International Journal of Chemical Studies

Siddharth Panda
Ph. D. Scholar, Orissa University
of Agriculture and Technology,
Bhubaneswar, Odisha, India

Shimantini Borkataki
Assistant Professor,
(Entomology), Assam
Agricultural University, Jorhat,
Assam, India

M Devender Reddy
Dean (Agri.), and Dean (Admin),
MSSSOA, Centurion University
of Technology and Management,
Paralakhemundi, Odisha, India

SP Nanda
Dean (Agri.), and Dean (Admin),
MSSSoA, Centurion University
of Technology and Management,
Paralakhemundi, Odisha, India

Domestication and evolution of maize

Siddharth Panda, Shimantini Borkataki, M Devender Reddy and SP Nanda

DOI: https://doi.org/10.22271/chemi.2020.v8.i1aa.8530

Abstract
Around ten thousand years ago, men mostly relied on hunting and gathering activities before shifting to agriculture and allied practices. By 4000 years ago, ancient people had completed the domestication of all major crop species upon which human survival is dependent, including rice, wheat, and maize. Recent advances have started to point out the genes that were responsible for this change of the cultivated maize crop. The list of genes to date tentatively suggests that diverse plant developmental pathways were the targets of Neolithic "genetic tinkering," Maize and its closest wild relatives, the teosintes, present a paradox. Even though maize and the teosintes exhibit extreme differences in their adult morphologies their genomes are so similar that they share the same chromosome number, similar or identical chromosome morphologies, and they can be easily cross-hybridized. A very high level of diversity exists among the maize landraces to explain this diversity many workers have proposed that maize landraces were the products of multiple independent domestication from their wild relative. Reports indicate that all maize arose from a single domestication in southern Mexico about 9,000 years ago. This phylogenetic work is consistent with a model based on the archaeological record suggesting that maize was the result of early Holocene domesticates. A few major genes or multiple linked minor genes on the maize chromosome largely govern the drastic change that is seen between teosinte and maize. Genes like teosinte branched1 (tb1) gene, teosinte glume architecture1 (tga1) and Zea Floricaula / Leafy2 (zfl2). There still remain some untold chapters in the origin and early diversification of maize. These questions will require additional archaeological and botanical exploration, more powerful molecular analyses, and perhaps DNA analysis of archaeological materials such that a perfect phylogenetic relationship can be established.

Keywords: Domestication, evolution, exploration, maize and teosinte

Introduction
Ten thousand years ago human beings realized the importance of agriculture; this realization came through a series of events. Initially they were hunters and gatherers, dependent on the animals they hunted and the plants or fruits they collected. This behavior was accompanied by seasonal migration schedules due to environmental variations. These people mostly followed the regular migratory traces visiting some specific geographical areas over the year in different seasons. The disturbance of the natural vegetation and middens at these sites provided fertile ground for the types of colonizing species that were the progenitors of our crops. Seeds discarded with the "kitchen" trash one year would sprout into a new crop by the time the group returned the following year. Sometimes if they preferred a particular variety and collected the seed or carried them to different places with the most desirable traits, then over time the frequency of plants with these favored phenotypes would increase in their garden crop. Eventually, no new wild seeds and fruits would be collected and a switch to deliberate sowing of seeds would occur. This phenomenon has been reasoned out for the realization of the importance of seeds and crops. Thus they started collecting fruits and seeds of specific plants for their propagation. Slowly the areas under specific crops started increasing and gradually the process of selection came into picture and then intensified. 4,000 years ago many of the modern day crops were already domesticated or selected upon, this resulted in the present day scenario.

Domestication and Domestication syndrome
Plant domestication is the genetic modification of a wild species to create a new form of a plant altered to meet human needs. For many crops, domestication has rendered the plant

Corresponding Author:
Shimantini Borkataki
Assistant Professor,
(Entomology), Assam
Agricultural University, Jorhat,
Assam, India

completely dependent on humans such that it is no longer capable of propagating itself in nature. Maize and cauliflower are good examples of such highly modified forms. However, other crops, such as hemp, carrot, and lettuce, have been more modestly modified compared to their progenitors, and they can either revert to the wild or become self-propagating weeds. There is a common suite of traits - known as the "domestication syndrome"- that distinguishes most seed and fruit crops from their progenitors [1]. Compared to their progenitors, food crops typically have larger fruits or grains, more robust plants overall, more determinate growth or increased apical dominance (the robust growth of the central stem in comparison to the side stems), and a loss of natural seed dispersal so that seeds remain attached to the plant for easy harvest by humans. Remarkably, crops often have fewer (although larger) fruits or grains per plant than their progenitors. A variety of physiological changes are also involved. These include a loss of seed dormancy, a decrease in bitter substances in edible structures, changes in photoperiod sensitivity, and synchronized flowering.

The early agricultural practices just described have left their signatures on the patterns of genetic diversity in the genomes of crop plants. Because early farmers used only a limited number of individuals of the progenitor species, much of the genetic diversity in the progenitor was left behind. Moreover, with each generation during the domestication process, only seed from the best plants formed the next generation. This winnowing caused a genetic bottleneck, which reduced genetic diversity throughout the genome [2]. The extent of this loss of diversity depends on the population size during the domestication period and the duration of that period. Notably, the loss in diversity was not experienced equally by all genes in the genome. The genes that do not influence favored phenotypes (which are called neutral genes), the loss in diversity is simply a function of the strength of the bottleneck in terms of the population size and duration. However, genes that influence desirable phenotypes experienced a more drastic loss of diversity because plants carrying favored alleles contributed the most progeny to each subsequent generation and other alleles were eliminated from the population [3]. One unknown in the domestication process is the extent to which new mutations versus preexisting genetic variation in the wild species contributed to the evolution of crop phenotypes. In a few cases, crops possess alleles of major genes that disrupt seed shattering [4] or the protective casing surrounding the seed [5] that are not found in the progenitor species. However, alleles of genes that contribute to increased fruit size in tomato or increased apical dominance in maize are also found in their wild or feral relatives, although at lower frequencies. Given the large store of genetic variation in the progenitor species, it seems most reasonable that domestication largely involved filtering out the best alleles from standing allelic variation in crop ancestors, although new mutations in key developmental pathways may have been instrumental for some traits.

Maize (*Zea mays* ssp. mays) provides perhaps the best example of how parallel genetic and archaeological research can be combined to provide a reasonably detailed and comprehensive account of a species' initial domestication and subsequent dispersal. Genetic analysis has identified populations of the wild grass teosinte growing in the central Balsas river valley of southern Mexico as the closest modern relative of maize, indicating that this general region is a candidate for the location of the initial domestication of maize [6]. The oldest archaeological maize ears come from Guilá

Naquitz Cave in the valley of Oaxaca, located only about 400 km northeast of the Balsas River, where two small cobs have been found dating to about 6300 BP (before present).

Maize domestication is one of the greatest feats of artificial selection and evolution, wherein a weedy plant in Central Mexico was converted through human-mediated selection into the most productive crop in the world. In fact, the changes were so astounding that it took much of the last century to identify modern maize's true ancestor. Grains such as wheat and rice have obvious wild relatives; there is no wild plant that looks like maize, with soft, starchy kernels arranged along a cob. The abrupt appearance of maize in the archaeological record baffled scientists.

Maize and its wild relatives present a paradox. There is nothing in nature today that resembles the cultivated corn with soft, starchy kernels arranged along a cob. The changes that were seen in maize after a period of domestication is as follows: parallel changes as in other domesticated cereals: increase in grain size, loss of dormancy, retention of the ripe grain on the ear rather than shattering of the inflorescence. Changes unique to maize: loss of the hard case surrounding the grain, doubling and redoubling of the rows of grain on the ancestral ear, enclosing the ear in husks with enormously elongated styles emerging at the tip of the ear for pollination.

Maize and Teosinte: An overlook
Maize and the teosintes exhibit such extreme differences in their adult morphologies that taxonomists initially considered the teosintes more closely related to rice than to maize, whereas the maize and teosinte genomes are so similar that they share the same chromosome number, similar chromosome morphologies, and they can be easily cross-hybridized. Moreover, F1 hybrids between maize and some forms of teosinte exhibit completely normal meiosis and full fertility.

The 'key' traits distinguishing maize and teosinte
The morphological differences between maize and teosinte, although complex, can be boiled down to five key traits. First, teosinte plants have elongated lateral branches that are terminated by male inflorescences. The teosinte plant therefore looks like candelabra. In maize, the lateral branches are short and terminated by female inflorescences (ears). Second, the teosinte ear is composed of a series of triangular units called cupulate fruitcases. Each teosinte cupulate fruit-case contains a single spikelet in which a single kernel develops. The corresponding structure in maize, called the cupule, has two (or paired) spikelets from which two kernels develop. Third, the teosinte ear bears grains on only two sides of its axis, a condition called two- ranked or distichous. In contrast, the maize ear bears its grains in at least four ranks (four sets of cupules), the polystichous condition. Fourth, the cupulate fruit cases of teosinte are separated by abscission layers that enable the fruitcases to separate (disarticulate) at maturity for dispersal. In maize, abscission layers are absent and the ear remains intact at maturity, which allows easy harvest. Fifth, the cupulate fruitcase of teosinte is sealed shut by the outer glume of the spikelet, obscuring the kernel from view. Both the cupulate fruitcase and this glume become highly indurated (hardened) at maturity, protecting the kernel from predation. In maize, this glume is much softer, and it is smaller relative to the size of the kernel. Thus, the maize kernels are visible on the ear once the husks are removed.

Initial studies in this direction were started influentially by George Beadle in the 1930s. Later scientists like Mangelsdorf

and Reeves, Rogers, Langham etc. ventured into this study proposing different hypotheses and progenitors of maize.

Different hypotheses for origin of maize
Teosinte hypothesis
The teosinte hypothesis states that teosinte is the sole progenitor of maize [7]. As proposed [7], the teosinte hypothesis states that (*i*) teosinte provided a useful food source and ancient peoples cultivated it (*ii*) during the cultivation of teosinte, mutations that improved teosinte's usefulness to humans arose and were selected by ancient people, (*iii*) as few as five major mutations would be sufficient to convert teosinte into a primitive form of maize, (*iv*) different mutations controlled different traits, e.g.*,* one mutation would have converted the disarticulating ear-type of teosinte into the solid eartype of maize, and (*v*) over the course of time, humans selected additional major mutations plus many minor ones. It was believed that missing ancestor is not needed to explain the origin [7]. Beadle could obtain completely fertile hybrids between maize and teosinte. He interpreted that these two species were conspecific and that they had only recently diverged. Beadle actually used Mangelsdorf and Reeves's own data against them and suggested that their four factors might correspond to four major genes. Each of these major genes controlled a single trait that transformed teosinte into maize. In modern form of teosinte hypothesis, *Zea mays* ssp. *Parviglumis* (wild Mexican grass teosinte) has been pin pointed as the likely progenitor since ssp. *parviglumis* is the closest living relative of maize. Further that maize arose through large changes in*parviglumis* - through artificial selection for specific traits. Most maize geneticists and evolutionists have accepted that maize is a domesticated derivative of *parviglumis*. However, the exact morphogenetic steps involved in transformation of wild teosinte into cultivated maize are yet to be known clearly.

Tripartite hypothesis
Tripartite hypothesis [8-10] stated that maize was domesticated from some unknown wild, now extinct maize plant that had structures similar to the ear of modern maize. The hypothesis comprised three parts: (i) the progenitor of maize was a wild maize prototype from South America, which is now either extinct or undiscovered. (ii) teosinte is the offspring of a cross between maize and *Tripsacum* (iii) sections of *Tripsacum* chromosomes had contaminated maize germplasm. Thus, Mangelsdorf and Reeves explained the extreme morphological differences between maize and teosinte by imagining a missing ancestor, while relied on *Tripsacum* to explain their similarities. The evidence/validation for this explanation came from their own experiment. Mangelsdorf and Reeves obatained few sterile maize - *Tripsacum* hybrids from the artificial crossing. They could identify a minimum of four factors with large effect that controlled defined morphological syndrome. Mangelsdorf and Reeves believed that each of these four factors with large effects represented a block of many linked genes. This interpretation was tied to their hypothesis that maize evolved in nature from a now extinct form of wild maize over a long evolutionary period. They believed that the differences between maize and teosinte were very large and hence it is not possible that teosinte was transformed into maize in the few thousand years during which virtually all crops were domesticated. Until the 1960s, the tripartite hypothesis was widely accepted.

However, data were not sufficient and their hypothesis could not withstand the test of time [11].

Catastrophic sexual transmutation theory
The catastrophic sexual transmutation was proposed [12] in which it was stated that maize was originated due to a sudden sexual transmutation that condensed the branches of teosinte and placed them in the female expression area of the plant. It states that the ear of maize was derived from the central spike of the tassel of teosinte. This has happened due to a phenomenon known as genetic assimilation [12]. This resulted in substantial alterations in the nutrient distribution of the plant and led to drastic morphological changes. The catastrophic sexual transmutation theory was fascinating in many ways. But it suffered criticism due to a misinterpretation of the genetic assimilation concept of Waddington [13] (1975) and the catastrophe theory [14] (Thom, 1977). Actually, the genetic assimilation concept is the Darwinist version of acquired traits. Using this Iltis described transformation into primitive maize through a possible morphogenetic and structural unbalance in the development of teosinte [12]. During the late 1980s, teosinte hypothesis started gaining importance and became the most accepted theory among the scientific and academic communities.

Tripsacum – *Zea diploperennis* hypothesis
Tripsacum–*Z. diploperennis* [15] hypothesis can be considered as a modern version of the tripartite hypothesis **[15]**. It proposed that maize arose from the progeny of a cross between *Zea diploperennis* and *Tripsacum dactyloides* [16]. This proposal was put forward with the observations on two putative hybrids originated from these two grasses, *viz*., Tripsacorn and Sundance. The rudimentary ear of these putative hybrids had exposed kernels attached to a central rachis, or cob. If such hybrids occurred naturally, then at least according to proponents of the hypothesis - the evolutionary puzzle of the origin of maize and its unparalleled architecture is solved. Thus, this hypothesis challenged the idea that maize is a domesticated form of teosinte. However, *Tripsacum* and *diploperennis* could not be hybridized successfully. The chromosome number of both Tripsacorn and Sundance is 2n = 20. These hybrids would be expected to have 28 or 46 chromosomes, If *Tripsacum* (2n = 36 or 72) had indeed been one of the parents.

Genetic evidences for teosinte hypothesis
All Zea species and subspecies have 10 chromosomes [17], with the sole exception of *Z. perennis*, (n= 20 chromosome doubling). However, most *Tripsacum* species have either 18 or 36 chromosomes [10]. Chromosomes of maize and teosinte are cytologically similar and hybrid between these two exhibits normal meiosis and full fertility. Crossing-over between maize and teosinte chromosomes occurs at frequencies similar to those observed in hybrids of two varieties of maize. Later, Beadle suggested that maize and Mexican annual teosinte were members of the same species. It is expected if maize were merely domesticated teosinte [7]. Chromosome arm lengths, centromere positions, and the sizes and positions of knobs in annual teosintes are identical to those of maize. Also annual teosintes possess at similar frequencies as that of maize [17]. Isozyme allele frequencies in annual teosinte, *Z. mays* ssp. parviglumis or Balsas teosinte, are essentially indistinguishable from those of maize. These data suggest that Balsas teosinte is the likely progenitor of maize [2].

Divergence studies using 18 currently sequenced genes in maize and *Tripsacum* [18] indicated that maize and *Tripsacum* alleles diverged around 5.2 million years ago. The domestication of maize cannot be older than significant human migration to the new world which took place about 15,000 years back [19]. Molecular dating by microsatellites data indicate that maize and Balsas teosinte diverged about 9000 years ago [20]. This agrees with archaeological evidence [21]. Phylogenetic analyses based on the microsatellite data strongly favour a single domestication which is derived from Balsas teosinte. The microsatellite data imply that the populations of Balsas teosinte in the central portion of its distribution (meeting region of Guerrero, Michoacan, and Mexico) are ancestral to maize.

What is teosinte?

The name, teosinte, is of Nahu´atl Indian origin, and it has been interpreted to mean "grain of the gods". It is the common name for a group of annual and perennial species of the genus *Zea* native to Mexico and Central America. These plants are taller and broader-leaved than most grasses. Their general growth form is similar to that of maize, although they have much longer lateral branches. Some species of teosinte are distinct from maize both genetically and taxonomically.

A single domestication for maize shown by multilocus microsatellite genotyping [21] was the first comprehensive phylogenetic analyses for maize and teosinte that provided evidence about the fact that maize was the result of a single domestication by using 99 microsatellite loci that provide broad coverage of the maize genome and a sample of 264 maize and teosinte plants. 193 maize (entire pre-Columbian range of maize from eastern Canada to northern Chile) samples were used. 67 Mexican annual teosinte (*Z. mays* ssp. *parviglumis* and ssp. *mexicana*) accessions {ssp. *mexicana* (33 accessions) and ssp.*parviglumis* (34 accessions)}.The microsatellite-based phylogeny of 264 maize and teosinte plant samples shows all maize in a single monophyletic lineage that is derived from within ssp. *parviglumis*, thus supporting a single domestication for maize.

Cradle of Maize Domestication

The region harboring those teosinte populations that are phylogenetically most closely allied with maize can be considered a candidate for the region in which maize was domesticated.

Dating the Domestication Event

When microsatellites adhere to the stepwise mutation model, they can provide an estimate of the time of separation of two populations. With this set of microsatellites, ssp. *parviglumis* and Mexican maize have a divergence time of 9,188 B.P.
Maize (*Zea mays* ssp. mays) provides perhaps the best example of how parallel genetic and archaeological research can be combined to provide a reasonably detailed and comprehensive account of a species' initial domestication and subsequent dispersal. Teosinte is distributed all over Mexico, from highlands to low lands and all over so the question was where to check for archeological evidence. A survey [22] was carried out by focusing on caves and rock shelters (because they were commonly used by ancient peoples and because they provide better protection for perishable materials, such as plant remains, than open-air sites.). The researchers located 15 caves and rock shelters that had been occupied sometime in prehistory, based on the stone and ceramic artifacts recovered from the site surfaces. The Xihuatoxtla Shelter,

excavations encountered undisturbed preceramic and ceramic deposits containing both chipped and ground stone tools, plant remains, and ceramics. 9,000 years ago people leaving in these caves, relied on grains as food and used grinding stones to make palletable. But searching for grain fossils in a tropical environment was not feasible, as they might be scavenged upon or being washed by the floods. So the search was for corn pieces being deposited on these grind surfaces of the stones as micro fossils. Finding maize microfossils on the surface of the grinding stones meant that humans leaving in the Xihuatoxtla Shelter were using maize as their food. Then the next attempt was made to date them back to their period of existence. Microfossils were too small to use radiocarbon dating method. So the researchers used charcoal found in the same sediment layer of the grinding stones to determine the age of micro fossils. The oldest charcoal was dated back to 8,700 years ago. This date coincides perfectly with the date provided by geneticists used micro satellite data.

Major genes that shaped the maize domestication
The *teosinte branched 1* gene

The teosinte branched1 (*tb 1*) gene is a candidate for the large effect QTL on chromosome arm 1L. It is a plant architecture mutant of maize that, as its name suggest, make the maize plant resemble a teosinte plant. Like teosinte, plants homozygous for the reference allele (*tb 1*-ref) have long lateral branches tipped by tassels at some upper nodes of the main culm. *tb 1*-ref plants also have many tillers at the basal nodes. *tb 1*-ref plants differ from teosinte in that they do not form normal ears, their secondary branches typically bearing only sterile, tassel-like inflorescences where teosinte bears its ears. The inability of *tb 1*-ref plants to form ears indicates that *tb 1* function is necessary for normal ear development. *tb 1* can be viewed as an apical dominance mutant, in that homozygous mutant plants exhibit unrestrained outgrowth of the axillary meristems. *tb 1* was identified as a candidate for a QTL on chromosome arm 1L because of their coincident chromosomal locations and similar phenotypic effects. This candidacy was confirmed by complementation tests, which indicated that our QTL and *tb 1* were allelic. As discussed below, the candidacy of *tb 1* for this QTL was further supported by evidence that *tb 1* was under selection during maize domestication and that the maize and teosinte alleles are differently regulated [23]. *tb 1* was molecularly cloned and found to be a class II member of the TCP family of transcriptional regulators. Class I TCP genes bind a conserved motif found in the promoters of several genes involved in the cell cycle or cell growth, and they appear to positively regulate the transcription of these genes. *tb 1* and other class II TCP proteins can bind the same sequence motif as class I TCP proteins, although their effects on transcription have not been assayed. An obvious hypothesis is that *tb 1* functions as a negative regulator of cell-cycle or cell-growth genes and thereby represses organ growth. *tb 1* may exert this negative regulation by competitively binding to the same sites as class I TCP genes. Thus, the evolution of maize require an increase in *tb 1* expression in the primary axillary branch primordium and its terminal inflorescence so that they form short ear shoots rather than elongated tassel-tipped branches [23].

The teosinte glume architecture1 locus

Developmental analyses of *teosinte glume architecture1* (*tga1*) revealed that it has pleiotropic effects on a small suite of traits. The teosinte allele lengthens and deepens inflorescence internodes, creating the invagination or cup

within which the kernel resides. The teosinte allele also makes the glumes longer, thicker, and angled upward to act as a closure over the cupule. The increased hardening of the glumes is correlated with a thicker abaxial mesoderm of lignified cells. Finally, the teosinte allele directs silica deposition in all abaxial epidermal cells of the fruitcase, giving this structure a stony appearance. The fact that *tga1* affects several distinc aspects of fruitcase development suggests that it acts as a regulatory locus. At what point in ear/fruitcase development does *tga1* act? Inflorescences in Zea are bisexual in their early development, having both male (stamens) and female (ovary) organ primordial [8]. During their development, adult sex is determined by an internal signal and then either the male organs are aborted to make an ear or the female organs aborted to make a tassel. In teosinte, if an inflorescence is determined to become female, then each internode will form a cupulate fruitcase. If it is determined to become male, the internodes remain soft and uninvaginated [8]. *tga1* may be a locus that is activated after the decision to become female is made and one that regulates the development of the cupulate fruitcase. In this latter capacity, *tga1* activates the programs for invagination of the internode, internode elongation.

Teosinte glume architecture1 (*tga1*), a member of the SBP-box gene family of transcriptional regulators, binding to DNA at GTAC motifs. Using nucleotide diversity data, it is now known that there is a single fixed nucleotide difference between maize and teosinte in is, this substitution transforms *tga 1* into a transcriptional repressor. While both alleles of *tga 1* can bind a GTAC motif, maize- *tga 1* forms more stable dimers than teosinte- *tga 1*. Seven nucleotide differences between maize and teosinte: six that are upstream of the start codon and one that is at position 18 of the ORF. Nucleotide difference at position 18 of the ORF which encodes a Lys6-to-Asn6 substitution from teosinte-*tga1* to maize-*tga1*, still remains a fixed difference. Thus, this is the only fixed difference in the causative region that defines the glume architecture difference between maize and teosinte.

Conclusion
The enigma still persists in this arena of research and survey, this call for further research on the origin and early diversification of maize. Microsatellite data identify ssp. Parviglumis of the Balsas River drainage below 1,800 m in elevation as the ancestor of maize. However, the microsatellite data and some archaeological evidence suggest maize from the highlands.

References
1. Hammer K. Das Domestikationssyndrom. Kulturpflanze. 1984; 32:11-34.
2. Doebley J. Isozymic evidence and the evolution of crop plants, In Isozymes in Plant Biology, D. Soltis, and P. Soltis, eds. (Portland, Oregon: Dioscorides Press). 1989, 165-191.
3. Wright SI, Bi IV, Schroeder SG, Yamasaki M, Doebley JF, Mc-Mullen MD *et al*. The effects of artificial selection on the maize genome. Science. 2005; 308:1310-1314.
4. Li C, Zhou A, Sang T. Rice domestication by reducing shattering. Science. 2006; 311:1936-1939.
5. Wang H, Nussbaum-Wagler T, Li B, Zhao Q, Vigouroux Y, Faller M *et al*. The origin of the naked grains of maize. Nature. 2005; 436:714-719.
6. Matsuoka Y, Vigouroux Y, Goodman MM, Sanchez GJ, Buckler E, Doebley J. A single domestication for maize shown by multilocus microsatellite genotyping. Proceedings of the National Academy of Sciences, USA. 2002; 99:6080-6084.
7. Beadle GW. Teosinte and the originof maize. Journal of Heredity. 1939; 30:245-47.
8. Mangelsdorf PC, Reeves RG. The origin of maize: present status of the problem. American Anthropologist. 1945; 7(2):235-243
9. Reeves RG, Mangelsdorf PC. The origin of corn: II. Teosinte, a hybrid of corn and *Tripsacum*. Botanical Museum Leaflet, Harvard University. 18(8):357-387
10. Mangelsdorf PC, Reeves RG. The origin of maize. Proceedings of the National Academy of Sciences. 1938; 24(8):303-312
11. Doebley JF. George Beadle's other hypothesis: one-gene, one-trait. Genetics. 2001; 158:487-93.
12. Iltis HH. From teosinte to maize: the catastrophic sexual transmutation. Science. 1989; 222(4626):886-94.
13. Waddington CH. The Evolution of an Evolutionist. Ithaca, NY: Cornell University Press. 1975, 2.
14. Thom R. Structural Stability and Morphogenesis: An Outline of a General Theory of Models. Reading, MA: Addison-Wesley, 1989.
15. Eubanks MW. Reevaluation of the Identification of Ancient Maize Pollen from Alabama. American Antiquity. 1997; 62(1):139-145
16. Eubanks MW. The Mysterious Origin of Maize. Economic Botany. 2001; 55(4):492-5144
17. Kato TA. Cytological studies of maize (*Zea mays* L.) and teosinte (*Zea mexicana* (Schrader) Kuntze) in relation to their origin and evolution. Massachusetts Agricultural Experiment Station Bulletin. 1976; 635:1-186.
18. Whitt SR, Wilson LM, Tenaillon MI, Gaut BS, Buckler ES. Genetic diversity and selection in the maize starch pathway. Proceedings of the National Academy of Sciences, USA. 2002; 99(20):12959-12962.
19. Dillehay TD. Monte Verde, a Late Pleistocene Settlement in Chile. Smithsonian Institution Press, Washington, DC, USA, 1989.
20. Matsuoka Y, Vigouroux Y, Goodman MM, Sanchez JG, Buckler E, Doebley J. A single domestication for maize shown by multilocus microsatellite genotyping. Proceedings of the National Academy of Sciences, USA. 2002; 99(9):6080-6084.
21. Piperno DR, Flannery KV. The earliest archaeological maize (*Zea mays* L.) from highland Mexico: new accelerator mass spectrometry dates and their implications. Proceedings of the National Academy of Sciences, USA. 2001; 98:2101-2103.
22. Ranere AJ, Piperno DR, Holst I, Dickau R, Iriarte J. The cultural and chronological context of early Holocene maize and squash domestication in the Central Balsas River Valley, Mexico. Proceedings of the National Academy of Sciences, USA. 2009; 106(13):5014-5018.
23. Doebley J. The genetics of maize evolution. Annual Review of Genetics. 2004; 38:37-59.