. The crossing-over of chromosomes of these hybrids is normal; therefore, it was deducted that there is a close relationship between both progenitors and, according to Beadle, the fact that teosinte can survive in the wild confirmed its ancestry of maize. Likewise, the maize's dependency on cultivation indicated a modern characteristic, resulting from the selection humans carried out. Regarding these evidences and the research on the origin of maize carried out until that moment, Beadle underpinned the study of the origin of maize from teosinte. Beadle's students and the main groups of maize researchers in the United States of America and in Latin America have followed Beadle's theories.

Other studies carried out from the cytogenetic point of view –on the chromosomal knobs of teosinte and maize, by Angel Kato of the Post-Graduated School of Agriculture (1976) allowed the identification of variation and traits of each species and came to the conclusion that teosinte was an ancestor of maize. This research strengthened the hypothesis of progressive evolution of teosinte into maize. On the other hand, in order to estimate the number of genes which would be necessary

to differentiate maize and teosinte, Beadle himself, Mario Gutierrez and Walton Galinat carried out segregation experiments with the hybrids of Chapalote maize and Chalco teosinte. On the result obtained, they concluded that “approximately five major differential genes, independently inherited from the progenitors”<sup>7</sup> could explain the transition from teosinte to maize. Besides, due to a series of anthropological investigations of the folklore related to teosinte, Beadle interpreted the results as a support element for his hypothesis. According to Garrison Wilkes' studies (1970, 1977), in many parts of Mexico teosinte was used, and is still used, to improve maize's fitness. What's more, references of the explorations of Lumholtz (1902) in Chihuahua mention the use of teosinte in order to recover the yield of maize fields in the communities of the Nobogame region (Sanchez and Ruiz Corral, 1997). For Beadle, these observations, along with his own interpretation of the word teosinte<sup>8</sup>, could constitute a case of “cultural memory” which would confirm the association of the pre-Hispanic cultures with the evolution of maize from teosinte.

It is noteworthy that the word teosinte, as used nowadays, is an inverted version of the word *cinteotl*, which, among Mexicas, designated the temple where the maize goddess – Xilonen- was worshiped. Johanna Broda, in her study on the political ritual relationships among Mexicas (Aztecs)<sup>9</sup> explains part of the worships in “...*the parties of Tecuilhuitontli (the minor party of the teteuctin or landlords) and Huey tecuilhuitl (the major party of the teteuctin): On the 10th day*

*of the month (june-july), [called] Huey tecuilhuitl, a representative of the maize goddess, Xilonen, was sacrificed. On that day, the warriors (tiachcahuan, telpopochtin, yaque, and tequihuaque) danced holding maize plants in their hands. This ritual dance was performed in front of the representative of the Xilonen goddess, who was accompanied by her priestess (cihuatlamacazque). Sahagun [Brother Bernardino] points out that after the Xilonen sacrifice in the Cinteotl temple, people would eat the tortillas of jilote [immature maize ear] (xilotlaxcalcaliztli) for the first time on the year, and they would make offerings consisting of green stalks of maize (ohuatl) and the plant [called] huahuhquilitl. According to Duran, they ate vegetable tamales, [called] quiltamalli, and offer them in the temples –along with strings of green chili and fresh maize cobs- as first fruits.”*

In all the American cultures, the sacred character of the rituals around maize is focused specifically on the plant itself. Nowhere have been found, or searched for, references to teosinte in the trace remains, mural paintings, chronicles or codex of the different American cultures. This gap in the information makes difficult to grant the pre-Hispanic cultures a particular interest on teosinte and, even less, to its relationship with the origin of maize.

<sup>6</sup> Beadle GW. 1980. “The ancestry of corn”; *Sci. American* 242, Pages 112-119, and Note 2.

<sup>7</sup> See Note 6. Beadle GW. 1980.

<sup>8</sup> According to Beadle, the word “teosinte” comes from the aztec word *teocentli*, which means “God's cob of maize.”

<sup>9</sup> Johanna Broda. 1978. “Relaciones políticas ritualizadas: El ritual como expresión de una ideología”; *Economía política e ideología en el México prehispánico*, Carrasco P. and Broda J. (eds), CIS-INAH. Editorial Nueva Imagen, Mexico, Mexico City; Pages 221-254.

For example, in the Popol Vuh (1986), maize was always mentioned as such and what is narrated is how the gods create “the human body and flesh” from the maize dough<sup>10</sup>, but its ancestor is never mentioned nor is it the way the gods created the maize. Therefore, and contradicting Beadle arguments (1980), with the anthropological elements gathered so far, it is not possible to link teosinte in the Mesoamerican or Andean cultures’ cosmovision with the origin of maize.

A theory linked to current research groups is the catastrophic sexual transmutation (Iltis, 1983<sup>11</sup>), which at that time represented a novel way of thinking on the origin of maize. This theory establishes that the female inflorescences (ear) of maize derived from the central spike of the male inflorescences (tassel) of teosinte. In a surprising twist, Iltis proposes that, unlike everything established so far, maize evolved thanks to a sudden sexual transmutation which condensed the branches of teosinte, placing them in the female expression area of the plant. Thus, severe alterations in the nutrient distribution of the plant happened, therefore unchaining a drastic morphological change. These modifications in the structure of the male tassel, so to turn it into a cob, did not involve mutations but, according to Iltis, a phenomenon known as genetic assimilation<sup>12</sup>. This abnormal quantum change would then be profited by human selection or, in other words, once humans discovered this “useful monstrosity”, produced by very particular conditions, the hunter-gatherers

availed the opportunity of domesticate it through a selection process.

Although it would take long to make a reference to all the aspects discussed in the work of Iltis, it is important to mention that this theory is marked by its affinity to some scientific theories which were popular and well established trends at the end of the 70s, specifically the catastrophes theory (Rene Thom<sup>13</sup>) and the concepts of genetic assimilation and epigenesis (Conrad Waddington<sup>14</sup>).

Although the catastrophic sexual transmutation theory set out by Iltis is fascinating in many ways, the criticism it suffered since it was published seemed to be due to a misinterpretation of the concepts of Waddington (1975a) and of the evolutionary models formalized through the catastrophe theory (Thom 1977). In particular, it was considered that the genetic assimilation is a form of “Lamarckism<sup>15</sup>”; as a result, its scientific worth was discredited. Actually, the genetic assimilation concept is the Darwinist version of acquired traits and it is a concept that allowed Iltis (1983) to describe a possible morphogenetic and structural unbalance (Thom, 1977) in the development of teosinte, which explained its transformation into primitive maize.

Towards the end of the decade of 1980, the hypothesis of the origin of maize from teosinte was gaining force and consolidating as the most accepted theory among the scientific and academic communities. Around that time, the new generations of researchers who

started to use molecular biology technologies came on the scene. Under the scheme of the dominant theory of teosinte, two schools of scientist discussed the issue of the characteristics of the center of origin of maize. That is, after establishing that the teosinte was the ancestor of maize, the researchers compared ideas and information regarding the details of the center of origin of maize. A group of specialists considered that the center was unicentric, for another group it was multicentric. Besides, at that time, a third group was still conducting studies, based on Mangelsdorf theories, and considered that the origin of maize was an event preceded by a wild ancestor already extinct and that teosinte was a hybrid of maize and tripsacum.

<sup>10</sup> Popol Vuh. 1986. Antiguas historias de los indios quichés de Guatemala por Albertina Saravia. Editorial Porrúa, Colección “Sepan cuantos...” Num. 36, Sixteenth edition. Mexico, Mexico City.

<sup>11</sup> Iltis H.H. 1983. “From teosinte to maize: The catastrophic sexual transmutation”. *Science* 222; Pages 886-894.

<sup>12</sup> The idea of genetic assimilation involves a phenomenon as well as mechanism due to which the phenomenon takes place. This phenomenon can be described as de change of an acquired trait into an inherited trait”. “Genetic assimilation is the proposed name for that process...” (Waddington, 1975a).

<sup>13</sup> René Thom, *Stabilité structurelle et morphogénèse*, Interédition, Paris, 1977 (*Estabilidad estructural y morfogénesis*, Editorial GEDISA, Barcelona, Spain, 1987). In this book, Thom applies his Catastrophes theory to the biology of development and morphogenesis.

<sup>14</sup> Conrad H. Waddington. 1975b. A catastrophe theory of evolution. In: “The evolution of an evolutionist” Waddington C.H. Cornell University Press, Ithaca, NY, United States of America, Pages 253-266

<sup>15</sup> “Lamarckism” term used for the studies which are based on the idea of the scientific Lamarck with regards to the “inheritance of the acquired traits”. In a simplistic manner, Lamarck has been pictured as an anti-scientist.

Image: Teosinte from Oaxaca / © David Lauer



# History of the research on the origin of maize 1990 to the present

During the decade of 1990, it seemed that scientists had reached an agreement on the prevalence of the theory of teosinte; nevertheless, from time to time new researches arisen involving the supposedly extinct wild maize -on the same line of thinking as Mangelsdorf and his collaborators<sup>16</sup>. As a summary, Figure 4 shows the diagrams developed in 1995 by Wilkes and Goodman<sup>17</sup> and which picture the different theories about the origin of maize. Also, at that time, the studies carried out with the help of new technologies on molecular biology were consolidated. Such studies would allow a deeper exploration on the origin of maize: millions of years in the evolutionary scale. Between 1990 and 1992, John Doebley, from the University of Minnesota, in order to define the differentiation of teosinte and maize and using molecular markers, formulated several variations from the pioneer studies of Beadle. With this research, John Doebley consolidated the theory of teosinte as ancestor of maize.

In one of the first works where the molecular markers methodology<sup>18</sup> was used to analyze the origin of maize, Doebley and collaborators<sup>19</sup> concluded that, in five segments of four chromosomes of the hybrids of teosinte and maize is found the genetic information which caused a morphological modification in the female ears and male tassels of these two species. They suggested that in maize, as consequence of that morphological change, an expression of secondary male sexual traits embedded in a female genetic context are produced. This research was, clearly, derived from the studies of Beadle and Illis -mentioned hereinabove -,

therefore, it is not surprising that the conclusions of Doebley and collaborators are a complement to the proposed theories of those scientists: a series of mutations result in the sexual transformation of the male inflorescence of teosinte into the female inflorescence of maize. Likewise, in that work they concluded that the Tunicate gene (also known as Tu) does not have any role in the origin of maize. This conclusion seems to bury one of the basic suppositions of the theory of Mangelsdorf (1939, 1959) which states that a kind of tunicate maize<sup>20</sup> participated in the origin of maize.

In 1991, Doebley and Stec<sup>21</sup>, when studying the morphology of the progeny of maize and teosinte, found that the molecular genetic analyses are coherent, once more, with the results of Beadle: they identified five genomic regions that control the differences between the two plants. These scientists highlight the importance of the gene Teosinte branched (or tb1) due to its effect on the inflorescence architecture and its impact on the morphological development of maize. Subsequently, in a review paper published in 1992<sup>22</sup>, Doebley stated that the works carried out so far, with the support of biotechnological methodologies, allowed to back up the theory of Beadle -the morphological differences between maize and teosinte started with a few mutations which had a strong influence on the morphology of the adult maize plant. On the other hand, in that work, Doebley anticipates that cloning the genes involved in the evolutionary change of teosinte -in order to give origin to the maize - would become a reality in the short term.

Some years later, Mary Eubanks published in 1995 a study which

shows the evidence of a hybrid produced by crossing a *Tripsacum dactyloides* (one of the tripsacum species) and *Zea diploperennis* (the perennial teosinte), two wild relatives of maize<sup>23</sup>. With the work, Eubanks revives the theory of Mangelsdorf, known as tripartite theory, and suggests that the hybrids of *Tripsacum-diploperennis* are one of the missing links which would solve the puzzle of the origin of maize. The main argument of Eubanks is that tripsacum and perennial teosinte hybrids represent the extinct wild maize, which is the principal element in the theory of Mangelsdorf (1939).

Meanwhile, Doebley and collaborators explored, at a molecular level, the genes of biochemical and enzymatic processes that could contribute to the evolutionary change from teosinte to maize<sup>24</sup>.

<sup>16</sup> Specially Mary Eubanks, from the Durham University in North Carolina, USA.

<sup>17</sup> Wilkes H.G. and Goodman M.M. 1995. "Mystery and missing links: The origin of maize". *Maize Genetic Resources*, Maize Program Special Report; Taba, S. (publisher), Mexico, Mexico City, Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT).

<sup>18</sup> The molecular markers methodology is based on a series of biochemical processes which involve extraction, purification and fragmentation of the deoxyribonucleic acid of the organisms in order to detect and identify segments which are specific in that genetic material. See Figure 7.

<sup>19</sup> Doebley J., Stec A., Wendel J., Edwards M., 1990. "Genetic and morphological analysis of a maize-teosinte F2 population: Implications for the origin of maize". *Proc Natl Acad Sci USA*, Volumen 87; Pages. 9888-9892.

<sup>20</sup> The tunicate maize is a type of maize where each grain is wrapped in vegetative tissue. See Figure 3, the second drawing, from left to right.

<sup>21</sup> Doebley J., Stec A. 1991. "Genetic analysis of the morphological differences between maize and teosinte". *Genetics*, Volumen 129; Pages. 285-295.

<sup>22</sup> Doebley J. 1992. "Mapping the genes that made maize". *Trends in Genetics*, Volumen 8, Número 9; Pages. 302-307.

<sup>23</sup> Eubanks M. 1995. "A cross between two maize relatives: *Tripsacum dactyloides* and *Zea diploperennis* (Poaceae)". *Economic Botany* 49(2); Pages 172-182.

<sup>24</sup> Hanson M.A., Gaut B.S., Stec A., Fuerstenberg S.I., Goodman M.M., Coe E.H., Doebley J. 1996. "Evolution of anthocyanin biosynthesis in maize kernels: The role of regulatory and enzymatic loci". *Genetics*, Volumen 143; Pages. 1395-1407.

This kind of studies were designed with the objective of finding evidences that contribute to test hypotheses of macro-evolutionary changes, such as the one that could have taken place in the origin and evolution of maize and that would explain the big step of teosinte transformation into maize.

The analysis of the results of the investigation of Doebley and collaborators led them to suggest that the changes in the genes that regulate the activity of proteins are a key factor in the evolution of teosinte into maize. That is: the generation of purple kernels in maize from colorless kernels in teosinte.

The refining of the molecular biology methods has allowed the advancement in the knowledge of the most ancient processes in the evolutionary path of maize. In this way, in 1997 Brandon Gaut and John Doebley developed an study<sup>25</sup> where, through the analysis of the divergences in the sequences of 14 pairs of genes, duplicated in the maize chromosomes, came to the conclusion that the configuration of the basic genome<sup>26</sup> -from which the most ancient ancestors of the

*Zea* genus derive-would be present since 20 million years ago. Moreover, these scientists suggest that 11 million years ago happened another crucial event in the evolution of the genus *Zea* when took place the hybridization of two ancestral species which make up the chromosomal number contained in maize (10 chromosomes).

The investigations that use molecular biology methodologies have also contributed to explain the evolution of the important traits of maize and its wild relatives. For example, the analysis of genes (tasselseed and gynomonoeicous sex form<sup>27</sup>) that intervene in the development of the monoecious inflorescences<sup>28</sup> of tripsacum and maize, led the team of Stephen Dellaporta<sup>29</sup> to suggest that the formation of male flowers in the group of grasses (*Andropogonae*) -where those two plant species are included- is a trait from just one ancestor group. This kind of studies allows us to explore the evolutionary history of the maize ears and tassels which, as we already mentioned, is very

important to understand the theories on the origin of maize.

Since the last part of 20th century and the beginning of 21st century, the study on the origin of maize has been consolidating thanks to the use of molecular biology. The constitution of the configuration and origin of the genome structure (or set of genes) which can be achieved with the use of molecular methodologies has been a significant factor to understand the evolution of maize. For example, it has been estimated that the chromosomal duplication of maize took place 11 million years ago and that, more than 5 million years ago its genetic configuration passed through a process of proliferation of genetic mobile elements<sup>30</sup>. These events set the base on which the diversification of genus *Zea* would take place. In this timeframe, the evolutionary history of maize is enclosed in a process where just natural factors take place and, thanks to them, the ancestors previous to teosinte and maize constituted the raw material which, after millions of years, would be managed by the human being.

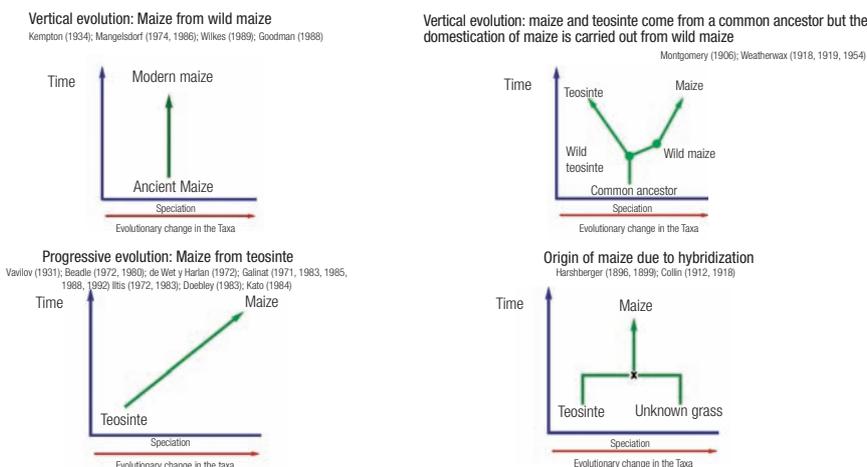


Figure 4. Theories on the origin of maize. Adapted by Antonio Serratos from the illustration of Wilkes and Goodman (Note 17).

<sup>25</sup> Gaut B.S. and Doebley J.F. 1997. "DNA sequence evidence for the segmental allotetraploid origin of maize". Proc. Natl Acad Sci USA, Volumen 94; Pages 6809-6814.

<sup>26</sup> The Genom is the set of genetic information contained in the sequence of genes of the chromosomes of the organisms.  
<sup>27</sup> Tassel seed2 Ts2 is a mutant of maize and Gynomonoeicous sex form gsf is a mutant of *Tripsacum dactyloides*. To obtain more information on maize mutants see: <http://www.maizegdb.org/cgi-bin/locusvarimages.cgi?id=12691>

<sup>28</sup> A monoecious plant is that one which has the two kind of unisexual flowers in the same individual. In the maize are know as inflorescences; the male one are located in the upper ears and the female ones in the cob.

<sup>29</sup> Li D., C.A. Blakey, C. Dewald, S.L. Dellaporta. 1997. "Evidence for a common sex determination mechanism for pistil abortion in maize and its wild relative *Tripsacum*". PNAS USA Volumen 94; páginas 4217-4222.

<sup>30</sup> See Note 1.

# Status of the knowledge on the center of origin and on the domestication of maize

At the beginning of the 21st century, the research on the origin of maize is determined by the importance of molecular biology methodologies. Based on these methodologies, it has been possible to explore evolutionary scenarios of millions of years where the genomic structures of plant organisms which are ancestors of the families to which maize and teosinte –and many other plants – belong to. In the same way, some genetic mechanisms that could be involved in the specific transformation of teosinte into maize have been described in timeframes ranging between seven and nine thousand years (estimated time during which the domestication of maize took place). Nevertheless, in more than seventy years of discussion and exchange of ideas regarding the origin of maize, there has been just one agreement among the scientific communities: teosinte is the ancestor of maize.

Although recent studies are still providing important data on the origin of maize, they are lacking a more precise definition of basic aspects such as how and where this plant had its origin. It is not yet possible to determine the supremacy of any theory on the location of the center, or centers, of origin and domestication of maize because we are still lacking data on the fossil and archeological records of this process. There are very few specific paleontological and archeological explorations which focused in the analysis of maize in America. The most well know are the ones of Puebla (Tehuacan) and Oaxaca (Guila Naquitz) in Mexico, New Mexico (Bat Cave) in the United States of America, and some more in other parts of Mexico (See Notes 60 and 61) and Ecuador (See Note 62).

The scarcity of crucial information on the fossil and archeological records of teosinte and maize, in comparison to the potential number of areas located throughout America, limits the correct definition and geographical location of the centers of origin, domestication and diversity of maize.

In practical terms, this scientific investigation would be of importance for issues as controversial as the review of the biosafety laws where, as happens in Mexico, is essential to have the scientific information which is relevant for the protection of native maize.

The process of domestication is a third element involved in how maize was originated. Either by a gradual selection or by a catastrophic sexual transmutation, human involvement is an essential condition for the transformation of teosinte into maize. On the other hand, determining domestication is key for locating the center of origin and diversification of the crop. Let us remember that with the emergence and discussion of the theories on the origin of maize, some domestication mechanisms closely linked to human work and agriculture were proposed, so, it has always been recognized that the farmers of the different American cultures can not be separated from the domestication and diversification of maize in subsequent times and up to the present.

The studies on the domestication of maize have given birth to contrasting theories related to the center of origin: the unicentric and multicentric theories. Although the controversy on the single or multiple character of the domestication center is a very old one, we cannot say it is already solved. A study by Yoshihiro Matsuoka, from the Doebley group<sup>31</sup>, concludes that all the maize as

we know it nowadays, developed from a unique domestication event which took place nine thousand years ago in the south of Mexico. The results of their analysis led to other conclusions that, according to the authors, definitely support the unicentric characteristic of the origin of maize. First of all, the *Zea mays ssp parviglumis* was identified as the only progenitor of maize, and the teosinte *Zea mays ssp mexicana* as a contributor to its diversification, mainly in the central plateau maize. Due to the fact that the distribution of these teosintes is limited to the Balsas region and to the highland plateau (altiplano) in the center of Mexico, respectively, Doebley and collaborators deduced that they could define the specific geographic location of the birthplace of maize. Nonetheless, it is important to be cautious because, as we already mentioned, the fossil and archeological records are very limited and, therefore, it is not prudent to draw a definitive conclusion.

In spite of the preference of the unicentric theory over the multicentric theory that many research groups have, it is not possible to fully discard the multicentric theory because it has contributed with very important pieces of evidence that supports it - particularly, the correlation between the chromosomal knobs of each racial composite and the geographical regions where those are located. This is a strong enough proof which points at not only to the origin and domestication of maize but also at its diversification. Kato (2005) analyzed the characteristic patterns of the chromosomal knobs<sup>32</sup> of teosinte and maize, and found that they could be associated to geographic patterns of the populations of each one of these species.

For example, a particular pattern of chromosomal knobs are called a “complex” which is associated to a set of races of maize or to populations of teosinte. When we associate maize or teosinte samples from different regions to the chromosomal knob patterns, it is possible to deduce the genetic relationship between samples, its geographic distribution and their dispersion/migration patterns. From his analysis, Kato concludes that the origin of maize is the result of several populations of teosinte and, as a consequence, there are at least four centers of origin/ domestication of maize throughout Mexico and Guatemala. The dispersion of racial complexes towards North and South America followed the same paths identified by other studies, including the one of Matsuoka and collaborators.

However, there are still some important questions to be solved regarding the domestication process and the definition of uni or multicentric origin and diversity of maize. Then, we can wrap up this section as Garrison Wilkes does in one of his papers<sup>33</sup>: *“There are many truths in all these contributions [on the study of the origin of maize], but there are still elements of mystery in what is yet to be solved”*.

<sup>31</sup> Matsuoka Y., Vigouroux Y., Goodman M.M., Sanchez-Gonzalez J., Buckler E., Doebley J. 2001. “A single domestication for maize shown by multilocus microsatellite genotyping”. PNAS USA, Volume 99, Number 9; Pages 6080-6084.

<sup>32</sup> The Chromosomal knobknobs are elements of the chromosomes with the shape of a knot . The knobs contain particular chemical substances (heterocromatine) that are visible with the help of a microscope. The location of the knobs is determined with special stains at the meiosis (formation of gametes for sexual reproduction) in the microsporocysts (immature pollen). See the article of Angel Kato (1997) where is detailed an analysis on the chromosomal knobs in teosinte and maize.

<sup>33</sup> Wilkes, G. 2004. Corn, Strange and Marvelous: But Is a Definitive Origin Known? In: “Corn: Origin, History, Technology, and Production” C. Wayne Smith (Publishing House), Wiley & Sons, Inc. Pages 3-63.



# The diversity of maize in the American Continent

## The studies on the diversity of maize 1940-1980

The research on the diversity of maize in the American continent started on the decade of 1940.

Those studies were supported mainly by the Rockefeller Foundation, the National Academy of Sciences and the National Research Council of the United States of America. At the Academy of Sciences a Committee was created for the Conservation of the Indigenous Maize Races; this committee functioned as coordinator for the collection and description of maize in America, carried out until mid 70s. In Mexico and Central America the Ministry of Agriculture of Mexico was in charge, jointly with the agricultural academic institutions, of the coordination and infrastructure of the field work. In South America, the Agricultural Institute of Colombia took over the functions of coordination and support of the field works which were carried out for the recollection of maize in the countries of that region.

For the storage and preservation of collections of maize, in Mexico, Colombia and Brazil were allocated some germplasm banks –besides the existing ones in the United States-. In these banks of ex situ conservation of maize germplasm are kept the seeds of the majority of the races of maize of America. The record of this work is kept in a series of documents on the races of maize of each one of the American countries that participated in the conservation of this crop<sup>34</sup>. These documents are the base for the knowledge, research and conservation of maize, not only in the American continent, but all over the world. Now it will be set forth a synthesis of the diversity of maize and its study, from the publication of the books on the races of maize up to the present time, as well as the research carried

out to systematize, sort and use the diversity of maize.

The first efforts to classify maize used the definition of race proposed by Anderson and Cutler (1942): “A group of individuals which are related, with enough traits in common as to allow its recognition as a group”. As this definition was the ground for the first studies of the diversity of maize in America, the classification of the groups or races of the different regions of the continent are based on this definition. Likewise, the association of the site or area where the maize is located (environment) with its race traits (genotype) generated the nomenclature of “Landrace of maize”<sup>35</sup>. In practice, it was included the biggest number of morphological traits in order to describe the plants of each one of the collected maize races. In this case, the traits of the female inflorescence (maize ear) are considered to be more important to differentiate between plants in the racial categories<sup>36</sup>.

In the Table 1 are listed the races catalogued in the American countries which have carried out exploration of maize in their territories. The information of maize in the majority of the countries is included in the Catalog of the Germplasm of Maize of CIMMYT, part of the Latin American Maize Project (LAMP)<sup>37</sup>, and other sources related with the books of the maize races –which are mentioned hereinbelow. Not all the sources tally in the number of races catalogued or in their name. Nonetheless, in this article the information was consolidated from the sources with the historical records of the first explorations in Mexico (which date from 1943).

The studies carried out with the help of numeric taxonomy<sup>38</sup>, in the decade of 1970, so to systematize and organize the diversity of maize, and the molecular analysis carried out at the end of the decade of 1980 with the same objective, used the same catalog numbers associated to the names of the races listed in the Table 1.

<sup>34</sup> (1) Wellhausen E.J., Roberts L.M., Hernández-Xolocotzi E., Mangelsdorf P.C. 1952. *Races of maize in Mexico*. Bussey Institute, Harvard University (Cambridge); (2) Hatheway W.H. 1957. *Races of maize in Cuba*. National Academy of Sciences, NRC Publication 453. Washington D.C.; (3) Roberts L.M., Grant U.J., Ramírez R., Hatheway W.H., Smith D.L., Mangelsdorf P.C. 1957. *Razas de maíz en Colombia*. Ministerio de Agricultura de Colombia, Oficina de Investigaciones Especiales, Technical report Num. 2. Editorial Máxima, Bogotá, Colombia; (4) Wellhausen E.J., Fuentes A., Hernández-Corzo A., Mangelsdorf P.C. 1958. *Razas de maíz en la América Central*. Technical brochure 31, Oficina de Estudios Especiales, Secretaría de Agricultura y Ganadería, Mexico DF; (5) Grobman A., Salhuana W., Sevilla R., Mangelsdorf P.C. 1961. *Races of maize in Peru*. National Academy of Sciences, NRC Publication 915. Washington D.C.; (6) Timothy D.H., Peña B., Ramírez R., Brown W.L., Anderson E. 1961. *Races of maize in Chile*. National Academy of Sciences, NRC Publication 847. Washington D.C.; (7) Ramírez R., Timothy D.H., Díaz E., Grant U.J., Nicholson-Calle G.E., Anderson E., Brown W.L. 1961. *Razas de maíz en Bolivia*. Ministerio de Agricultura de Colombia, oficina de Investigaciones Especiales, Boletín técnico Num. 9. Publishing House ABC, Bogotá, Colombia; (8) Grant U., Hatheway W.H., Timothy D.H., Cassalet C., Roberts L.M. 1963. *Races of maize in Venezuela*. National Academy of Sciences, NRC Publication 1136. Washington D.C.; (9) Timothy D.H., Hatheway W.H., Grant U.J., Torregróza M., Sarria D., Varela D. 1966. *Razas de maíz en Ecuador*. Instituto Colombiano Agropecuario, Ministerio de Agricultura de Colombia, Boletín Técnico Num. 12. Bogotá Colombia; (10) Paterniani, E. and Goodman, M.M. (1978). *Races of Maize in Brazil and Adjacent Areas*. Mexico: International Maize and Wheat Improvement Center, Mexico City.

<sup>35</sup> In Spanish “raza local”.

<sup>36</sup> See Note 34, Reference 1: “the cob and not the ear shows diagnosis traits which are more useful than any other part of the plant because the cob is the most specialized organ of the plant of maize and it is the structure that allow us, more than any other one, to differentiate the Zea mays from all the other gramineae species”. Specifically, the external traits of the cob are measured, such as: length, diameter of the middle part, number of kernel rows, diameter of the stem, width, thickness, depression and strain of the kernel, etc.; as well as internal traits such as the length of the rachilla, diameter of the cob, index of cob/raquis, glume/kernel and rachilla/kernel.

<sup>37</sup> Latin American Maize Project (LAMP), 1991. ARS-USDA, CIMMYT, Pioneer Hi-Bred International Inc., Universidad Agraria La Molina (Peru); CIMMYT, 1999. A core subset of LAMP, from the Latin American Maize Project 1986-1988. Mexico, Mexico City.

<sup>38</sup> The numeric taxonomy is a group of mathematical techniques through which the organisms are classified according to its similarities or resemblance. Usually morphological traits are used, although in real life any kind of traits are used to group the operational taxonomical units (i.e. races, species, families, etc.)

This table contains the nomenclature found in the books of the races of maize in America which had been preserved heretofore in the germplasm banks. Other specific codes and data of the passport of the accesses corresponding to each collection are in each germplasm bank (i.e. CIMMYT).

These early works of classification and sorting of maize in America have their grounds on the description of the races under morphological, physiological, genetic and agronomic bases and cytogenetic traits (chromosomal nodes), which allowed to determine preliminary genealogy relationship patterns. In the books on maize from the American Continent (Note 34), besides the classification in groups and the affinity and kinship relationships, the maps of distribution of the different races are included. This information is the ground base for the knowledge on the diversity of maize, and it has been used so far as the standard for the description of races. Of course, there has been a lot of advancement in the classification of the races of maize; but the nomenclature and data of the passport of the recollections, also known as accessions, of the maize races in the continent, still keeps the information of those pioneer works of exploration of maize in the continent.

Each book tells the history of the study of maize in each country. So, we learned that the diversity of maize in Mexico (Note 34, Subsection 1) was first noticed by Fray Bernardino de Sahagun (1539) and, after that, in the 19th century and the 20th century, Mexican scientists such as de la Rosa (1846) and Lopez y Parra (1908) go into greater detail about the study of the variability of maize in Mexico. Similarly, in Peru (Note 34, Subsection 5), the maize cultivation mentions

date back to 1609 - with the Inca historian Garcilaso. At the beginning of the 20th century, the Russian scientists Kuleshov and Vavilov (Note 34, subsections 1, 3, 4 and 5) made important contributions to the diversity of maize in the American continent: the first one for its study in Mexico, Centro America and Colombia.

The study and description of maize races in Mexico and Colombia allowed having a first approach to what would have been the prehistory and pre-Hispanic migrations -and later during the Viceroyalty- of the different types of maize in the continent. The book on the races of maize in Central America shows in a very evident way the relationship of Guatemala maize with the southwest races in Mexico, specifically with the race Nal-tel of the Mayan culture. Southwards, the rest of the countries of Central America have some races and hybrids, representative of Colombia and the Andean region, particularly Peru. An important characteristic in Peru is that the cultivation of maize in the Inca culture was carried out in conditions considered as "advanced agriculture", which produced a great diversity in the kernels and ears. The agriculture in the Inca culture lead Grobman and collaborators to propose a theory about the multiple centers of domestication. Following Kuleshov, Grobman (Note 34, Subsection 5) defined the domestication as independent from the botanic center of origin. Therefore, even the teosinte would be ruled out as ancestor of maize because Grobman would be supposing that the extinct wild maize was the precursor of modern maize in that region. The current genetic and taxonomic studies reject this version of the

origin and domestication of maize, nevertheless, recent archeological research carried out in the Andean area shows interesting information about the antiquity of maize in South America because remains of maize as old as the ones located in Mexico (Notes 60 to 62) had been found.

In the decade of 1970 a great amount of information on the diversity of maize in America was gathered. During those years, thanks to development of statistical methods that handled a great amount of variables and to the computer systems -towards the end of the decade of 1960-, it was possible to analyze in a systematic way the variability of maize in the continent through the use of numerical taxonomy (Note 38). Using the information of the books on the races of maize and the methods developed some years ago, Major Goodman and Robert Bird (1977) started the study on the taxonomic relationship of maize races in all America.

The results of this work allowed the discovery of 14 complexes of maize races in the American continent. In Figure 5 is shown a partial compilation of the results of Goodman and Bird, which were published in 1977<sup>39</sup>.

<sup>39</sup> Goodman, MM, Bird RMck. 1977. The races of maize IV: Tentative grouping of 219 Latin American races. *Economic Botany* 31: 204-221.

Table 1. Compilation of the races of maize catalogued per country. By Antonio Serratos, based on several information sources (Notes 34 and 37). See the map on Figure 8.

Country	Race
<b>Argentina</b> (47)	Amarillo Ocho Hileras, Amarillo de Ocho, Altiplano, Amargo, Avatí Morotí, Avatí Morotí Mita, Avatí Morotí Ti, Avatí Pichingá, Azul, Blanco Ocho Hileras, Calchaqui, Camelia, Canario de Formosa, Capia Blanco, Capia Garrapata, Capia Rosado, Capia Variiegado, Catete Oscuro, Chaucha Amarillo, Chaucha Blanco, Chulpi, Colita Blanco, Complejo Tropical, Cravo, Cristalino Amarillo, Cristalino Amarillo Anaranjado, Cristalino Blanco, Cristalino Colorado, Cristalino Naranja, Cristalino Rojo, Culli, Cuzco, Dentado Blanco Rugoso, Dentado Amarillo, Dentado Blanco, Dentado Amarillo Marlo Fino, Dentado Blanco Marlo Fino, Dulce, Marrón, Morochito, Negro, Pericarpio Rojo, Perla, Perlita, Pisingallo, Socorro, Tuzón, Venezolano
<b>Bolivia</b> (77)	Achuchema, Amarillo Subtropical, Altiplano, Aperlado, Argentino, Ayzuma, Bayo, Blanco Mojo, Blanco Yungueño, Blando Amazónico, Blando Blanco, Blando Cruceño, Camba, Canario, Cateto, Chake Sara, Checchi, Cholito, Chuncula, Chuspillu, Concebideño, Colorado, Cordillera, Confite Puneño, Coroico, Coroico Amarillo, Coroico Blanco, Cubano Amarillo, Cubano Blanco, Cubano Dentado, Cuzco Boliviano, Cuzco Huilcaparú, Duro Amazónico, Duro Beniano, Enano, Harinoso de Ocho Hileras, Huaca Songo, Hualtaco, Huilcaparu, Jampe Tongo, Janka Sara, Kajbia, Karapampa, Kcello, Kellu, Kellu Huilcaparu, Kepi Siqui, Kulli, Morado, Morochillo, Morocho, Morocho Chaqueño, Morocho Chico, Morocho Grande, Morocho Ocho Hileras, Morocho Catorce Hileras, Niñuelo, Oke, Parú, Pasankalla, Patillo, Patillo Grande, Perla, Perla Amarillo, Perla Primitivo de los Llanos, Perola, Pisankalla, Pojoso Chico, Pororo, Pura, Purito, Reventón, Tuimuru, Uchuquilla, Yungueño
<b>Brasil</b> (44)	Caiano, Caingang, Canario de Ocho, Caribe Precoz, Cateto, Cateto Sulino, Cateto Sulino Precoce, Cateto Sulino Escuro, Cateto Sulino Grosso, Cateto Assis Brasil, Cateto Grande, Cateto Nordista Precoce, Chavantes, Cravo, Criollo de Cuba, Cristal Semidentado, Cristal Sulino, Cravo Riograndense, Cravo Paulista, Dente Amarelo, Dente Riograndense, Dente Riograndense Rugoso, Dente Riograndense Liso, Dente Paulista, Dente Branco, Dente Branco Riograndense, Dente Branco Paulista, Dente Colorado, Entrelazado, Guaraní Popcorns, Hickory King, Indígena, Lenha, Morotí Precoce, Morotí Guapí, Perola, Pinha, Pipoca, Saint Croix, Semidentado Riograndense, Semidentado Paulista, Semidente Amarelo, Semidente Azul, Tusón
<b>Colombia</b> (23)	Amagaceño, Andaquí, Cabuya, Cacao, Capio, Cariaco, Chocoseño, Clavo, Común, Costeño, Güirua, Imbricado, Maíz Dulce, Maíz Harinoso Dentado, Montaña, Negrito, Pira, Pira Naranja, Pollo, Puya, Puya Grande, Sabanero, Yucatán
<b>Cuba</b> (11)	Cubano Amarillo, Chandelle, Coastal Tropical Cristalino, Cuban Flint, Maíz Criollo, Tusón, Argentino, Canilla, White Pop, Yellow Pop, White Dent
<b>Chile</b> (29)	Amarillo Malleco, Amarillo Ñuble, Araucano, Capio Chico Chileno, Capio Grande Chileno, Capio Negro Chileno, Camelia, Choclero, Chulpi, Chutucuno Chico, Chutucuno Grande, Cristalino Chileno, Cristalino Norteño, Curagua, Curagua Grande, Dentado Comercial, Diente Caballo, Dulce, Harinoso Tarapaqueño, Limeño, Maíz de Rulo, Marcame, Morocho Blanco, Morocho Amarillo, Negrito Chileno, Ocho Corridas, Pisankalla, Polulo, Semanero
<b>Ecuador</b> (31)	Canguil, Sabanero Ecuatoriano, Cuzco Ecuatoriano, Mishca, Patillo Ecuatoriano, Racimo de Uva, Kcello Ecuatoriano, Chillo, Chulpi Ecuatoriano, Morochón, Huandango, Montaña Ecuatoriano, Blanco Harinoso Dentado, Cónico Dentado, Uchima, Clavito, Pojoso Chico Ecuatoriano, Tusilla, Gallina, Candela, Maíz Cubano, Tuxpeño, Chocoseño, Blanco Blandito, Cholito Ecuatoriano, Yunga, Enano Gigante, Yunquillano, Yungueño Ecuatoriano
<b>Guatemala</b> (33)	Criollo, Huesillo, Nal-Tel, Nal-Tel Amarillo, Nal-Tel Amarillo Tierra Baja, Nal-Tel Blanco Tierra Baja, Nal-Tel Amarillo Tierra Alta, Nal-Tel Blanco Tierra Alta, Nal-Tel Ocho, Imbricado; Serrano, San Marceño, Quiché, Quicheño Rojo, Quicheño Grueso, Quicheño Ramoso, Negrita, Negro, Negro Chico, Negro Chimaltenango Tierra Fria, Negro Chimaltenango Tierra Caliente, Salpor, Salpor Tardío, Salvadoreño, San Marceño, Olotillo, Olotón, Comitico, Dzit Bacal, Tehua, Tepecintle, Tusón, Tuxpeño
<b>El Salvador, Honduras, Costa Rica, Nicaragua, Panamá</b> (11)	Nal Tel Blanco, Nal Tel Amarillo, Nal Tel Rojo, Nal Tel Panamá, Clavillo, Salvadoreño, Negro, Chocoseño, Cariaco, Huesillo, Cubano Amarillo Cristalino
<b>Mexico</b> (65:69 collated; 6 impresise)	Ancho, Apachito, Arrocillo Amarillo, Arrocillo, Azul, Blandito, Blando Sonora, Bofo, Bolita, Cacahuacintle, Carmen, Celaya, Chalqueño, Chapalote, Clavillo, Comitico, Conejo, Cónico, Cónico Norteño, Coscomatepec, Cristalino Chihuahua, Complejo Serrano Jalisco, Cubano Amarillo, Dulce de Jalisco, Dulcillo Noroeste, Dzit Bacal, Elotes Cónicos, Elotes Occidentales, Elotero de Sinaloa, Fasciado, Gordo, Harinoso, Harinoso de Ocho, Jala, Lady Finger, Maíz Dulce, Maízón, Motozinteco, Mushito, Nal Tel, Nal-Tel de Altura, Olotillo, Olotón, Onaveño, Palomero de Chihuahua, Palomero Toluqueño, Pepitilla, Ratón, Reventador, San Juan, Serrano de Jalisco, Tablilla, Tablilla de Ocho, Tabloncillo, Tabloncillo Perla, Tehua, Tepecintle, Tunicata, Tuxpeño Norteño, Tuxpeño, Vandeño, Xmejenal, Zamorano Amarillo, Zapalote Chico, Zapalote Grande
<b>Paraguay</b> (10)	Avatí Mita, Avatí Morotí, Avatí Ti, Avatí Guapí, Opaco, Pichinga Redondo, Sape Morotí, Sape Pyta, Tupí Morotí, Tupí Pyta
<b>Perú</b> (66)	Ajaleado, Alazán, Alemán, Amarillo Huancabamba, Ancashino, Arequipeño, Arizona, Arizona Mochero, Blanco Ayabaca, Cabaña, Capio, Chancayano, Chancayano Amarillo, Chancayano Blanco, Chancayano Pintado, Chaparpeño, Chimlos, Chullpi, Chuncho, Colorado, Confite Introducido, Confite Morocho, Confite Puneño, Confite Puntigudo, Coruca, Cubano Amarillo, Cubano Amarillo Piricincin, Cuban Yellow Dent, Cuzco, Cuzco Cristalino Amarillo, Cuzco Gigante, Enano, Granada, Híbrido Amarillo Duro, Huachano, Huancavelicano, Huarmaca, Huayleño, Jora, Kculli, Maraño, Mochero, Mochero Pagaladroga, Morocho Cajabambino, Morocho Canteño, Morocho, Opaco, Pagaladroga, Pardo, Pardo Amarillo, Paro, Perla, Perilla, Piricincin, Piscorunto, Rabo de Zorro, Rienda, Sabanero, San Gerónimo Huancavelicano, Sarco, Shajatu, San Gerónimo, Tambopateño, Tumbesino, Tuxpeño, Uchuquilla
<b>Uruguay</b> (8)	Cateto Sulino, Cristal, Dentado Branco, Dentado Rugoso, Morotí Amarillo, Morotí Blanco, Pisingallo, Semidentado Rugoso
<b>United States of America</b> (16)	Argentino, Canilla, Cariaco, Chapalote, Confite Morocho, Corn Belt Dent, Creole, Early Caribbean, Haitian White, Northern Flint, Northern Flour, Palomero Toluqueño, Saint Croix, Southern Dent, Tuson, White PopCorn
<b>Venezuela</b> (19)	Aragüito, Cacao, Canilla Venezolano, Cariaco, Chandelle, Chirimito, Común, Costeño, Cuba Amarillo, Guaribero, Huevito, Negrito, Pira, Pollo, Puya, Puya Grande, Sabanero, Tusón, Tuxpeño

Although these studies were preliminary, they set the ground for studying the traits, affinities and relationships of the races of maize; besides, they contributed to the evaluation of the genetic resources (that, at that time, had a great economic value).

In Mexico, after a series of studies on the relationships and affinities between some racial composites<sup>40</sup>, Tarcicio Cervantes, from the Postgraduate School, and collaborators<sup>41</sup> classified –using numerical taxonomy – the 25 races of maize identified in 1952 by Wellhausen and collaborators. Although the sets of races set in the dendrograms<sup>42</sup> were not an exact match with the genealogical relationships deduced from the previous studies, they had a general agreement. For example, the race Maiz Dulce (Sweet Maize) is associated with the race Cónico of the Highlands (Figure 6) and not with Cacahuacintle, as Wellhausen and collaborators had proposed (1952).

Years later, thanks to the adaptation of biochemical and molecular techniques to determine genetic variation, the analysis of the races of maize in Latin America and

Mexico is carried out once more. A study on the pollen proteins<sup>43</sup>, which was meant to determine the link between some Mexican races, found that there was a general consistency between the morphological and agronomic studies with regard to the formation of racial groups. Nevertheless, in connection with those immunological studies, remarkable differences between Chalqueño race and the rest of the other analyzed races were discovered. Also, it was found a great similarity between the races Palomero Toluqueño (Toluqueño Popcorn) and Maiz Dulce (Sweet Maize). On the other hand, the analysis on the variation of the enzyme content of the Mexican maize races and with special statistical techniques (principal components and clusters) did not found a clear difference among racial complexes; nevertheless, the pyramidal races of Mexican Altiplano, the races of the North and Northwest, and in a third group, all the other Mexican races were identified (Doebley and col., 1985). In the case of the races of Latin-American maize, mitochondrial ADN extracts were used to generate electrophoretic

patterns which determined 18 different racial groups. These racial groups coincided with the clusters generated by taxonomy and numerical analysis of morphological and cytogenetic characteristics (Weissingner and col., 1983).

In practically all the world, during two decades, the numerical taxonomy of quantitative traits was the technique of choice for the study of populations, races, and racial complexes of maize. For example, in Italy, at the end of the decade of 1970 and beginning 1980, 102 Italian maize populations were examined in its germplasm bank and the scientists were able to classify three groups of Italian maize: Cinquantino group (representative populations: Cinquantino y Tecchinese), Heterogenic group (representative populations: Rostrato, Bastardo, Giallot, Primitivo and Locale); and the Distante group (representative populations: Bani and Otesa)<sup>44</sup>. The importance of these studies, back then and nowadays, is the knowledge obtained about the variability of maize for the programs of improvement of maize all over the world.

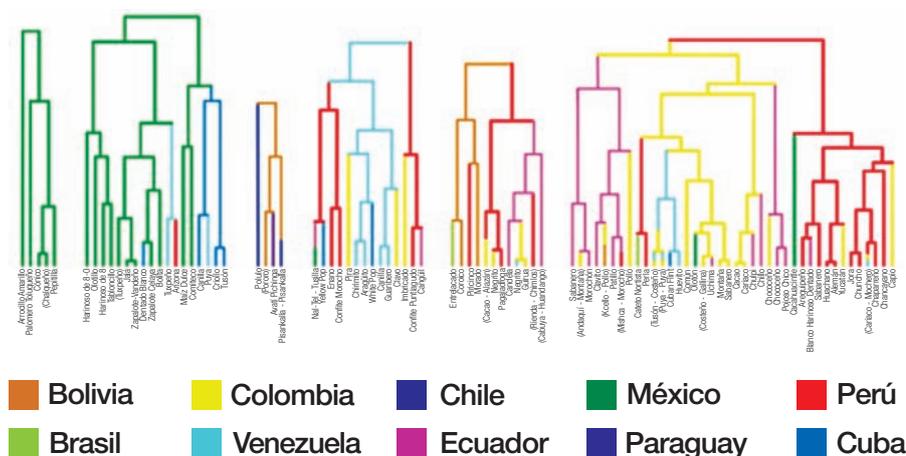


Figure 5. The classification -done by using numerical taxonomy- of the maize races in the American continent. Adapted by Antonio Serratos, with information from Goodman and Bird (See Note 39).

<sup>40</sup> Since 1968, Eduardo Casas, Dan Hanson and Edwing Wellhausen, implemented the taxonomic and number analysis of some races of Mexican maize in their study, published in the magazine *Genetics*: "Genetic relationships among collections representing three Mexican racial composites of Zea mays", Volume 59, Pages 299-310.

<sup>41</sup> Cervantes T., Goodman M.M., Casas-Díaz E., Rawlings J.O. 1978. Use of genetic effects and genotype by environmental interactions for the classification of Mexican races of maize. *Genetics*, Volume 90; Pages 339–348.

<sup>42</sup> A Dendrogram is a graph which shows the closeness of groups of organisms due to its similarity or its remoteness due to its lack of similarity, represented by statistic coefficients.

<sup>43</sup> Yakoleff-Greenhouse V, Hernández-Xolocotzin E, Rojkind-de-Cuadra C, Larraalde C. 1982. Electrophoretic and immunological characterization of pollen protein of Zea mays races. *Economic Botany* 36(1): 113-123.

<sup>44</sup> Camussi A., Spagnoletti P.L., Melchiorre P. 1983. "Numerical taxonomy of Italian maize populations: Genetic distances on the basis of heterotic effects". *Maydica* Volume 28; Pages 411-424

## The studies on the diversity of maize. 1990-to the present

During the decade of 1990, genetic and biochemical traits associated to factors which are considered of great agronomic importance for the protection of the crop were linked to the numerical analysis. Through the analysis of the content of the chemical substance DIMBOA (2,4-dihydroxi-7-metoxi-(2H)-1,4-benzoxasin-3-(4H)-ona) – the assessment of damages caused by the insect *Ostrinia nubilalis* (the European corn borer) and by the fungi *Giberella zea* and *Ustilago maydis* – Lana Reid and collaborators<sup>45</sup> were able to determine that the group of maize classified by Wellhausen and collaborators as Prehistoric Mestizo (See Note 34 Subsection 1) was more resistant to the attack of the assessed insect and fungi. This work was one of the first characterizations of the Mexican maize germplasm related to its

resistance to pests and diseases, linked to secondary chemical substances of the maize plant.

Scientists from Ottawa University, the National Institute for Forestry, Agriculture and Livestock Research (INIFAP, in Spanish) and the International Center for the improvement of maize and wheat (CIMMYT, in Spanish)<sup>46</sup>, carried an investigation, on the basis of the discovery of resistance factors in native races<sup>47</sup>, to explore the diversity of Mexican maize and classify it based on its resistance to post-harvest pests. They found that some races of the maize groups Ancient Indigenous and Prehistoric Mestizos, by the description of Wallhausen and collaborators (Note 34, Subsection 1), are sources of resistance to the infestation of the insect *Sitophilus zeamais*, one of the most destructive pests of stored maize. This type of studies

showed that there is a great, but unexplored<sup>48</sup>, richness of useful traits in the native Mexican maize germplasm that also could be extrapolated to all the races of maize in the American continent.

On the other hand, at the beginning of the 90s the scientists Jesus Sanchez and Major Goodman (1992a, b) worked again the classification of maize diversity in Latin America and reviewed the racial description of Mexican maize made in 1952 by Wellhausen and collaborators (Note 34, Subsection 1). In a similar work to the one of Cervantes and collaborators (1978), Sanchez and Goodman (1992a) concluded that conventional taxonomy results agreed with the numerical taxonomy in the classification of maize. In their study with Mexican races, they could define with a greater precision the races that so far were not defined.

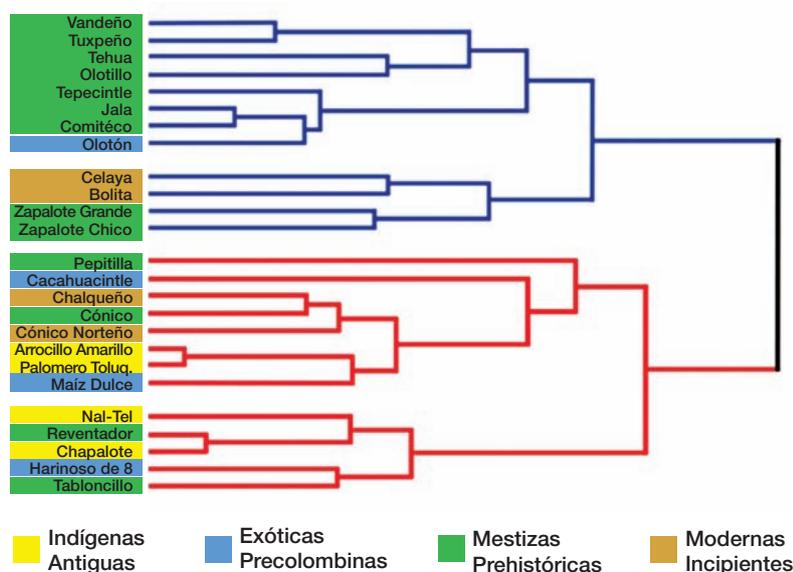


Figure 6. Classification of Mexican maize races. The blue and red lines correspond to the two main groups of Mexican races generated with data from genetic effects and environment-genotype interaction. The groups described by Wellhausen and collaborators are included as a comparison element (Note 34, Subsection 1): Ancient Indigenous, Pre-Columbian Exotic, Prehistoric Mestizos and Modern Incipient. Modified by Antonio Serratos with information from the Notes 34, 40 and 41.

<sup>45</sup> Reid L., Arnason J.T., Nozzolillo C., Hamilton R. 1990. "Taxonomy of Mexican landraces of maize, based on their resistance to European corn borer, *Ostrinia nubilalis*". *Euphytica*, Volume 46; Pages 119-131

<sup>46</sup> Arnason JT, Baum B, Gale J, Lambert JDH, Bergvinson D, Philogene BJR, Serratos A, Mihm J, Jewell DC. 1994. "Variation in resistance of Mexican landraces of maize to maize weevil *Sitophilus zeamais*, in relation to taxonomic and biochemical parameters". *Euphytica*, Volume 74; Pages 227-236.

<sup>47</sup> Serratos A, Arnason JT, Nozzolillo C, Lambert JDH, Philogene BJR, Fulcher G, Davidson K, Peacock L, Atkinson J, Morand P. 1987. Factors contributing to resistance of exotic maize populations to maize weevil, *Sitophilus zeamais*. *Journal of Chemical Ecology* 13: 751-762.

<sup>48</sup> Nevertheless, we recommend checking the works of Hernandez Casillas (1986), Hernandez-Xolocotzi (1988), Gonzalez (1994) and Garcia Lara and collaborators (2003).





Traits, as the ones used for identifying the maize races during the 50s, represent for the scientists a reflection of what happens at gene level. The differences or similarities of any trait of maize represent differences or similarities based on genetic grounds. Therefore, the direct analysis of DNA means a fundamental advancement for the phylogenetic review of organisms. In recent years, the systematization and the study of maize diversity have been enriched thanks to the use of molecular biology, allowing the scientist to complement the characterization of maize in America. As for the study of the origin of maize, the molecular markers have been useful for deepening the knowledge on the genetic relationships and associations existing in the crop's germplasm.

After the use of isoenzymes and phytochemical methods for the study of diversity and classification of plants, some of which have been mentioned hereinabove, molecular markers had been used for the same purpose. There are several kinds of molecular markers employed for measuring the diversity of maize and the basic principle they are grounded on is practically the same.

These markers or "traits" of the DNA sequences, in order to be used for tracking the inheritance patterns of organisms, must be polymorphic, that is, they have to include variations which allow us to distinguish them in the individuals who have them and to be able to trace them in the progeny of the individuals being studied.

Examples of molecular markers are the Restriction Fragment Length Polymorphisms (RFLP) used first in molecular genetic studies. With the development of the Polymerase Chain Reaction (PCR), a biochemical technique which revolutionized the field of molecular genetics, it has been possible to implement another series of molecular markers which, nowadays, are the preferred technique by molecular geneticists.

As an example, let us imagine that we are analyzing with RFLP the Mexican maize races Palomero, Jala and Tuxpeño, and that we want to establish their phylogenetic affinity (See figure 7). Let's suppose that when we extracted their DNA and processed it with biochemical methods we obtained a series of fragments we identified by means of their chemical properties and weight. To identify these fragments we placed them in a gel through which runs an electrical current, so we are able to separate the fragments thanks to these chemical properties. When we dye the fragments immobilized in the gel, some patterns of the different DNA sizes can be identified. With this data, we can generate association diagrams that allow us to establish phylogenetic relationships.

Although we have simplified the genetic and molecular analysis processes, the fundamentals of the biotechnological methodology used in the research on the diversity of maize have been preserved. With these elements we can follow up the most representative studies that are carried out nowadays with the support of molecular biology.

With molecular methodologies, similar to the ones depicted in the Figure 7, current investigations have been carried out to describe the diversity of maize. In this way the genetic resources of maize in Brazil<sup>49</sup> have been re-assessed, where, through the use of the molecular study of 79 landraces of that country, it was possible to define that the farmers' maize management contribute to the maintenance of the genetic variability, besides preserving the identity of those races. This conclusion coincides on the majority of investigations about the diversity of maize in several countries, and at different time frames, that links the farmer with the diversity of maize.

Another molecular study carried out by Joanne Labate and collaborators describe the diversity of dent maize in the corn belt of USA<sup>50</sup> with a historical perspective of its germplasm. Nowadays, the diversity of maize is very limited in that country; nevertheless, in its germplasm banks are kept hundreds of varieties which show the original diversity of its landraces. Thanks to the molecular methods used in its analysis, Labate and her team confirmed the divergence and distinctive traits of the two major groups which constitute the maize germplasm in USA: flint and dent maize. For those researchers it is clear that, besides of the historical knowledge of their germplasm, the description of maize genetic variability allows a better use of germplasm for practical purposes of genetic improvement. As already

mentioned, the diversity of maize was recognized since the first studies on the American races, described in the books sponsored by the National Academy of Sciences of USA (See Note 34). The analysis of the germplasm variability, from the morphological and botanical studies to the isoenzymes and phytochemical studies, accounts for the great diversity of maize. With the molecular methodologies, not only phylogenetic relationships have been defined but also the germplasm diversity has been confirmed, allowing its taxonomical systematization. With all those elements, gathered throughout a lot of years of scientific research, it has been possible to recognize –as is shown in the work of Matzuoka and collaborators (2001) – the historical path of maize in every part of the American continent. The evident variability of maize germplasm in the continent had led many scientists to ask how the evolution and diversification of maize took place under domestication, since its origin to the present. As we can observe, this question leads us directly to a fundamental issue on the study of maize where social and natural sciences work together, with the human intervention in the process and development of the culture (or agriculture) of the representative crop of America.

<sup>49</sup> Carvalho VP, Ruas CF, Ferreira JM, Moreira RMP, Ruas PM. 2004. Genetic diversity among maize (*Zea mays* L.) landrace assessed by RAPD markers.

<sup>50</sup> Labate JA, Lamkey KR, Mitchell SE, Kresovich S, Sullivan H, Smith JSC. 2003. Molecular and historical aspects of corn belt dent diversity. *Crop Science* 43: 80-91

Image page 20: tender blue Maize, State of Mexico  
Image in this page: Blue maize from Oaxaca  
© David Lauer



# The maize migration and diversification in America

Domestication is a process driven by humans. For researchers such as Antonio Turrent<sup>51</sup>, the genetic improvement process carried out by farmers in the rural and indigenous communities in most parts of Mexico, since ancient times, is a continuous process that reaches the present. As we may remember, humans are a key factor in any and all the theories about the maize origin, and to explain its evolution under domestication. Although one of the arguments against teosinte as ancestor of maize lies in its lack of appealing as food and its low yield, a team coordinated by George Beadle<sup>52</sup> in the 70s was able to determine that teosinte satisfactorily complied with the yield and could be used as food under “primitive” experimental conditions. Therefore, Beadle considered that human intervention in the evolution of teosinte on domestication was a determining factor for explaining the change of teosinte small ears into the maize ear, and its subsequent diversification. In Figure 8 is integrated the data of

the main information sources on landraces in America to illustrate the regions where the races diversity is distributed throughout the continent (Table 1).

In order to explain the early diversification of maize in America we will use the scenarios described by Robert Bird<sup>53</sup>, where he summarizes all the information derived from the research and exploration of maize in Americas at the beginning of the decade of 1980. Bird sets the evolution of maize in a timeframe of 2 thousand 500 years, linked to the cultural history of Mesoamerica and South America, and proposes the correlation of morphological and cytogenetic studies of races and racial complexes of maize with certain general characteristics of the civilizations and human groups in the continent. Without forgetting the complex interaction between the first types of maize and teosinte in the early stages of race diversification, in which we could assume there was a minor human intervention, Bird identifies

and defines the race complexes in the different cultural areas of the continent. In accordance with their particular environmental and cultural traits, Bird describes six main regions, as shown in Table 2.

Based on the information and on the analysis of racial complexes, Bird proposes the hypothesis of diversification of these complexes, in the different regions of the continent, from seven ancient types of maize and from the introgression of teosinte. Although that hypothesis was not developed further, in the present document the information and analysis of Robert Bird is used as a reference showing the different regions of the continent where is located the diversity of maize (Figure 8).

<sup>51</sup> Turrent A, Serratos JA. 2004. Context and Background on Maize and its Wild Relatives in Mexico; *Maize and Biodiversity: The Effects of Transgenic Maize in Mexico*. CCA, Montreal Canada. 55 pp.

<sup>52</sup> In collaboration with the researchers Garrison Wilkes, Mario Gutiérrez, Robert Drennan and Rafael Ortega, and with the support of the International Center for the Improvement of Maize and Wheat in Mexico.

<sup>53</sup> Bird, RMck. 1980. "Maize Evolution from 500 BC to the present". *Biotropica*, Volume 12, Number 1, Pages 30-41.

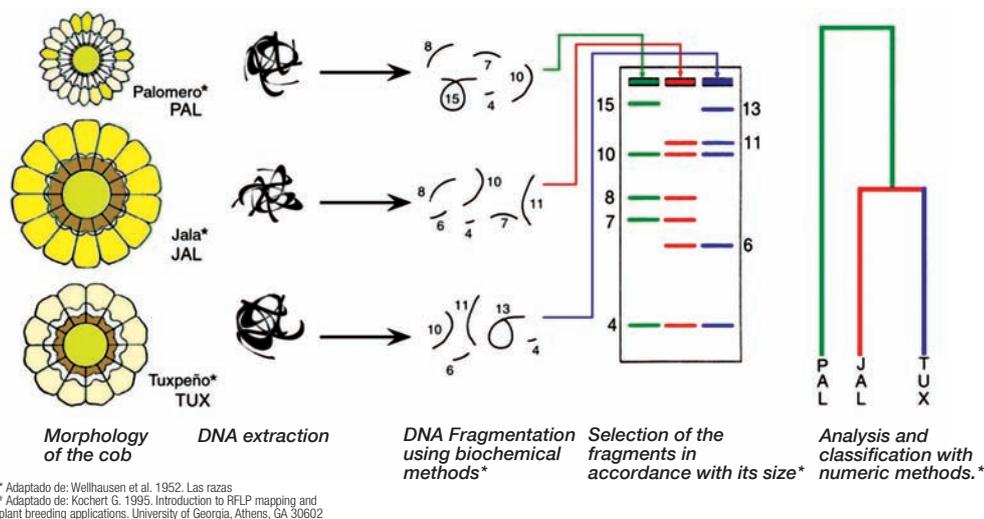


Figure 7. Illustration of the molecular methodology used to analyze the genetic affinity among individuals and populations. The explanation is in the article. Elaborated by Antonio Serratos and based on the references in the diagram.

In the analysis of the maize races from North and South America, Sanchez and Goodman<sup>54</sup> strengthen the conclusions of the researches carried out during the 80s on the paths of dispersion of maize in the continent. They add complementary data regarding the relationship of popcorn maizes in Mexico with the ones in South America; as well as the relationship of Nal-Tel race with the tropical dent maizes from the Caribbean area of Colombia and Venezuela, and furthermore the affinity of flint maize of Northwest of Mexico with the north flint maize of USA. An interesting taxonomic relationship found thanks to this work was the morphological and genetic affinity between the races of the Mexican and Guatemalan Altiplano with the maize of Ecuadorian and Colombian Altiplanos. This data would back up the studies of Wellhausen and collaborators, because they describe the Cacahuacintle maize as ancient exotic maize in the Mesoamerican region. However, recent studies do not support this result. With regards to

the description of the diversification of maize towards the north of America, the study of Labate and collaborators reports that the most ancient maizes in the United States of America are the north flint ones, and that they date 1000 years BC. This maize had been traced in the southwest of USA and it is recognized that from there they dispersed towards the north, through the Great Prairies until the year 1000 of our time, when they were established in that region. Another component of maize in USA, dent maize, was introduced by Spaniards in the 16th century, and it comprised Mexican maize races (See Table 1).

In the study of Matsuoka and collaborators (2001), along with the proposal of the unicentric domestication of maize, the phylogenetic relationships of the maize races in America are defined. In that study are included the 193 types of maize and 71 collections of teosinte representative of all the regions of the continent, from the northwest of USA and Canada to the south of Brazil and the center-north of Argentina,

with a very wide range of altitudes and agro-ecological conditions. With the results obtained from the numeric analysis of molecular markers (Figure 7), Matsuoka and his group proposed an explanation to the diversification of maize in America. They advanced that the oldest maize is from the Mexican Altiplano, where it diversified thanks to the interaction with the *teosinte Zea mexicana* and from where they spread throughout the American continent: "We could track one of the paths through the west and north of Mexico towards the southwest of USA, and from there to the east of USA and Canada. The second path runs outside of the Altiplano towards the west low lands and south of Mexico, and from there to Guatemala, the Caribbean Islands, the low lands of South America and, finally, to the Andean mountains"<sup>55</sup>.

<sup>54</sup> Sánchez-González, J.J. and M.M. Goodman. 1992a. Relationships among the Mexican races of maize. *Econ. Bot.* 46(1): 72–85. Sánchez-González, J.J. and M.M. Goodman. 1992b. Relationships among Mexican and some North American and South American races of maize. *Maydica* 37: 41–51.  
<sup>55</sup> Page 6083 of: Matsuoka and col. 2001. PNAS USA 99(9): 6080-6084.

Table 2. Groups of racial complexes representative of the macro geographical regions of America, and its general cultural traits. By Antonio Serratos, with information from Bird (Note 53).

Region and cultural traits	Racial composites
<b>1. Central Andes.</b> Over 1800 m above sea level, from the center-north of Peru to the northwest of Argentina. The predominant languages are Quechua and Aymara.	Harinosos Redondos de los Andes Centrales, Harinosos Pequeños del Altiplano, Cristalinos Pequeños del Altiplano, Cristalinos Bolivianos, Confite Morocho, Chutucuno Chico
<b>2. South Basin and West Amazons.</b> Covers an arch area from Paraguay to Venezuela in the region of tropical forests. Several groups of tribes.	Harinosos Imbricados del Amazonas, Palomeros Elongados Paraguayos, Morotí Camba
<b>3. North Andes and the Central American Altiplano.</b> Comprises from north of Peru (Huanuco), Colombia and Venezuela to Guatemala. The predominant languages are Chibcha and Paezan, in the Andean north, and Mayan in the Guatemalan Altiplano.	Cristalinos del Norte Andino, Pollo Serrano, Montaña, Rienda-Clavo
<b>4. The Caribbean and Low Lanás.</b> Coasts from Venezuela to Belize and the Caribbean islands. The Caribbean tribes have a more complex social structure in comparison to the one of the tribes in the tropical forests.	Dentados Anchos Caribeños, Harinosos del Bajío Tropical, Canilla-Chandelle, Palomeros Redondos Caribeños
<b>5. The Central Altiplano of Mexico or "Mesa Central".</b> State of Mexico, Federal District, Tlaxcala, Hidalgo, Morelos and Puebla. Three of the most important civilizations of Mesoamerica: Teotihuacans, Toltecs and Aztecs. At least, there is some commercial and cultural influence from northwest of Mexico to Nicaragua.	Dentados Cónicos Mexicanos, Palomeros
<b>6. The east of USA.</b> Oriental woods of USA, the Dakotas and Carolinas.	Cristalinos Norteños

## The peoples and cultures in America and the maize diversity

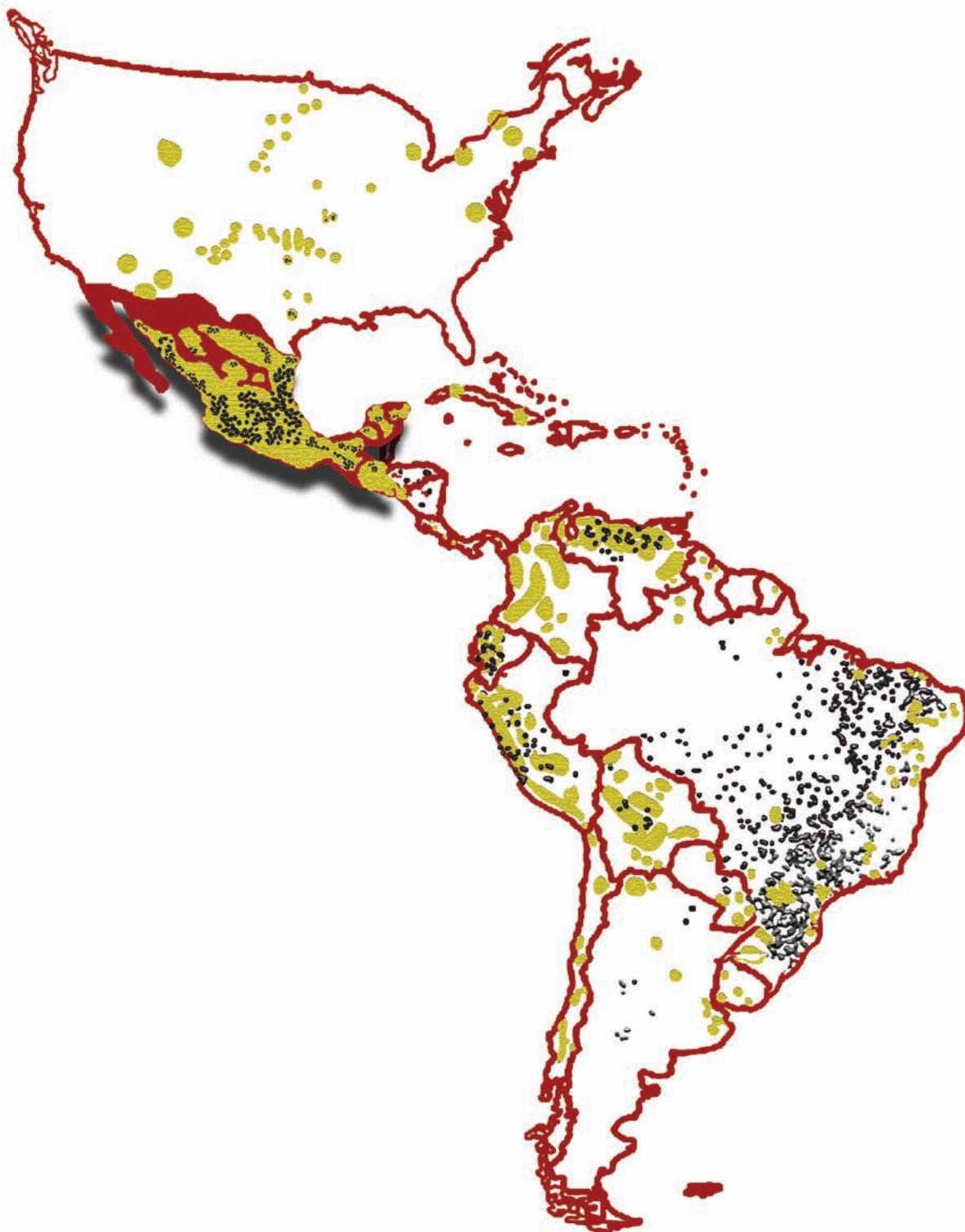


Figure 8. Distribution of maize races in the American continent. The areas in green correspond to the zones where native germplasm has been collected. The black dots are the current areas of maize production in Latin America. By Antonio Serratos based on information from different sources<sup>58</sup>.

The link between the different cultures of the American continent with the cultivation of maize has been established with the myths of the founders of these civilizations, particularly the Mesoamerican ones, which tell us about that close relationship. Enrique Florescano accounts the story of those legends which encourage the development of peoples and cultures in Mexico. According to Florescano, the Olmecs were the first people founded on the cultivation of maize and its myths, between 1500 and 3000 BC<sup>56</sup>. In this way, says the specialist, the Olmecs' legacy to all the other cultures of Mesoamerica was Quetzalcoatl, the first god of maize. With modifications and adaptations, in their origin stories and myths, the Mayas, Teotihuacans, Toltecs, Mixtecas and Mexicas show the maize as fundamental life element for the human being. From the search and re-discovery of maize as sustenance of the people, according to the *Legend of the Suns* of the Mexicas, and the creation of humans with maize dough according to the Mayans-quiches, to the depicting of maize as the axis between the Mayan and Mexicas worlds, all are expressions of the unity and continuity of the foundation myths of the Mesoamerican cultures, as Miguel Leon-Portilla explains<sup>57</sup>.

On the other hand, in the Andean region in South America, the Inca Empire achieved a very advanced agriculture level, where maize played an important role. For Grobman and collaborators<sup>58</sup>, the process of masal selection, used in the early stages of the development of the Inca people, was enough as to achieve the great variety of shapes and colors existing in the maize of that region.

Later, with the consolidation of the Inca confederation and a complex state organization, the races of maize for specific uses flourished with the boost of advanced farming techniques, such as terraces, irrigation, row sowing and fertilization techniques used by the Incas and other Andean cultures before the arrival of the Spaniards to America. In this sense, it is not surprising that the number or catalogued races for Bolivia or Peru are among the ones with a greater number in all America, although due to the variation of kinds of each race, it is in Mexico where the major number of collections or accessions is found. With this information we can imagine that the flow, exchange, and adoption of maize throughout the continent must have been spectacular since the very first stages of the maize domestication, as it is shown by the findings of archeological cobs in Guila Naquitz, Oaxaca<sup>60</sup> -which are 5 thousand 400 years old-, the archeological pollen -5 thousand 100 years old- found in San Andres, Tabasco<sup>61</sup>, both in Mexico, and the maize phytoliths in the Ecuadorian Amazon<sup>62</sup> dated 5 thousand 300 years BC.

At the end of the conquest and at the beginning of the Spaniard Colonial times, in all America the existing power relationships were disrupted and, as a result, the community structures changed in all the regions of the continent. However, we can figure out that the communities linked to maize production suffered a slower process of changes in its structure and social networks, which allowed continuity in the interaction of agricultural workers with maize and its ancient forms of cultivation and production.

<sup>56</sup> Florescano, E. 2003. "Imágenes y significados del dios del maíz"; *Sin maíz no hay país*, Esteva G, Marielle C (coord), Dirección General de Culturas Populares e Indígenas, CONACULTA, México, DF.

<sup>57</sup> León-Portilla, M. "Mitos de los orígenes en Mesoamérica". *Arqueología Mexicana*, Volume X, Number 56, Pages 20-29. Raíces-INAH Publishing House.

<sup>58</sup> Bird, See Note 53; Turrent and Serratos, See Note 51; Matsuoka and col., See Note 31; Various authors, See Notes 34 and 37; McClintock, B, Kato and TA and A. Blumenschein, 1981. *Chromosome Constitution of Races of Maize. Its Significance in the Interpretation of Relationships between Races and Varieties in the Americas*. Colegio de Postgraduados, Chapingo, Mexico; CIMMYT, Programa de Recursos Naturales.

<sup>59</sup> See Note 34, Subsection 5.

<sup>60</sup> Benz BF. 2001. "Archaeological evidence of teosinte domestication from Guila Naquitz, Oaxaca". PNAS Volume 98, Number 4, Pages 2104-2106. This work shows that the agricultural selection of domesticated teosinte was practiced more than 4 thousand years a.C. In another article, Dolores Piperno and Kent Flannery ("The earliest archaeological maize (*Zea mays* L.) from highland Mexico: New accelerator mass spectrometry dates and their implications", PNAS 2001, Volume 98, Number 4; Pages 2101-2103), with the results obtained from the same location in Guila Naquitz, came to the conclusion that the cultural practices that lead to the domestication of maize took place in other area of Mexico.

<sup>61</sup> Pope, KO, Pohl MED, Jones JG, Lentz DL, von Nagy C, Vega FJ, Quitmyer IR. 2001. "Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica". *Science*, Volume 292, Pages 1370-1373.

<sup>62</sup> 1) Bush MB, Piperno DR, Colinvaux PA. 1989. "A 6000 year history of Amazonian cultivation". *Nature*, Number 340, Pages 303-305; 2) Tykot RH, Staller JE. 2002. The importance of early maize agriculture in coastal Ecuador: New data from La Emerenciana. *Current Anthropology*, Volume 43, Number 4, Pages 666 - 677.

Table 3. Races of maize catalogued in Mexico. \* The number in parenthesis is the number of collections registered in the catalog of LAMP (1991). \*\* The groups are set as described in Sanchez and Goodman (1992a).

State*	Maize races catalogued (Cardenas, F. in Taba 1995a)
<b>Aguascalientes (59)</b>	Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos
<b>Baja California Sur (11)</b>	Tuxpeño, Tabloncillo Perla
<b>Campeche (182)</b>	Dzit-Bacal, Nal-Tel, Clavillo
<b>Chihuahua (348)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Tabloncillo, Reventador, Tabloncillo Perla, Bolita, Maíz Dulce, Harinoso de Ocho, Palomero, San Juan, Dulcillo del Noroeste, Tuxpeño Norteño, Azul, Lady Finger, Blandito, Cristalino de Chihuahua, Gordo, Tehua, Apachito, Maizon
<b>Chiapas (795)</b>	Tuxpeño, Celaya, Cónico, Elotes Occidentales, Olotillo, Tabloncillo Perla, Dzit-Bacal, Vandeño, Nal-Tel, Tepecintle, Oloton, Zapalote Chico, Zapalote Grande, Clavillo, Comiteco
<b>Coahuila (124)</b>	Tuxpeño, Celaya, Cónico Norteño, Elotes Occidentales, Tuxpeño Norteño, Tehua
<b>Colima (29)</b>	Tuxpeño, Tabloncillo, Reventador, Tabloncillo Perla, Vandeño, Jala
<b>Durango (270)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Occidentales, Tabloncillo, Reventador, Tabloncillo Perla, Bolita, Pepitilla, San Juan, Dulcillo del Noroeste, Bofo, Blandito de Sonora, Blandito, Cristalino de Chihuahua, Gordo, Tablilla, Tunicata
<b>Guerrero (383)</b>	Tuxpeño, Elotes Cónicos, Elotes Occidentales, Olotillo, Tabloncillo, Reventador, Vandeño, Nal-Tel, Pepitilla, Mushito, Tepecintle, Ancho, Conejo
<b>Guanajuato (370)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Reventador, Maíz Dulce, Mushito, Fasciado
<b>Hidalgo (236)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Olotillo, Bolita, Dzit-Bacal, Mushito, Cacahuacintle, Arrocillo Amarillo, Olotón, Arrocillo
<b>Jalisco (683)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Tabloncillo, Reventador, Tabloncillo Perla, Bolita, Vandeño, Pepitilla, Maíz Dulce, Harinoso de Ocho, San Juan, Azul, Jala, Zamora, Complejo Serrano de Jalisco
<b>State of Mexico (724)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Bolita, Pepitilla, Cacahuacintle, Palomero, Arrocillo Amarillo, Ancho, Azul
<b>Michoacán (528)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Olotillo, Reventador, Dzit-Bacal, Vandeño, Pepitilla, Maíz Dulce, Mushito, Cacahuacintle, Palomero, Conejo, Zamora
<b>Morelos (165)</b>	Tuxpeño, Chalqueño, Olotillo, Tabloncillo, Vandeño, Pepitilla, Tuxpeño Norteño, Ancho
<b>Nayarit (336)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Occidentales, Olotillo, Tabloncillo, Reventador, Tabloncillo Perla, Vandeño, Maíz Dulce, Harinoso de Ocho, Bofo, Jala, Tablilla de Ocho

<b>Nuevo León (118)</b>	Tuxpeño, Cónico Norteño, Tabloncillo, Tablilla de Ocho
<b>Oaxaca (562)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Olotillo, Bolita, Vandeño, Nal-Tel, Mushito, Tepecintle, Olotón, Conejo, Zapalote Chico, Zapalote Grande
<b>Puebla (943)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Olotillo, Bolita, Pepitilla, Mushito, Cacahuacintle, Palomero, Arrocillo Amarillo, Arrocillo
<b>Quintana Roo (132)</b>	Tuxpeño, Olotillo, Dzit-Bacal, Nal-Tel, Tepecintle
<b>Querétaro (115)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Bofo, Onaveño, Fasciado
<b>Sinaloa (187)</b>	Tuxpeño, Tabloncillo, Reventador, Tabloncillo Perla, Maíz Dulce, Harinoso de Ocho, San Juan, Dulcillo del Noroeste, Blandito de Sonora, Lady Finger, Onaveño, Chapalote, Harinoso
<b>San Luis Potosí (206)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Olotillo, Tabloncillo, Dzit-Bacal, Harinoso de Ocho
<b>Sonora (183)</b>	Tuxpeño, Tabloncillo, Reventador, Tabloncillo Perla, Nal-Tel, Harinoso de Ocho, San Juan, Dulcillo del Noroeste, Blandito de Sonora, Lady Finger, Onaveño, Chapalote
<b>Tabasco (35)</b>	Tuxpeño, Olotillo, Vandeño, Nal-Tel, Zapalote Grande
<b>Tamaulipas (148)</b>	Tuxpeño, Dzit-Bacal, Carmen
<b>Tlaxcala (332)</b>	Cónico, Chalqueño, Elotes Cónicos, Cacahuacintle, Palomero, Arrocillo Amarillo, Arrocillo
<b>Veracruz (741)</b>	Tuxpeño, Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Olotillo, Bolita, Dzit-Bacal, Nal-Tel, Pepitilla, Mushito, Cacahuacintle, Palomero, Tepecintle, Arrocillo Amarillo, Olotón, Coscomatepec
<b>Yucatán (249)</b>	Tuxpeño, Olotillo, Dzit-Bacal, Nal-Tel, Tepecintle, Zapalote Chico, Xmenejal
<b>Zacatecas (263)</b>	Celaya, Cónico, Cónico Norteño, Chalqueño, Elotes Cónicos, Elotes Occidentales, Tabloncillo, Bolita, Maíz Dulce, San Juan, Dulcillo del Noroeste, Bofo, Tablilla



Figure 9. Distribution of races of maize in Mexico, per state.



Due to the survival of the approximately 300 maize races in the continent, we can say that the indigenous-campesino culture in the communities of the native peoples and, later, with the Mestizo and Creole farmers, was a key factor for the survival of their cultures and the diversity of maize. In other words, maize constituted the support for the indigenous resistance for more than 500 years, after the destruction of all their ancient ways of life.

The maize and the indigenous and farming peoples had had, since then and still nowadays, a very close relationship that had turned the farmers into guardians of this genetic richness. For example, when re-assessing the traditional indigenous Mexican agriculture, Ekart Boege<sup>63</sup> showed the link between the indigenous peoples existing nowadays and the diversity of maize each ethnic group has. A study carried out by Perales and his group<sup>64</sup> on the maize diversity related with the ethnolinguistic diversity among the tzeltales and tzotziles in Chiapas, concluded that the differentiation and preservation of the races of particular ethnic groups is related to language and, therefore, with the amount of reliable information each farmer can use for preserving their patrimony by growing and producing “their maize”. It is in this kind of studies where we can appreciate the value of the maize collections preserved in germplasm banks and described in other sections herein, as well as the culture developed around them. Therefore, maize collections become base lines for studies from different disciplines which contribute to obtain a better knowledge and valorization of maize and its diversity, thus accounting the importance of the farmers management of maize and the development and diversity of this crop.

From the biological point of view, the inner mechanisms of diversification had been studied to understand the morphological diversity with which the farmer directly works, and “preserve the long term maize selection potential”<sup>65</sup>.

With the aim of knowing the evolutionary mechanisms of maize in the traditional agricultural ecosystems, Gael Pressoir and Julien Berthaud, in two separate research works, assessed the genetic diversity, the agroecological factors and the farmer’s management of seed in six communities in the Central Valleys in Oaxaca. They described the impact of the selection carried out by the farmer on the differentiation and diversification of maize. What they concluded was that in these communities, distance has no influence on the isolation of maize populations and that there is a high level of seed flow inside and outside of the communities, therefore ensuring the conservation of the diversity of maize. The great variation on the interval of flowering and anthesis is a key factor for the structuring of the population which partly explains the morphological evolution of maize in that region of Oaxaca.

<sup>63</sup> Boege-Schmidt E. 2006. “Territorios y diversidad biológica. La agrobiodiversidad de los pueblos indígenas de México”; *Biodiversidad y conocimiento tradicional en la sociedad rural*, Concheiro Bórquez L and López Barcenás F (coord.). Centro de Estudios para el Desarrollo Rural Sustentable y la Soberanía Alimentaria, LX Legislatura, Congreso de la Unión, México.

<sup>64</sup> Perales H, Benz BF, Brush SB. 2005. “Maize diversity and ethnolinguistic diversity in Chiapas, Mexico”. *PNAS* Volume 102, Number 3, Pages 949-954.

<sup>65</sup> 1) Pressoir G, Berthaud J. 2004. “Patterns of population structure in maize landraces from the Central Valleys of Oaxaca in Mexico”. *Heredity*, Volume 92; Pages 88-94. 2) Pressoir G, Berthaud J. 2004. “Population structure and strong divergent selection shape phenotypic diversification in maize landraces”. *Heredity*, Volume 92; Pages 95-101.

## Analysis and perspective of the diversity of maize in the american continent

Through the history of the study and exploration of the diversity of maize, we can see that there are two major strategies for the conservation of these resources: the recollection and storage of maize samples in germplasm banks or ex situ conservation, and the in situ conservation, which implies supporting the reproduction of social and environmental conditions of the farmer, allowing him to preserve the maize.

From the pioneering works of the Committee for the Conservation of maize of the Academy of Science of USA, it is clear that their conservation strategy is focused in the extensive and exhaustive recollection of maize genetic resources. We can see that in the books of the races of maize in Latin American countries (Note 34), the effort was focused in botanical, genetic, agronomic and technical aspects of maize germplasm. Although in those books the importance of farmers for the diversification and conservation of the crop is mentioned, they do not go deeper on that factor and, as a matter of fact, the farmer and his agricultural system are placed just as context for maize. This strategy could not be focused otherwise, if we take into account the technological path USA was been building since back then. In that country, the implementation and adoption of maize hybrids was promoted since the beginning of the 20th century, and all the research system was brought together around that technology. The public policies and the government's direct economic support allowed generating a great concentration of control on the maize production throughout the American Corn Belt. In a classical work on agricultural economy, Zvi Griliches describes the process of adoption of hybrids

in USA. In this work is described what in capitalism is considered the paradigm of technological innovation process, the process of adoption and distribution of inventions which are specific to different markets and the rate of acceptance of these processes among entrepreneurs<sup>66</sup>. In that sense, the agrotechnological path of USA conceive the genetic resources and the ex situ conservation as a capital stock in germplasm banks for industrial application and as insurance for future risks. Then, conservation of maize is carried out through the alienation of the germplasm resources from the farmers, which were generated during centuries of communal work.

Based on the general strategy for maize production that lies on the intensive use of hybrids and on the control of native genetic material, this model is exported to the less developed countries. In this way, the explorations of maize diversity in Latin America began, and generated the resources which make up the first maize germplasm banks in Mexico, Colombia, Brazil and Peru, around which regularly cooperate regional networks of plant genetic resources or continental networks, such as the Latin American Maize Project. This project was the soundest effort to concentrate the information on maize diversity in the Continent. Although it is based in the agricultural research strategy of USA, its paramount importance is undeniable, because is key for the analysis and a source of agronomic information of the core collections of the diversity of maize in America. We cannot deny the great value that ex situ conservation has, nevertheless, in order to develop all its potential, it is necessary to

include the information from the farmers and, as a priority service, grant preferential access to that maize for improvement programs and projects.

All the studies on maize and its relationship with the traditional agricultural systems show that farmer and ethnic groups management in different areas of America, is fundamental for the continuity of crop diversity. This fact have been recognized during decades, but there has not been a definitive attention to in situ conservation programs that would allow the sustainability and feasibility of traditional or agroecological systems.

This kind of agriculture and the research linked to it has had different stages and degrees of success. Nevertheless, the research "from bottom to top", that is, with participation of farmers and of alternative type, had always been marginal in comparison to the dominant agricultural research.

<sup>66</sup> Griliches Z. 1957. "Hybrid corn: An exploration in the economics of technological change". *Econometrica*, Volume 25, Number 4, Pages 501-522.

Despite the efforts that, in different times and carried out by international and national organizations, had been done in order to preserve the genetic resources of maize and the communities where these are located, it has not been possible to achieve a greater impact in the agricultural sector as a whole. This problem deepens when we talk about maize because in Latin America the financial resources allocated for agriculture are each time more and more slender.

Likewise, development models are uncritically copied by Latin American countries from the ones of industrialized countries -that have very different conditions- rendering severe social, economical and environmental problems in the countries that adopt these models. The deterioration of the social, economic and political conditions of the agricultural and livestock sectors, in general, and of the farmers, in particular, risks the diversity of maize throughout the American continent. It is necessary to underline that the key factor for solving this problem is the conservation of the means and modes of production of campesinos. We cannot overlook the fact that maize diversity in the continent needs support for the rural society who lives out of the agriculture, as well as the fact that farmers need to improve their life and work conditions so they do not abandon agriculture as their way of life. Implementing ways of protecting in situ the diversity of maize requires taking into account

much more complex situations that need governmental support so they can develop and that involve political and social stakeholders who need the support of programs that promote actions towards social organization and communal work.

The indigenous and farmer peoples where the survival of the maize diversity lies, are threaten by economic factors, making them leave their lands and emigrate to obtain better life conditions. The destruction of the social net in these communities increases the risk of extinction of maize and its diversity by disrupting the key factors for its survival: farmers, indigenous people, and agroecological producers. In this scenario, it is essential to move towards a new stage where is included a revalue of maize in the entire American continent as an agglutinating focal point for the defense and sustainability of the rural farming and indigenous lands.

In view of all the scientific, social and humanistic evidences analyzed, which show us that the diversification of maize is a process that took place throughout America and in all the civilizations of the continent, it is necessary to revalue the meaning of maize in the continent. We can say; the maize is, as the Olmecs, Mayans, Aztecs or Incas said, the axis of the life of the peoples of America and, therefore, it must be regarded as the most representative crop of the American continent. The protection of maize must involve all the peoples of America, independently of political borders that divide them.

# References

- Anderson E, Cutler H. 1942. Races of *Zea mays* I: their recognition and classification. *Ann Missouri Bot Gard*, 21: 69–88
- Arnason TJ. 1936. Cytogenetics of hybrids between *Zea mays* and *Euchlaena mexicana*. *Genetics* 21: 40-60
- Arnason JT, Baum B, Gale J, Lambert JDH, Bergvinson D, Philogene BJR, Serratos A, Mihm J, Jewell DC. 1994. Variation in resistance of Mexican landraces of maize to maize weevil *Sitophilus zeamais*, in relation to taxonomic and biochemical parameters. *Euphytica*, Volume 74; Pages 227-236.
- Beadle GW. 1932. The relation of crossing over to chromosome association in *Zea-Euchlaena* hybrids. *Genetics* 17: 481-501.
- Beadle G.W. 1939. Teosinte and the origin of maize. *J. Heredity* 30; Pages 245-247.
- Beadle G.W. 1978. Teosinte and the origin of maize. En: *Maize breeding and genetics*, D.B. Walden (Ed.), Wiley Interscience; Pages 113-128.
- Beadle G.W. 1980. The ancestry of corn, *Sci. American* 242; Pages 112-119.
- Benz BF. 2001. Archaeological evidence of teosinte domestication from Guilá Naquitz, Oaxaca. *PNAS* Volume 98, Number 4, Pages 2104–2106.
- Bird, RMck. 1980. *Maize Evolution from 500 BC to the present*. *Biotropica*, Volume 12, Number 1, Pages 30-41.
- Boege-Schmidt E. 2006. Territorios y diversidad biológica. La agrobiodiversidad de los pueblos indígenas de México. In: *Biodiversidad y conocimiento tradicional en la sociedad rural*, Concheiro Bórquez L and López Barcenás F (coord.). Centro de Estudios para el Desarrollo Rural Sustentable y la Soberanía Alimentaria, LX Legislatura, Congreso de la Unión, México.
- Broda J. 1978. Relaciones políticas ritualizadas: El ritual como expresión de una ideología. In: *Economía política e ideología en el México prehispánico*, Carrasco P. and Broda J. (eds), CIS-INAH. Editorial Nueva Imagen, Mexico, DF; Pages. 221-254.
- Bush MB, Piperno DR, Colinvaux PA. 1989. A 6000 year history of Amazonian cultivation. *Nature*, Number 340, Pages 303-305.
- Camussi A., Spagnoletti P.L., Melchiorre P. 1983. Numerical taxonomy of Italian maize populations: Genetic distances on the basis of heterotic effects. *Maydica*, Volume 28; Pages 411-424.
- Carvalho VP, Ruas CF, Ferreira JM, Moreira RMP, Ruas PM. 2004. Genetic diversity among maize (*Zea mays* L.) landrace assessed by RAPD markers. *Genetics Mol Biol* 27(2): 228-236.
- Casas-Díaz E, Hanson D, Wellhausen E. 1968. Genetic relationships among collections representing three Mexican racial composites of *Zea mays*. *Genetics* Volume 59, Pages 299–310.
- Cervantes T., Goodman M.M., Casas-Díaz E., Rawlings J.O. 1978. Use of genetic effects and genotype by environmental interactions for the classification of Mexican races of maize. *Genetics*, Volume 90; Pages 339–348.
- CIMMYT, 1999, A core subset of LAMP, from the Latin American Maize Project 1986-1988. Mexico, D.F.
- Collins GN. 1921. Teosinte in Mexico. *J. Heredity* 12: 339-350.
- Creighton HB, McClintock B. 1931. A correlation of cytological and genetical crossing-over in *Zea mays*. *PNAS* Volume 17, Number 8, Pages 492–497
- Doebley J, Goodman JJ, Stuber CW. 1985. Isozyme variation in the races of maize from Mexico. *American Journal of Botany* 72(5): 629-639.
- Doebley J, Stec A, Wendel J, Edwards M. 1990. Genetic and morphological analysis of a maize-teosinte F2 population: Implications for the origin of maize. *PNAS*, Volume 87; Pages 9888-9892.
- Doebley J., Stec A. 1991. Genetic analysis of the morphological differences between maize and teosinte. *Genetics*, Volume 129; Pages 285-295.
- Doebley J. 1992. Mapping the genes that made maize. *Trends in Genetics*, Volume 8, Number 9; Pages 302-307.
- Emerson RA. 1924. Control of flowering in teosinte. *J. Heredity* 15, Pages 41-48.
- Emerson RA, Beadle GW, 1932. Studies of *Euchlaena* and its hybrids with *Zea*. II. Crossing over between the chromosomes of *Euchlaena* and those of *Zea*. *Z Indukt Abstamm Ver* 62: 305-315.
- Eubanks M. 1995. A cross between two maize relatives: *Tripsacum dactyloides* and *Zea diploperennis* (Poaceae). *Economic Botany* 49(2); Pages 172-182.
- Florescano, E. 2003. Imágenes y significados del dios del maíz. In: *Sin maíz no hay país*, Esteve G, Marielle C (coord), Dirección General de Culturas Populares e Indígenas, CONACULTA, México, DF.
- García-Lara S, Burr AJ, Serratos JA, Díaz-Pontones DM, Arnason J, Bergvinson DJ. 2003. Defensas naturales en el grano de maíz al ataque de *Sitophilus zeamais* (Motsch. Coleoptera: Curculionidae): Mecanismos y bases de resistencia. *Revista de Educación Bioquímica* 22(3): 138-145.
- Gaut BS, Doebley JF. 1997. DNA sequence evidence for the segmental allotetraploid origin of maize. *PNAS*, Volume 94; Pages 6809-6814.
- Goodman, MM, Bird RMck. 1977. The races of maize IV: Tentative grouping of 219 Latin American races. *Economic Botany* 31: 204-221.
- González R LP. 1994. Caracterización de microorganismos de mucigel de raíces adventicias y suelo rizosférico de maíz de la región Mixe, Oaxaca. Doctorate Thesis, Universidad Autónoma Benito Juárez de Oaxaca. 95 p.

- Grant U, Hatheway WH, Timothy DH, Cassalet C, Roberts LM. 1963. Races of maize in Venezuela. National Academy of Sciences, NRC Publication 1136. Washington D.C.;
- Griliches Z. 1957. Hybrid corn: An exploration in the economics of technological change. *Econometrica*, Volume 25, Number 4, Pages 501-522.
- Grobman A, Salhuana W, Sevilla R, Mangelsdorf PC. 1961. Races of maize in Peru. National Academy of Sciences, NRC Publication 915. Washington D.C.
- Hanson MA, Gaut BS, Stec A, Fuerstenberg SI, Goodman MM, Coe EH, Doebley J. 1996. Evolution of anthocyanin biosynthesis in maize kernels: The role of regulatory and enzymatic loci. *Genetics*, Volume 143; Pages 1395-1407.
- Harshberger, JW. 1893. Maize: A Botanical and Economic Study (Monograph). In: Contributions from the Botanical Laboratory of the University of Pennsylvania, volumen 1 Number 2.
- Hatheway WH. 1957. Races of maize in Cuba. National Academy of Sciences, NRC Publication 453. Washington D.C.
- Hernández-Boncalo F. (1515/1517 – 1578): <http://www.franciscoteixido.com/default.asp?q=6&p=2&lg=sp>  
<http://www.madrimasd.org/cienciaysociedad/patrimonio/personajes/biografia.asp?id=27>  
<http://www.publicaciones.cucsh.udg.mx/pperiod/esthom/esthompdf/esthom20/19-37.pdf>
- Hernández-Casillas JM. 1986. Estudio de caracteres químicos del grano de las razas mexicanas de maíz y clasificación racial. Tesis de Maestría. Colegio de Postgraduados, Montecillo Estado de México. 79 p.
- Hernández-Xolocotzi E. 1988. Experiences in the collection of maize germplasm. In: Recent advances in the conservation and utilization of genetic resources: Proceedings of the Global Maize Germplasm Workshop. CIMMYT, Mexico DF, Pages 1-8.
- Ittis H.H. 1983. From teosinte to maize: The catastrophic sexual transmutation. *Science* 222; Pages 886-894.
- Kato-Yamakake TA. 1976. Cytological studies of maize (*Zea mays* L.) and teosinte (*Zea mexicana* Schrader Kuntze) in relation to their origin and evolution. Massachusetts Report Agric Expt Station Number 635.
- Kato-Yamakake TA. 1996. Revisión del estudio de la introgresión entre maíz y teocintle. In: Flujo genético entre maíz criollo, maíz mejorado y teocintle: implicaciones para el maíz transgénico, Serratos JA, Willcox MC y Castillo F (eds), CIMMYT México DF. ([http://www.cimmyt.org/ABC/geneflow/geneflow\\_pdf\\_spa/FG-Revision.pdf](http://www.cimmyt.org/ABC/geneflow/geneflow_pdf_spa/FG-Revision.pdf))
- Kato-Yamakake TA. 2005. Cómo y dónde se originó el maíz. *Investigación y Ciencia* Agosto 2005: 68- 72.
- Labate JA, Lamkey KR, Mitchell SE, Kresovich S, Sullivan H, Smith JSC. 2003. Molecular and historical aspects of corn belt dent diversity. *Crop Science* 43: 80-91.
- León-Portilla, M. Mitos de los orígenes en Mesoamérica. *Arqueología Mexicana*, Volume X, Number 56, Pages 20-29. Editorial Raíces-INAH.
- Li D, Blakey CA, Dewald C, DellaportaSL. 1997. Evidence for a common sex determination mechanism for pistil abortion in maize and its wild relative *Tripsacum*. *PNAS* Volume 94; Pages 4217-4222.
- Linneo C. 1748. *Systema Naturae*. Estocolmo, Suecia: [http://gdz.sub.uni-goettingen.de/no\\_cache/dms/load/img/?IDDOC=233236](http://gdz.sub.uni-goettingen.de/no_cache/dms/load/img/?IDDOC=233236)
- Lumholtz 1902 (1986). *El México desconocido*. Instituto Nacional Indigenista, 2 tomos, México DF.
- Mangelsdorf, PC y Reeves RG. 1938. The origin of maize. *PNAS* 24(8); Pages 303-312.
- Mangelsdorf, PC y Reeves, RG. 1959. The origin of corn. *Bot. Mus. Leaflet. Harv. Univ.*, 18: 389-411.
- Matsuoka Y, Vigouroux Y, Goodman MM, Sánchez-González J, Buckler E, Doebley J. 2001. A single domestication for maize shown by multilocus microsatellite genotyping. *PNAS*, Volume 99, Number 9; Pages 6080-6084.
- McClintock B. 1929. Chromosome morphology in *Zea mays*. *Science*, Volume 69, Number 1798, Page 629
- McClintock B. 1930. A Cytological Demonstration of the Location of an Interchange between two Non-Homologous Chromosomes of *Zea mays*. *PNAS* Vol. 16, Number 12; Pages 791-796
- McClintock, B, Kato Y. TA y Blumenschein A. 1981. Chromosome Constitution of Races of Maize. Its Significance in the Interpretation of Relationships between Races and Varieties in the Americas. Colegio de Postgraduados, Chapingo, Mexico; CIMMYT, Programa de Recursos Naturales.
- Paterniani, E y Goodman, MM. 1978. Races of Maize in Brazil and Adjacent Areas. Mexico: International Maize and Wheat Improvement Center, Mexico City.
- Perales H, Benz BF, Brush SB. 2005. Maize diversity and ethnolinguistic diversity in Chiapas, Mexico. *PNAS* Volume 102, Number 3, Pages 949-954.
- Piperno D y Flannery K. 2001. The earliest archaeological maize (*Zea mays* L.) from highland Mexico: New accelerator mass spectrometry dates and their implications. *PNAS*, Volume 98, Number 4; Pages 2101-2103.
- Pope, KO, Pohl MED, Jones JG, Lentz DL, von Nagy C, Vega FJ, Quitmyer IR. 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. *Science*, Volume 292, Pages 1370-1373.
- Popol Wuj. 1986. Antiguas historias de los indios quichés de Guatemala por Albertina Saravia. Editorial Porrúa, Colección "Sepan cuantos..." Num. 36, Decimosexta edición. México, D.F.

- Pressoir G, Berthaud J. 2004a. Patterns of population structure in maize landraces from the Central Valleys of Oaxaca in Mexico. *Heredity*, Volume 92; Pages 88-94.
- Pressoir G, Berthaud J. 2004b. Population structure and strong divergent selection shape phenotypic diversification in maize landraces. *Heredity*, Volume 92; Pages 95-101.
- Latin American Maize Project (LAMP). 1991. ARS-USDA, CIMMYT, Pioneer Hi-Bred International Inc., Universidad Agraria La Molina (Perú).
- Ramírez R, Timothy DH, Díaz E, Grant UJ, Nicholson-Calle GE, Anderson E, Brown WL. 1961. Razas de maíz en Bolivia. Ministerio de Agricultura de Colombia, Oficina de Investigaciones Especiales, Boletín técnico Num. 9. Editorial ABC, Bogotá, Colombia;
- Reid L, Arnason JT, Nozzolillo C, Hamilton R. 1990. Taxonomy of Mexican landraces of maize, based on their resistance to European corn borer, *Ostrinia nubilalis*. *Euphytica*, Volume 46; Pages 119-131.
- Roberts LM, Grant UJ, Ramírez R, Hatheway WH, Smith DL, Mangelsdorf PC. 1957. Razas de maíz en Colombia. Ministerio de Agricultura de Colombia, Oficina de Investigaciones Especiales, Boletín técnico Num. 2. Editorial Máxima, Bogotá, Colombia
- Sánchez-González, J.J. and M.M. Goodman. 1992a. Relationships among the Mexican races of maize. *Econ. Bot.* 46(1): 72-85.
- Sánchez-González, J.J. and M.M. Goodman. 1992b. Relationships among Mexican and some North American and South American races of maize. *Maydica* 37: 41-51.
- Sánchez González JJ, Ruíz Corral JA. 1996. Distribución del teocintle en México. In: Flujo genético entre maíz criollo, maíz mejorado y teocintle: implicaciones para el maíz transgénico, Serratos JA, Willcox MC y Castillo F (eds), CIMMYT México DF ([http://www.cimmyt.org/ABC/geneflow/geneflow\\_pdf\\_spa/FGDistribucion.pdf](http://www.cimmyt.org/ABC/geneflow/geneflow_pdf_spa/FGDistribucion.pdf))
- Schrader H. 1833. *Index Seminum Hort Acad Gottingen 1832*: 25-26. See: <http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?16116>
- Serratos A, Arnason JT, Nozzolillo C, Lambert JDH, Philogene BJR, Fulcher G, Davidson K, Peacock L, Atkinson J, Morand P. 1987. Factors contributing to resistance of exotic maize populations to maize weevil, *Sitophilus zeamais*. *Journal of Chemical Ecology* 13: 751-762.
- Thom R. 1977. *Stabilité structurelle et morphogénèse. Interédition*, París (Estabilidad estructural y morfogénesis, Editorial GEDISA, Barcelona, España, 1987).
- Timothy DH, Peña B, Ramírez R, Brown WL, Anderson E. 1961. Races of maize in Chile. National Academy of Sciences, NRC Publication 847. Washington D.C.
- Timothy DH, Hatheway WH, Grant UJ, Torregroza M, Sarria D, Varela D 1966. Razas de maíz en Ecuador. Instituto Colombiano Agropecuario, Ministerio de Agricultura de Colombia, Boletín Técnico Num. 12. Bogotá Colombia.
- Turrent A, Serratos JA. 2004. Context and Background on Maize and its Wild Relatives in Mexico. In: *Maize and Biodiversity: The Effects of Transgenic Maize in Mexico*. CCA, Montreal Canadá. 55 pp.
- Tykot RH, Staller JE. 2002. The importance of early maize agriculture in coastal Ecuador: New data from La Merenciana. *Current Anthropology*, Volume 43, Number 4, Pages 666 - 677.
- Waddington CH. 1975a. Genetic assimilation. In: *The evolution of an evolutionist*, Waddington CH Cornell University Press, Ithaca, NY, Estados Unidos, Pages 59 - 92.
- Waddington CH. 1975. A catastrophe theory of evolution. In: *The evolution of an evolutionist*, Waddington CH Cornell University Press, Ithaca, NY, Estados Unidos, Pages 253 - 266.
- Weissinger AK, Timothy DH, Levings III CS, Goodman MM. 1983. Patterns of mitochondrial DNA variation in indigenous maize races of Latin America. *Genetics* 104: 365-379.
- Wellhausen E.J., Roberts L.M., Hernández-Xolocotzi E., Mangelsdorf P.C. 1952. *Races of maize in Mexico*. Bussey Institute, Harvard University (Cambridge)
- Wellhausen E.J., Fuentes A., Hernández-Corzo A., Mangelsdorf P.C. 1958. Razas de maíz en la América Central. Folleto técnico 31, Oficina de Estudios Especiales, Secretaría de Agricultura y Ganadería, México DF
- Wilkes HG. 1970. Teosinte introgression in the maize of the Nobogame valley. *Botanical Museum Leaflets*, Harvard University, Volume 22, Number 9, Pages 297 - 311.
- Wilkes HG. 1977. Hybridization of maize and teosinte, in Mexico and Guatemala and the improvement of maize. *Economic Botany*, Volume 31, Number 3, Pages 254 - 293.
- Wilkes HG y Goodman MM. 1995. Mystery and missing links: The origin of maize. *Maize Genetic Resources*, Maize Program Special Report; Taba, S. (editor), México, DF, Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT).
- Wilkes, G. 2004. Corn, Strange and Marvelous: But Is a Definitive Origin Known?. In: *Corn: Origin, History, Technology, and Production*, C. Wayne Smith (ed), Wiley & Sons, Inc. Pages 3 - 63.
- Yakoleff-Greenhouse V, Hernández-Xolocotzin E, Rojkind-de-Cuadra C, Larralde C. 1982. Electrophoretic and immunological characterization of pollen protein of *Zea mays* races. *Economic Botany* 36(1): 113-123.

## **Editorial review**

Aleira Lara  
Cecilia Navarro

## **Design**

Atzin Aguilar

Greenpeace is a global, environmental, non governmental and politically and economically independent organization. It takes action to protect the environment, promote social and environmental peace and justice and to change attitudes and habits. It works through campaigns to: promote clean energies and mitigate climate change, protect the oceans from overexploitation and contamination, protect the forests and the people living in them, avoid the release of GMO to the environment and promote a sustainable agriculture, create a future free of toxics and promote the environmental justice and peace.

Photograph on the cover:  
Diversity of native maize © Greenpeace

## **Greenpeace México**

Santa Margarita 227, Col. del Valle,  
C.P. 03100, Mexico, Mexico City

More information in:  
[www.greenpeace.org.mx](http://www.greenpeace.org.mx)

Contact us:  
[greenpeace.mexico@greenpeace.org](mailto:greenpeace.mexico@greenpeace.org)

Join Greenpeace calling the phone numbers:  
5687 8780 / 5687 8869



Paper made without elemental chlorine and acids free.