

The story of how a hard fruit cased plant attracted humans: a successful domestication or a lucky accident

The Mayan
corn god



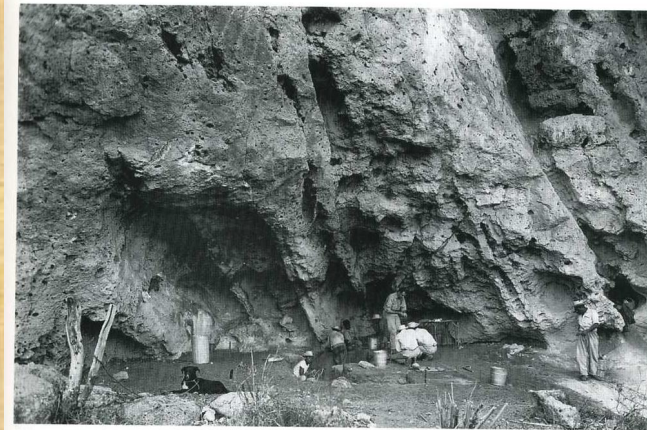
Claudia Irene Calderon
10-03-2006

Ancient Maize

- Origin: south central Mexico
- Archeological remains of the earliest maize cob, found at Guila Naquitz in the Oaxaca Valley of Mexico (6250 years ago).
- Microfossil evidence suggesting dispersal by 7,000 – 5,000 BP
- Estimation of domestication of maize: 12,000-6,000 BP
- SSR phylogeny indicates a single domestication event (Matsuoka 2002).



http://en.wikipedia.org/wiki/Image:Mesoamerica_english.PNG



Excavation of Guila Naquitz in 1966.

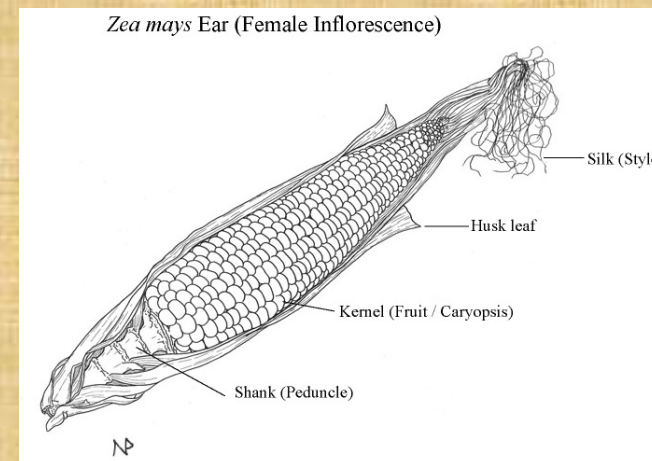
From “The emergence of Agriculture” by Bruce D. Smith,
1995

Changes in Maize

- 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

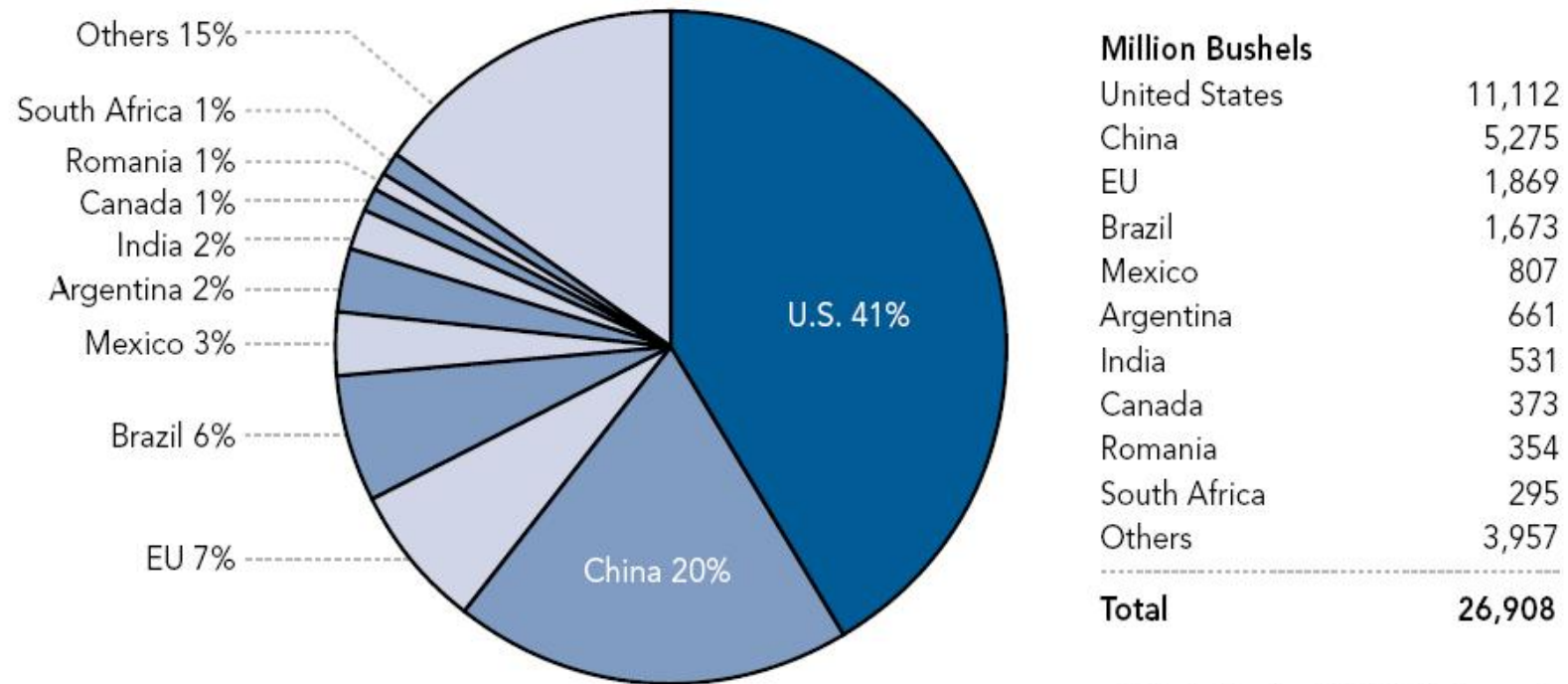


From "The emergence of Agriculture" by Bruce D. Smith, 1995



http://www.gramene.org/zea/maize_illustrations.html

World Corn Production, 2005-06*



*Estimates based on USDA, FAS Attachee reports
Source: USDA/Foreign Agriculture Service, Grain: World Markets and Trade, Jan. 13, 2006

World of Corn 2006 (NCGA)

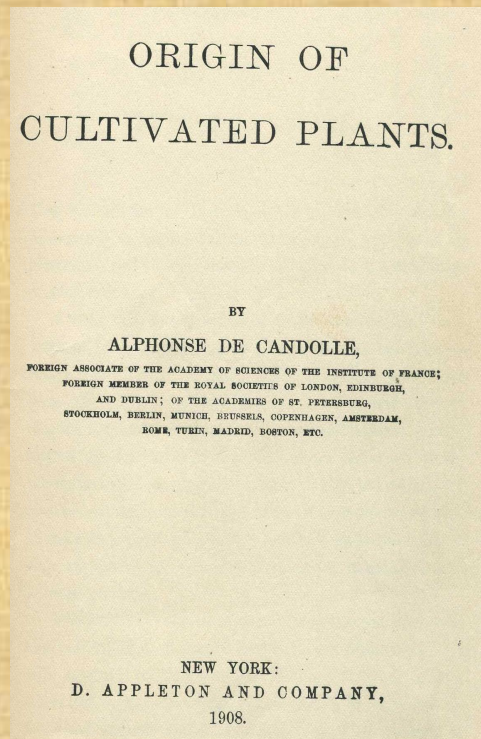


- Unlike most crops, maize does not have a morphological equivalent wild form. Particularly, maize has no wild relative having a cob-like pistillate inflorescence (ear).
- Interpreting the relation between maize and its wild relative generated a big debate over the 20th century.

http://www.gramene.org/zea/maize_anatomy_and_taxonomy.html

Alphonse de Candolle (Father of crop evolution)

Misleading origin of maize (16th century):



Maize = Ble de
Turquie (Turkish
wheat), Indian corn.
East of France
(Roman corn), in
Tuscany – Italy
(Sicilian corn), in
Sicily (Indian corn) ,
in south of France
(Spanish corn)
Turks (Egyptian
corn), Egyptians
(Syrian dourra)



nceas.ucsb.edu/%7Ealroylef/lefa/deCandolle

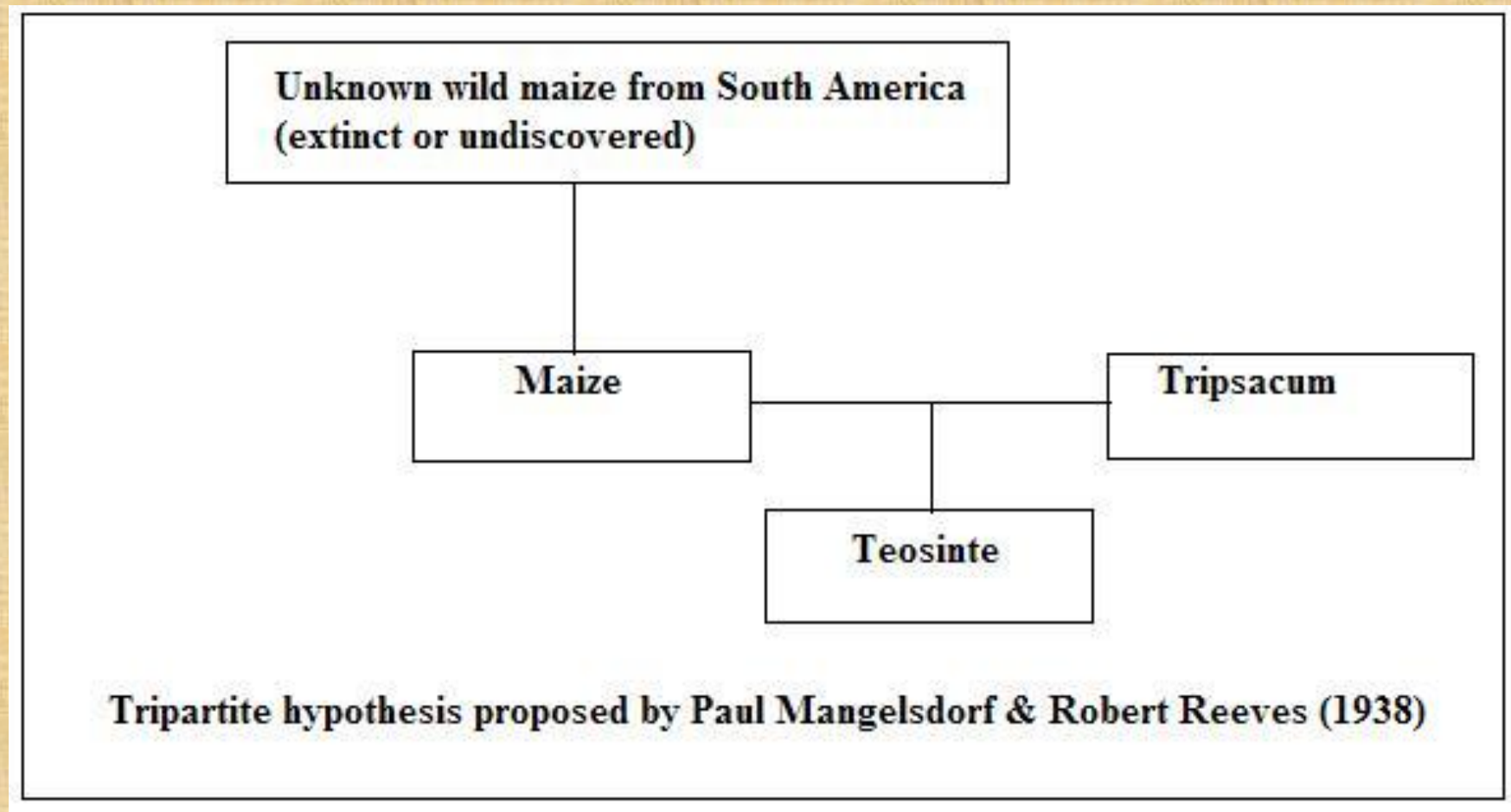
Origin of Maize: three hypothesis

- Tripartite hypothesis
- Teosinte hypothesis
- Recombination hypothesis



www.maizemap.org

Tripartite hypothesis



Counter arguments

- Differences in chromosome number and constitution between *Zea* (10 chromosomes) and *Tripsacum* (18 or 36 chromosomes).
- Basing their assumption on a “missing wild maize”

Three hypothesis

- Tripartite hypothesis
- Teosinte hypothesis
- Recombination hypothesis



www.maizemap.org

Teosinte hypothesis

As stated by Beadle (1939)

- Ancient people cultivated teosinte because it provided a useful food source
- During cultivation, mutations that improved teosinte's usefulness to humans arose and were selected
- As few as 5 major mutations would be sufficient to convert teosinte in a primitive form of maize
- Over the course of time, humans selected additional major mutations plus many minor ones



plantsciences.ucdavis.edu

What is teosinte?

Teosinte from the *Nahuatl* “grain of the Gods”

- Is the common name of a group of annual and perennial species of the genus *Zea* native to Mesoamerica.
- One form of Teosinte (*Zea mays ssp parviglumis*) shares close genetic relationship with maize (isozyme and microsatellite evidence)



<http://hila.webcentre.ca/research/teosinte/>

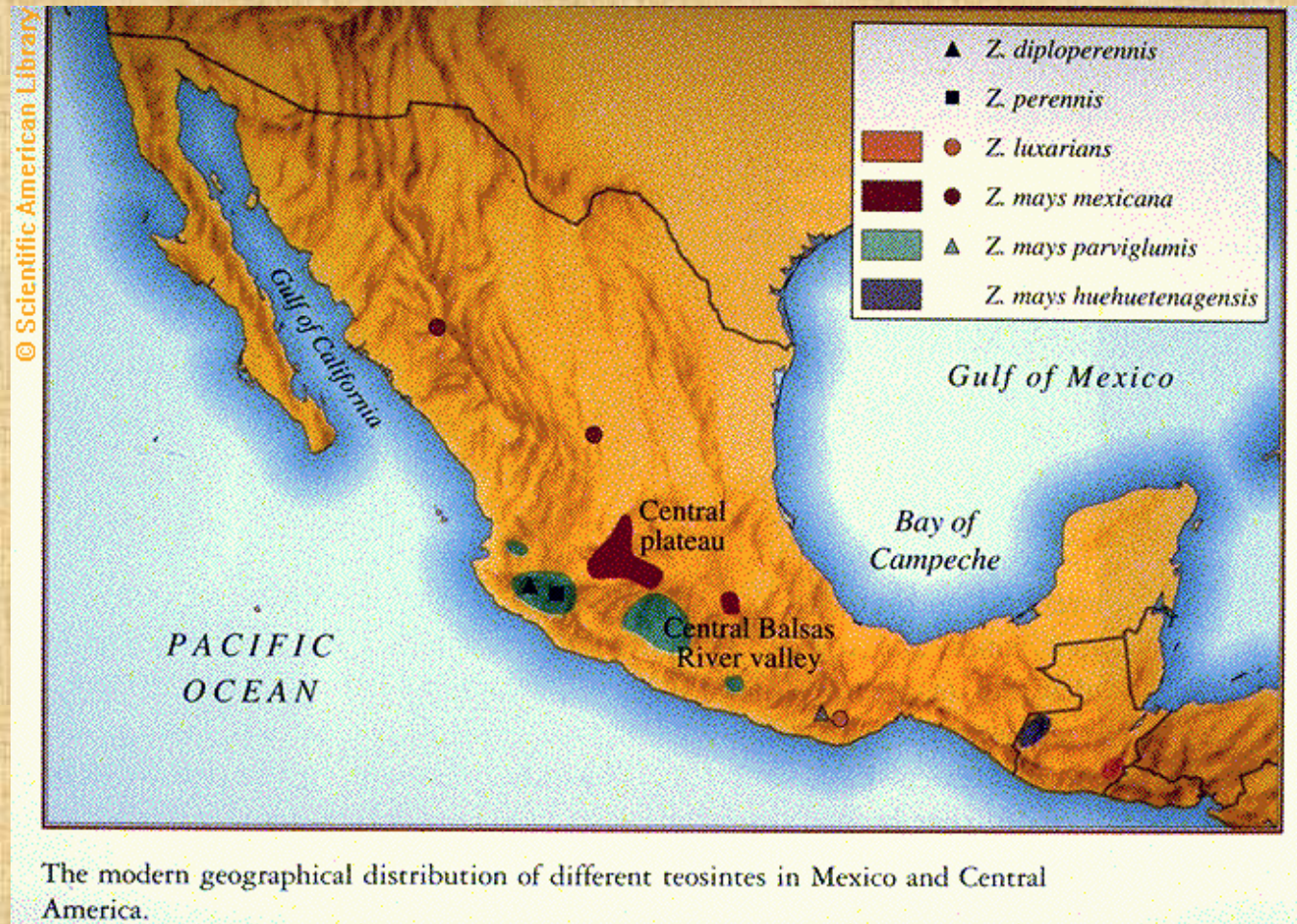


<http://teosinte.wisc.edu/images.html>



<http://hila.webcentre.ca/research/teosinte/>

Distribution of Teosinte



Counter arguments

- Evolution proceeds slowly over time, through the accumulation of many small changes in numerous genes.
- Critics in methods of Matsuoka paper: only one plant per accession tested, just 3 species of teosinte, non inclusion of *Tripsacum* in the analysis.

Three hypothesis

- Tripartite hypothesis
- Teosinte hypothesis
- Recombination hypothesis



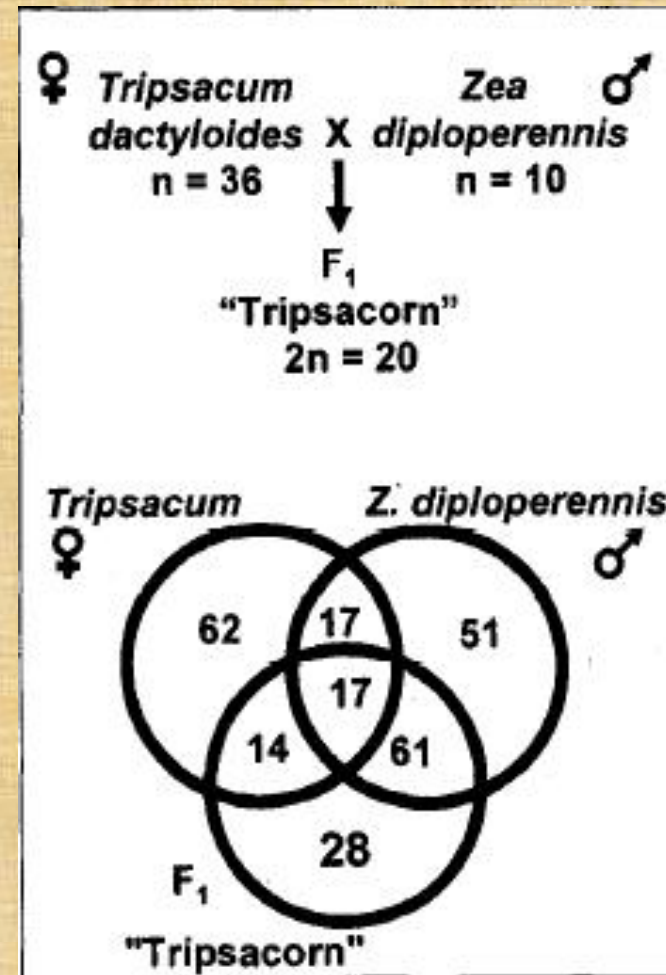
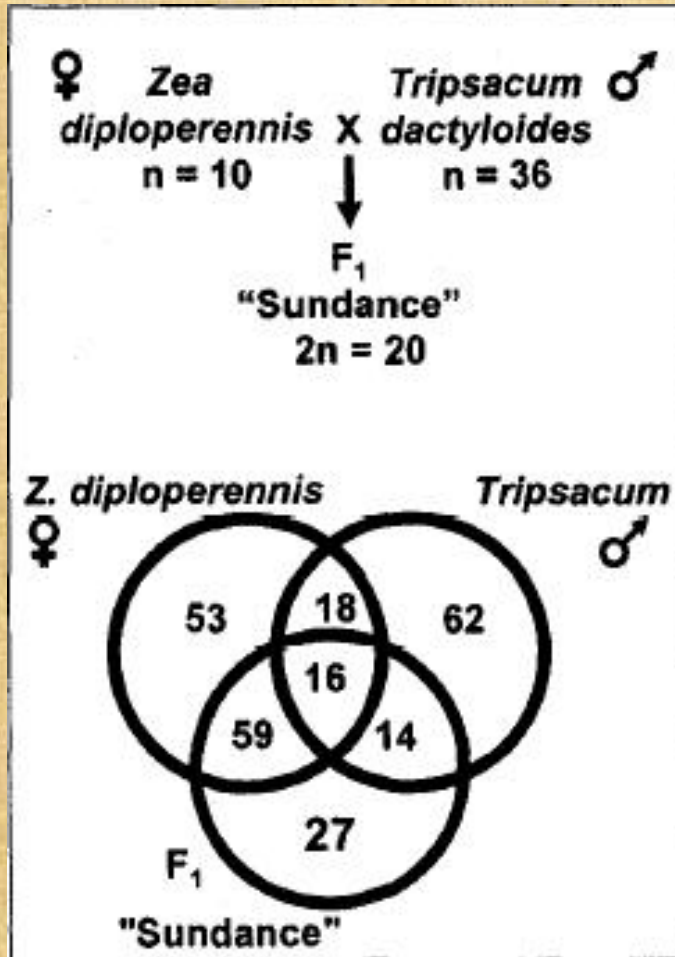
www.maizemap.org

GAMA GRASS (*Tripsacum* sp)

TEOSINTE (*Zea mays* ssp.)

MAIZE (*Zea mays* ssp *mays*)

The recombination hypothesis (MacNeish and Eubanks 2000)



From Darwin's harvest 2006

First empirical demonstration of how teosinte could have been transformed into maize via *Tripsacum* introgression. Hybrids show intermediate form: have partially fused rachis, 2 kernel per rachis (instead of 1) and the kernels are partially exposed at the tips

Tripsacum



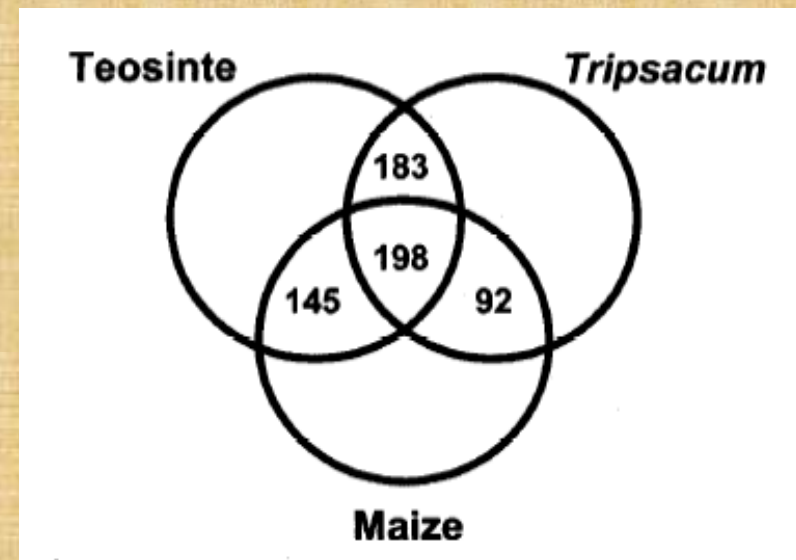
- It's a polyploid ($x=18$), with 36-108 chromosomes.
- There are 12 species
- F1 progeny of crosses between maize and gamagrass have high degree of female sterility and are male sterile



http://www.missouriplants.com/Grasses/Tripsacum_dactyloides_page.html

Counter-argument

- 23% of the molecular markers are not found in either progenitor
⇔ 120 point mutations/gene (3 million times the normal rate of mutation: 6×10^{-9} substitutions per site per year)
- Only 1 sp of *Z.m ssp parviglumis* included
- Tripsacum/maize similarity could be inflated by the inclusion of a *Zea-Tripsacum* hybrid
- Studies of divergence times between Tripsacum/maize estimate 5.2 million years ago (suggesting that the domestication of maize predates the human migrations to the new World ~15,000 years ago).



Shared ancestral polymorphisms between Teosinte, maize and Tripsacum, based on RFLP (Eubanks 2001).

Modern Argument

- With more molecular analysis and archaeological findings, teosinte appears to be sufficiently similar on a genetic level to maize:
 - Cytological evidence: same chromosome numbers, complete chromosome pairing, full fertility (Emerson & Beadle 1932) . Chromosome arm length, centromere position, sizes in annual teosintes are identical to those in maize (Longley 1941). Longley (1941) & Kato (1976) later suggested that from all teosintes, mexican were the more similar to maize.

- Evidence at the **protein level**: classification of teosinte populations based on isozyme allele frequencies. It allowed to pinpoint the Mexican teosinte that had allele frequencies “essentially indistinguishable” from maize: *Z. mays ssp parviglumis*. (Doebley et al 1984).
- Evidence at the **molecular level**: a study of the microsatellite diversity in maize and teosinte (Matsuoka 2002) confirmed the isozyme results. They also demonstrated a single domestication event, and that Balsas teosinte diverged ~9188 ya. Jaenicke-Despres (2003): ancient DNA studies support that teosinte was rapidly transformed into maize around 9000-7000 years ago.

Archaeological data

The two oldest maize cobs in the New World from Guilá Naquitz Cave. The cob at the bottom is from excavation square D10 and is about 2.5 cm long. The cob at the top is from square C9.



Increase in maize cob size

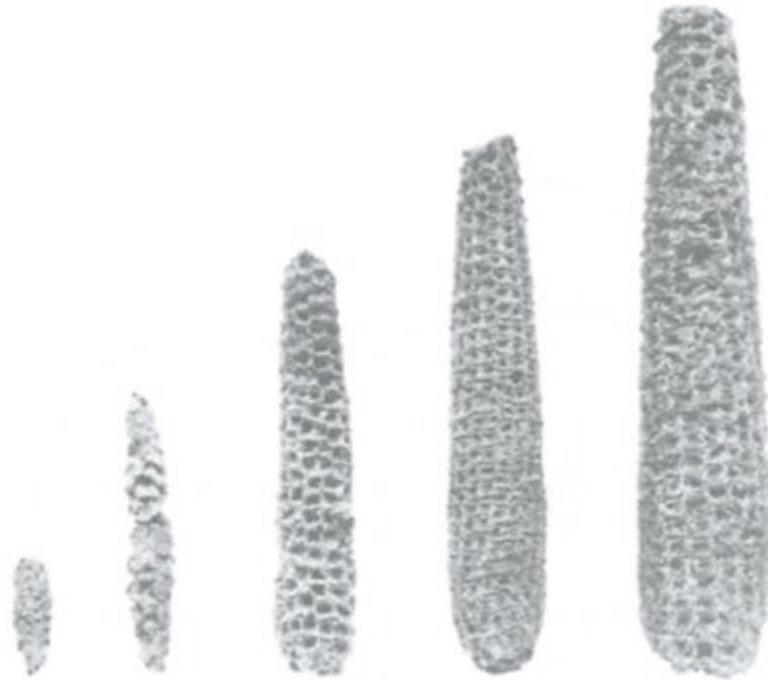
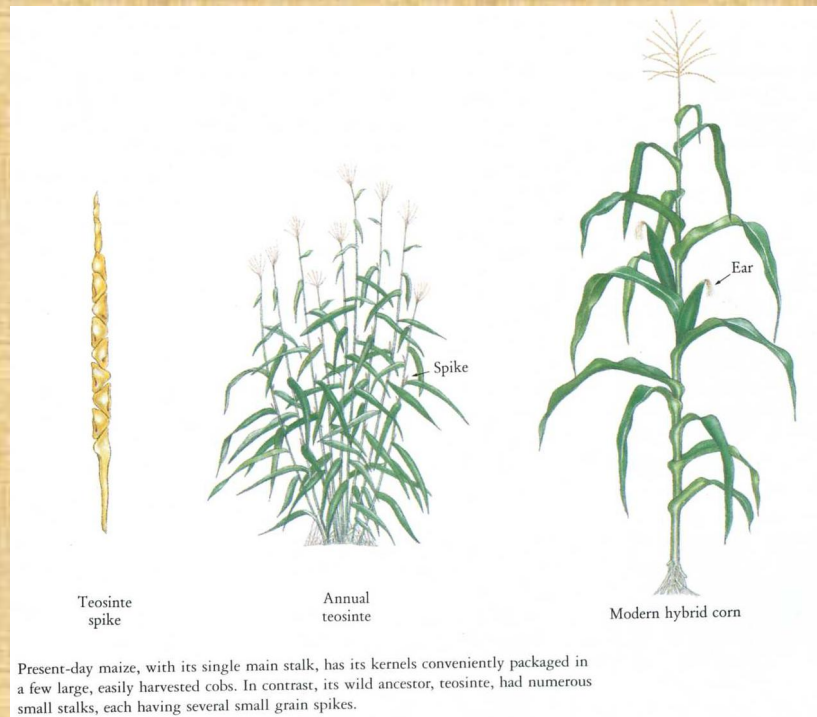
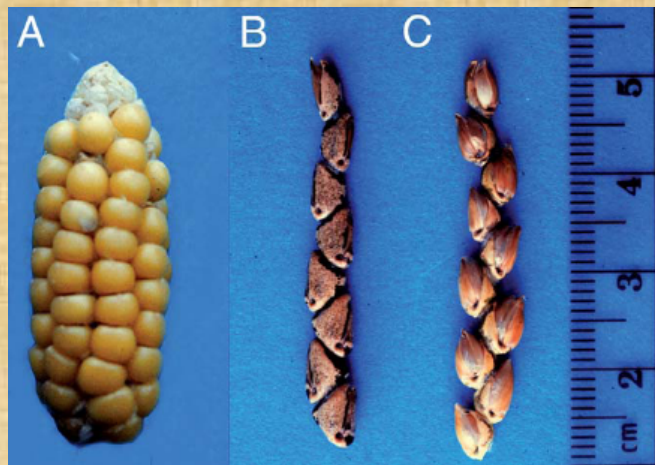


Fig. 2.9. Increase in maize cob size between 7000 and 3500 BP in Tehuacan Valley, Mexico. The cob on the left was about 1 inch long. (Used with permission from D.S. Byers (ed.), © 1967, *The Prehistory of the Tehuacan Valley*, Vol. 1. Andover Foundation for Archaeological Research, University of Texas, Austin.)

Plant evolution and the origin of crop species (Hancock 2004)



From "The emergence of Agriculture" by Bruce D. Smith, 1995



Genetics of maize evolution, J. Doebley 2004

- Maize lost 30% of gene diversity relative to **teosinte** (nucleotide sequence data)
- Finding of genes with big effect on morphology of maize:
 - **tga1** (teosinte glume architecture 1) → dvt of glume lacking in maize present in teosinte (forms the cupule)
 - **tb1**: (teosinte branched1) → dictates difference in plant architecture (long lateral branches terminated by male tassels in teosinte vs short lateral branches tipped by female ears in maize)
- Genes under current investigation: shattering vrs solid cobs, single versus paired spikelets, distichous vers polystichous condition.

Wrapping up

- Maize domestication has proven that evolution can happen rapidly when it combines the following elements:
 - High genetic variability (it has allowed maize to respond to centuries of artificial selection)
 - Large starting population
 - Selection on a few genes of major effect (transcriptional factors) and several of minor effect
- Allowing for new epistatic interactions (cryptic variants, novel phenotypes) it is easier to accept that teosinte is the wild progenitor of maize... see redomestication of maize project “*I want to select natural teosinte variants and thereby move the phenotype in the direction of maize*” (J. Doebley)
- The evolution of maize is extremely complex and goes beyond plant architecture, inflorescence development

Questions to be addressed

- How does evolution proceed?
 - slowly (small changes in numerous genes) or rapidly over time (a few changes in significant genes) ?
- Evidence for a single domestication event.. Can “post-domestication” hybridization between teosinte/maize be ruled out of the domestication process?
- What kind of experimental design (which species? from which areas?) should be included in a study to determine the origin of maize?
- Support for introgressive hybridization: genes enter the genome of one species through transfer from another species (comparative genomics study of Eubanks)
- What other targets of selection remain to be studied?

Thank you very much!

Maize God figure
painted in mural,
San Bartolo,
Guatemala



<http://www.peabody.harvard.edu/SanBartolo.htm>