Popped Secret: The Mysterious Origin of Corn

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Film Guide
Educator Materials

OVERVIEW

In the HHMI film *Popped Secret: The Mysterious Origin of Corn*, evolutionary biologist Dr. Neil Losin embarks on a quest to discover the origin of maize (or corn). While the wild varieties of common crops, such as apples and wheat, looked much like the cultivated species, there are no wild plants that closely resemble maize. As the film unfolds, we learn how geneticists and archaeologists have come together to unravel the mysteries of how and where maize was domesticated nearly 9,000 years ago.

KEY CONCEPTS

A. Humans have transformed wild plants into useful crops by artificially selecting and propagating individuals with the most desirable traits or characteristics—such as size, color, or sweetness—over generations.
B. Evidence of early maize domestication comes from many disciplines including evolutionary biology, genetics, and archaeology.
C. The analysis of shared characteristics among different species, including extinct ones, enables scientists to determine evolutionary relationships.
D. In general, the more closely related two groups of organisms are, the more similar their DNA sequences will be. Scientists can estimate how long ago two populations of organisms diverged by comparing their genomes.
E. When the number of genes is relatively small, mathematical models based on Mendelian genetics can help scientists estimate how many genes are involved in the differences in traits between species.
F. Regulatory genes code for proteins, such as transcription factors, that in turn control the expression of several—even hundreds—of other genes. As a result, changes in just a few regulatory genes can have a dramatic effect on traits.

CURRICULUM CONNECTIONS

Standards	Curriculum Connections
NGSS (2013)	LS1.A, LS3.A, LS3.B, LS4.A
AP Biology (2015)	1.A.4, 1.C.2, 3.A.1, 3.A.3, 3.B.1, 3.C.1
AP Environmental Science (2013)	II.C
IB Biology (2016)	2.7, 3.1, 3.4, 5.1, 9.3, 10.2
IB Environmental Systems and Societies (2017)	5.2
Common Core (2010)	ELA.RST.9-12.2, WHST.9-12.4
Vision and Change (2009)	CC1, CC2, CC3

PRIOR KNOWLEDGE

Students should

- be able to describe the process of artificial selection and explain how it differs from natural selection;
- be familiar with the Mendelian principles of segregation and independent assortment as well as related terms such as *allele, cross, hybrid,* F_1*,* F_2*, and phenotype;*
- be able to use Punnett squares to predict genotype and phenotype frequencies in F_1 and F_2 mono- and dihybrid crosses; and
- understand that gene expression is regulated, often by the products of other genes.

PAUSE POINTS

The film may be viewed in its entirety or paused at specific points to review content with students. The table below lists suggested pause points, indicating the beginning and ending times in minutes in the film.

	Begin	End	Content Description	Review Questions
1	0:00	06:55	• Humans have transformed wild plants into useful crops via artificial selection (domestication) over generations. • The origin of maize was a mystery. There is no wild plant that looks like maize, and the earliest fossil ears of maize look like those of modern maize. • George Beadle suggested that teosinte is the ancestor of maize when he observed that teosinte and maize have nearly identical chromosomes and can be crossbred to produce fertile offspring. • Because maize and teosinte have many physical differences including branching pattern, seed number, and fruit form, many botanists doubted Dr. Beadle's conclusion. • Late in his career, Dr. Beadle designed a crossbreeding experiment to estimate the number of genes responsible for the differences between teosinte and maize. Based on F_2 phenotypes, Dr. Beadle concluded that four or five genes are responsible for observed differences between the plants, meaning that maize could have been rapidly domesticated from teosinte, as Dr. Beadle predicted.	• Why did botanists expect the wild relative of maize to look similar to modern maize? • Why did Dr. Beadle use so many plants in his experiments? Would his data have been as meaningful if he had grown only 1,000 plants?
2	06:55	12:10	• By comparing the DNA of modern maize and varieties of wild teosinte, scientists were able to 1) trace the origin of maize to a population of teosinte near the Balsas River basin in southwestern Mexico, and 2) estimate that the original domestication event occurred about 9,000 years ago. • Archaeological evidence from Mexico—including stone tools and plant microfossils—independently verified the genetic data and support the conclusion that maize was originally domesticated from teosinte around 9,000 years ago in Mexico.	• Why is it important to know the average mutation rate when using DNA comparisons to determine how long ago lineages split? • How did archaeological evidence support the molecular evidence for the timing and geographic location of maize domestication?
3	12:10	15:35	• Crossbreeding experiments that introduced teosinte genes into maize and maize genes into teosinte led scientists to conclude that both the fruitcase trait and the branching trait are each mostly controlled by a single gene. • A small number of genes can produce dramatic changes if the genes are regulatory genes, meaning each one affects the expression of hundreds of others.	• Did Dr. Doebley's genetic experiments confirm Dr. Beadle's predictions that only a few genes are mostly responsible for the differences between teosinte and maize? • Explain the comparison between regulatory genes and the conductor of an orchestra.

4	15:35	17:27	• Teosinte doesn't seem to be a very good food crop. Dr. Losin and Dr. Doebley recreate Dr. Beadle's experiment to show that teosinte can be popped and eaten like popcorn, which explains why people originally started domesticating teosinte.	• What does the fact that teosinte can be "popped" help to explain?

BACKGROUND

AGRICULTURE AND THE DOMESTICATION OF PLANTS

Domestication is the process of adapting wild organisms to fulfill human needs. Domestication is achieved by the process of **artificial selection**, in which humans select and cross (or breed) individuals with desirable traits over many generations to maximize the expression of these traits within the population. In this way, humans have produced plants with larger, more nutritious fruits and seeds, and animals that produce more milk or that have increased muscle mass. A domesticated crop cannot generally survive without human help. For example, maize seeds don't disperse effectively. Without human intervention, the plant's seeds would all fall to the ground attached to the cob and would all germinate at the same time, in the same place. The resulting plants would compete intensely for sunlight and nutrients, and few would survive. When humans collect, distribute, and nurture seeds, however, maize plants thrive.

Maize is just one of many crop plants that humans domesticated around the world at roughly the same time: 8,000 to 10,000 years ago during the transition from hunter-gatherer to agricultural societies. In Central America, beans, squash, avocados, cacao, strawberries, and pecans were common. In the Near East, wheat, oats, peas, carrots, apples, almonds, and walnuts were domesticated.

DOMESTICATION OF MAIZE

For many years, scientists thought the precursor of maize was extinct, as there was no obvious candidate among wild plants. In 1939, however, Dr. George Beadle presented evidence that teosinte—a wild grass found in Central America—was maize's ancestor. Teosinte is the common name of four species of grass belonging to the genus *Zea*. The name "teosinte" comes from the Nahuátl Indians, interpreted to mean "grain of the gods." Botanists, however, were skeptical. Teosinte, at first glance, seems an improbable ancestor of modern maize (Figure 1).

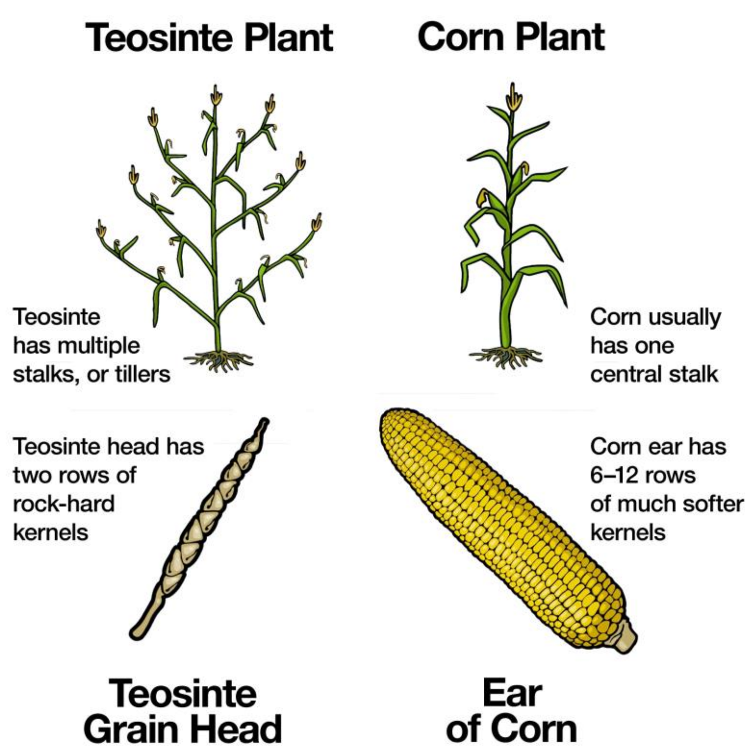

Figure 1. Teosinte and maize differ in many traits. Teosinte is highly branched, and its ears have only two rows of hard kernels. Maize has a central stalk and ears with hundreds of "naked" kernels in six to 18 rows.

Teosinte is highly branched; its bushy form has many stems (called "tillers") and produces heads with two rows of five to 12 seeds at the top of each stalk. By contrast, a maize plant usually has just one central stalk that produces a few ears, each with hundreds of kernels in six to 18 rows. Another stark difference is that teosinte's seeds, or kernels, are surrounded by a hard fruitcase. This protective covering enables seeds to survive the digestive tracts of birds and grazing animals. When the seeds are excreted with animal waste, they can germinate, effectively using the animals as dispersal agents to spread the plants to distant locales. In contrast, the fruitcase of maize is greatly reduced and develops into part of the cob. This leaves the kernel exposed or naked and thus easily digested by animals.

GENETIC EVIDENCE OF MAIZE DOMESTICATION

Dr. Beadle conducted a massive experiment in the 1970s. He crossed teosinte with maize to produce F_1 hybrids, and then crossed the F_1s to produce an F_2 generation. Based on classical genetics and making some reasonable assumptions, Beadle developed a mathematical model for predicting how many genes differed between the plants based on the frequency of F_2 offspring that looked like either parent.

He planted 50,000 F_2s and once grown, he found that about 100 plants had an ear that looked like maize, and 100 plants had an ear that looked like teosinte. From these data and his mathematical model, he concluded that four or five genes were responsible for the differences between teosinte and maize, supporting his claim that maize could have been domesticated rapidly from teosinte.

In the 1990s, modern molecular genetics tools allowed geneticists John Doebley and Adrian Stec to reexamine Dr. Beadle's hypothesis. Dr. Doebley and Dr. Stec identified five genetic regions, which correspond to about five genes or blocks of genes, that together account for most of the variation between maize and teosinte, further supporting Dr. Beadle's hypothesis.

How could so few genes cause the dramatic differences between these plants? Scientists found that at least two of the genes are **regulatory genes** that code for proteins that turn other genes off or on. Thus having a different version of a single regulatory gene can affect the expression of hundreds of others.

One gene, dubbed *tga1* (for teosinte glume architecture—glume is a technical term for the hard fruitcase of teosinte), controls the expression of traits associated with the seeds. The teosinte version of this gene results in tightly encased seeds, and the maize version produces naked seeds. When the teosinte *tga1* gene was incorporated into the maize genome, some of the maize seeds became enclosed in a fruitcase. When the maize *tga1* gene was bred into teosinte, the seeds were partially exposed. Scientists now recognize that the teosinte version of *tga1* differs from the version in maize by just one nucleotide. The one difference causes a change in the resulting protein from the amino acid lysine in teosinte to asparagine in maize.
The results were similar when variants of the *tb1* (teosinte branched 1) gene were transplanted across species. When the teosinte *tb1* gene was introduced into maize, the maize became more branched and developed many ears. When the maize *tb1* gene was transplanted into teosinte, the teosinte became less branched and had fewer, larger seed-containing ears.

Together, these two regulatory genes played major roles in changing the plant's architecture, transforming teosinte to maize. Since domestication, humans have continued to change maize through artificial selection; one recent study showed that 1,200 genes of the maize genome have been affected in some way. Changes in these genes resulted in more subtle differences in the evolution of early maize plants to present-day maize; for example, present-day maize has much bigger ears and sweeter seeds.

WHEN WAS MAIZE DOMESTICATED?

Genetic comparisons of maize and four different teosinte varieties—all the same species but genetically specialized for different habitats—showed that the origin of domesticated maize can be traced to teosinte from the Balsas region in southwest Mexico. The same study used a "molecular clock" to calculate that corn first originated about 9,000 years ago. Molecular clocks use known mutation rates to estimate the time since two organisms, or groups of organisms, diverged based on their genetic differences.

Archaeological evidence supports these conclusions. Archaeologist Dolores Piperno searched in caves and shelters in the Balsas region of Mexico for evidence of maize domestication. The conditions inside these caves are ideal for the preservation of plant remains, and Dr. Piperno's team found layered deposits that included the remains of maize, beans, and squash.

To establish the age of relatively recent carbon-containing specimens, archaeologists typically use carbon-14 dating. If a fossil is large enough, a so-called **macrofossil**, it can be dated directly. Maize macrofossils are rare because more often than not, large pieces of nutritious food would be either consumed or degraded over time. The oldest maize specimen directly dated using carbon-14 dating comes from the Guilá Naquitz cave in Oaxaca, Mexico, and is about 6,250 years old (Figure 2). Those maize fossils look similar to modern maize except for their size: the "ears" are less than 5 cm (2 in.) long, with few rows and kernels.

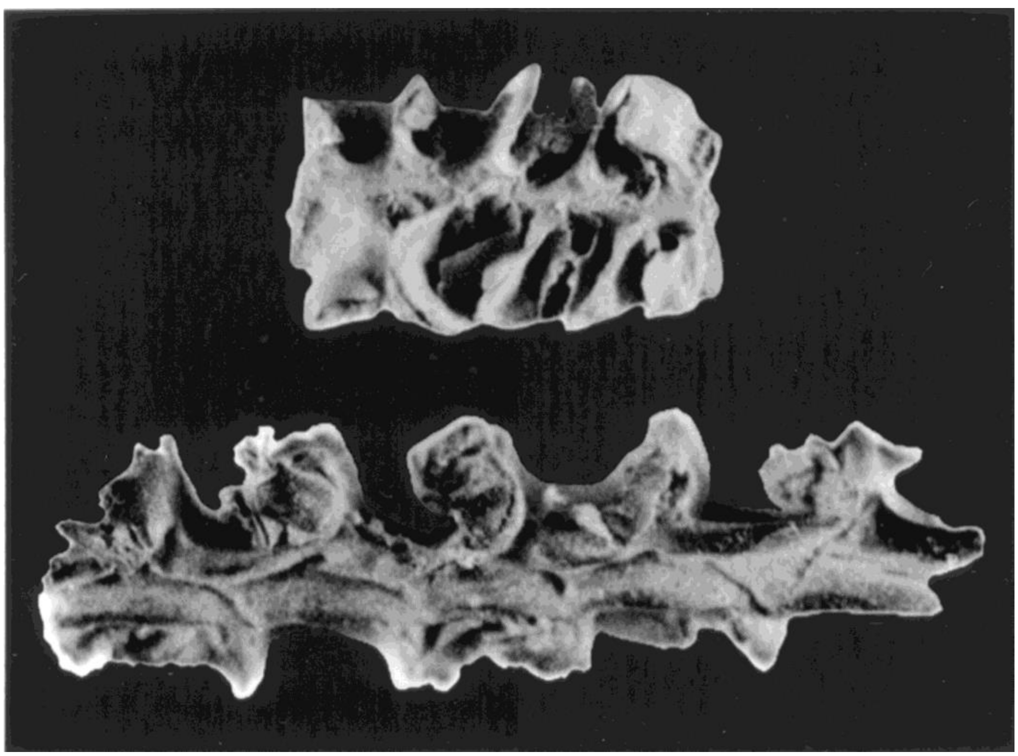

Figure 2. The two oldest maize cobs in the New World, from Guilá Naquitz cave. (Source: Proceedings of the National Academy of Sciences. vol. 98 no. 4 D. R. Piperno, 2101–2103, doi: 10.1073/pnas.98.4.2101. Copyright (2001) National Academy of Sciences, U.S.A.)

Archaeologists were able to push maize's origin back further in time by looking at microscopic remains, or microfossils. Microfossils are too small for direct carbon-14 dating. Instead, archaeologists determine the age of carbon deposits in the same layer as the microfossil. Maize microfossils include pollen, starch grains, and phytoliths, which are stable, silica-based crystals in plant tissue. Domesticated maize has distinctively irregular starch grains that can be distinguished from round grains of wild teosinte. Based on microfossil analysis, Dr. Dolores Piperno found the oldest evidence of domesticated corn from 8,700-year-old charcoal found beside corn microfossils extracted from grinding stones in the Xihuatoxtla cave shelter in the central Balsas River valley of Guerrero, Mexico.

DISCUSSION POINTS

- To avoid confusion, point out that the words "corn" and "maize" can be used interchangeably. Maize is the name for any of the countless varieties of *Zea mays*. Corn is the name given to maize in the United States.
- Make sure that students understand that modern species are not the ancestors of other modern species. So the teosinte that is growing today is not the ancestor to corn. Corn's ancestor is a variety of teosinte that existed about 9,000 years ago. Teosinte has been evolving for the past 9,000 years too, though much less dramatically than corn.
- The world's first farmers likely didn't set out to purposefully domesticate plants. As individual wild plants were selected and gathered for their desired traits, some would have accidentally spilled and germinated, while others would eventually be planted. Get students to think about maize domestication by asking them why plants with fewer ears and more kernels per ear would have been desirable to early farmers. *Answer:* Fewer ears with more kernels per ear would have been easier to harvest and process.
- Domestication has led to plants that are easier to cultivate and eat, and are more calorie-dense. Over 30,000 edible plants exist in the world, but only a few hundred plants have been domesticated. Incredibly, three of these domesticated crops—corn, rice, and wheat—make up 60% of global human calorie intake. If domesticated livestock such as cattle that rely on those crops for food are included as part of the calculations as well, the percentage increases even further (reference: http://www.fao.org/news/story/en/item/174330/icode/). Domesticated plants are less genetically diverse than their wild ancestors. That's because alleles that are favored by farmers arise to fixation faster, and nearby genes travel with them, decreasing overall genetic diversity in the population. Ask your students to consider the pros and cons of domestication.
- Ask students why scientists go to remarkable efforts to identify the wild relatives of modern crops and create seed banks that include the seeds of wild relatives. One answer is that knowing the wild ancestors of modern crops allows scientists to increase diversity within a crop by breeding back to the wild close relatives. In fact, in the early 1900s explorers noted that in certain regions of Mexico, people said that teosinte growing near corn was "good for the corn." The reason is that genetic crosses between corn and teosinte helped increase genetic diversity in the corn and helped alleviate problems with extensive inbreeding. Another reason is that identifying which genes control traits that changed during domestication may provide ways to improve those crops further.
- Searching for answers to scientific questions often requires an interdisciplinary approach. Ask students to identify the different disciplines of science that were highlighted in the film. (*Answer:* genetics and archaeology.) Discuss how each discipline contributed to the evidence that teosinte is the ancestor of maize.
- The ability to generate fertile teosinte-maize hybrids may cause your students to ask whether maize and teosinte are different species. The familiar definition of a species as a population that can generate fertile offspring is known as the biological species concept. However, this definition can be particularly problematic as applied to plants because many species of closely related plants readily form fertile hybrids, and some plants reproduce asexually. Whether teosinte and maize are separate species depends on the definition of species, which is a topic of much discussion among biologists. What is important is that there are distinct structural differences between the two taxa, which makes it possible to determine whether a microfossil is teosinte or early maize.
- The graphics showing Dr. Beadle's F_1 crosses in the film are simplified to illustrate the concept. They show only three phenotypes: a teosinte phenotype, a maize phenotype, and a hybrid phenotype that is half teosinte and half maize. In reality, the hybrid offspring would show varying degrees of "maize-ness" and "teosinte-ness," and Dr. Beadle had to determine which phenotypes were likely to represent a homozygous or heterozygous genotype for any one trait.

- If your students have ever been to a farmer's market, they may be familiar with the term "heirloom crop," which means a crop that is different from the most common commercially grown varieties. Large, irregular heirloom tomatoes are fairly common, for example, as are purple heirloom potatoes and yellow heirloom carrots. Heirloom crops can be more flavorful and more nutritious than their commercial cousins. Ask your students: How might selecting for certain traits, such as shape, size, or color, have resulted in the loss of other valuable traits, such as flavor or nutritional content?
- Students may have learned that evolution is always slow and gradual. A debate about the pace and magnitude of evolutionary changes can be traced all the way back to Darwin, who famously said "*Natura non facit saltum*," or "nature does not take leaps." This idea can make it hard to understand how novel structures evolve quickly. Highlight the message in the film that minor changes in regulatory genes can produce rapid evolutionary changes. For example, a change in a single nucleotide in the fruitcase gene, *tga1*, results in a much smaller fruitcase that leaves the seed exposed. Through mutations in regulatory genes, dramatic changes can occur quite quickly.
- Recently, researchers have been able to modify a plant's genetic code—either by introducing genes from another plant species or microbe—to create genetically modified organisms (GMOs). One example, Bt corn, is named for the introduction of a gene encoding a natural insecticide from the bacterium *Bacillus thuringiensis*. Another example is the introduction of genes that make plants resistant to a widely used herbicide known as glyphosate, or by the brand name "Roundup." Although the tools are different, the goal of these technologies is the same as the goal of classic artificial breeding: to produce crops with desirable traits.
- You may want to discuss GMOs with your class. Ask students what they think it means to be a GMO and explore the pros and cons of GMO use by reading relevant articles and news stories.

ADDITIONAL RESOURCES

The Panzea website provides teaching resources at http://www.panzea.org/#!for-teachers/c1b5b, including a traveling exhibit on maize domestication.

STUDENT HANDOUT

We designed the student handout as a learning assessment that probes students' understanding of the key concepts addressed in the film, which can be used before or during the film to assess students' prior knowledge and to guide students as they watch the film. We encourage you to choose the use that best fits your learning objectives and your students' needs. Moreover, because the vocabulary and concepts are complex, we encourage you to modify the handout as needed (e.g., reducing the number of questions, explanations of complicated vocabulary for English learner students).

ANSWERS

1. (Key Concept A) Which of the following statements describes domestication?
   a. It is the process by which animals are trained to do tricks useful for human needs.
   b. ***It is the process by which wild species have been turned into species with traits that are useful for human needs.***
   c. It is the process by which animals build nests to attract mates and raise young.
   d. It is the process by which plants have evolved to fill in ecological niches over time.

2. (Key Concept A) To illustrate how common corn is in a typical American diet, the narrator gives many examples, from corn-on-the-cob to foods that contain cornstarch and corn syrup. The narrator also mentions meat. What is the connection between the meat we eat and corn? ***The animals rely on a corn-based diet.***

3. (Key Concepts B and C) Dr. Beadle concluded that teosinte was the likely ancestor of maize. On what evidence did he base this conclusion? Select all that apply.
   a. Teosinte looks like maize. ***False; teosinte looks very different from corn. The differences are so pronounced that Dr. Beadle's hypothesis was not widely accepted.***
   b. Teosinte and maize have nearly identical chromosomes. ***True***
   c. A cross between teosinte and maize produces fertile hybrid offspring. ***True***
   d. Christopher Columbus discovered written records of maize's domestication from teosinte. ***False; Christopher Columbus encountered maize when he landed in North America but not written records of its domestication.***

4. a. (Key Concept C) Fill in the table below to compare teosinte and maize:

	Extent of branching	Number of rows of kernels per cob	Kernel type (naked or enclosed in a hard fruitcase)
Teosinte	***Many branches***	***Few kernels in few rows***	***Enclosed in hard fruitcase***
Maize	***Few branches***	***Many kernels organized into many rows***	***Naked***

   b. (Key Concept A) Pick one of the characteristics of maize from the table and explain how it makes the crop more useful to humans than teosinte? ***Answers will vary. One answer is that having naked kernels makes the crop easier to eat. Another answer is that having few branches makes it easier to harvest.***

5. (Key Concepts B and E) Dr. Beadle conducted an experiment to determine how many genes control the differences between maize and teosinte. He crossed teosinte with maize (the two parental plants) to produce F_1 hybrids, and then crossed the F_1 plants to produce an F_2 generation (offspring). He then looked at the appearance, or phenotype of the offspring. Based on classical genetics, he predicted if just one gene was responsible for all the differences between maize and teosinte, a parental phenotype was expected in one of every four offspring—in other words ¼ of the offspring would look like maize and ¼ would look like teosinte. If two genes are involved, one out of every 16 offspring would look like maize and one out of 16 like teosinte. This relationship can be summarized by this equation: $X = (1/4)^n$
   a. In the equation above, X represents the proportion of offspring expected to have a parental phenotype. What does *n* represent? n ***represents the number of genes responsible for the differences in phenotype.***
   b. Dr. Beadle planted 50,000 plants and discovered that 1 out of 500 offspring had the phenotype of one parent and 1 out of 500 of the other parent. Approximately how many plants had a teosinte phenotype? A maize phenotype? What phenotype(s) did the rest of the plants have? ***About 100 would be expected to show the teosinte phenotype, and about 100 would be expected to show the maize phenotype. The rest of the plants would show a mixture of maize and teosinte traits.***
   c. Use the equation $X = (1/4)^n$ to explain how Dr. Beadle came to conclude that four or five genes are responsible for the differences between maize and teosinte. ***About 1/500 F_2 plants had a parental phenotype. $(1/4)^4$ is 1/256 and $(1/4)^5$ is 1/1024; 1/500 is between these two numbers, so four or five genes are responsible for the differences.***
   d. (Key Concept F) Explain how changes in a small number of genes can result in very different-looking plants. ***Regulatory genes, such as transcription factors, control the expression of many other genes. As a result, changes in regulatory genes can have a big impact on phenotype.***

6. (Key Concepts B, C, and D) The film describes two independent sources of evidence that have been used to estimate when maize was first domesticated: genetic evidence and archaeological evidence. Do these two sources of evidence support each other? Explain your answer.

Yes. The oldest macrofossils (maize cobs) are only about 6,000 years old, but using the microfossil data, archaeologists date maize domestication to about 8,700 years ago. This date is highly consistent with the genetic data, which estimates a domestication date of about 9,000 years ago.

7. (Key Concepts B and F) To demonstrate how two different genes can explain different traits in teosinte and maize, Dr. Doebley and colleagues used careful breeding to transplant genes from one organism to the other. In the table below, draw and/or describe the results of each cross and explain what you can infer about the function of the genes.

Gene	Moved from	Moved into	Draw the result	What can you infer about the function of the gene?
fruitcase gene	Teosinte	Maize	***More closed fruitcase***	***That the fruitcase gene has a major effect on how open the fruitcase is. Note that the gene doesn't completely control all the differences between maize and teosinte.***
	Maize	Teosinte	***More open fruitcase***	
branching gene	Teosinte	Maize	***More branched***	***That the branching gene has a major effect on how branched the plant is. Note that the gene doesn't completely control all the differences between maize and teosinte.***
	Maize	Teosinte	***Less branched***	

8. (Key Concepts A, B, and C) Humans have been selecting maize for desirable characteristics ever since domestication of the crop began. Figure 1 below describes the traits of maize cobs found in four archaeological deposits from the Tehuacán cave in Puebla, Mexico. Rachis diameter refers to the diameter of the cob at its base. Average number of rows refers to the number of rows of kernels per cob.
   a. Which archaeological layer contains the oldest maize remains? The youngest?
   The oldest layer is Layer A, which is about 5,500 years old. The youngest layer is Layer D, which is about 1,850 years old.
   b. Use data to compare and contrast the oldest and youngest maize cobs in the archaeological record.
   The oldest maize cobs have a smaller diameter (0.26 vs. 0.4) and fewer rows of kernels (7.3 vs. 9.7) compared to the youngest maize cobs.
   c. The authors compared the ancient maize to two different modern maize varieties: arrocillo and tabloncillo. How do these two varieties compare to the cobs found in the archeological record? Why do you think the study selected these two varieties to use for their comparisons?
   Arrocillo cobs are short and fat, with an average of 8.1 rows and an average rachis diameter of 1.09 cm. Tabloncillo cobs are longer and thinner, with an average of 17 rows and an average rachis diameter of 0.9 cm. In general, both varieties have more kernels per cob than the ancient cobs. The authors used two different varieties because modern corn has a range of phenotypes. These two varieties represent two extremes.
   d. Based on these data, what can you say about the kinds of traits that have farmers been selecting for in maize over the past 5,000 years?
   The trend over the past 5,000 years has been for cobs to become wider and with a greater number of rows of kernels. Farmers have been selecting plants with more kernels per cob.

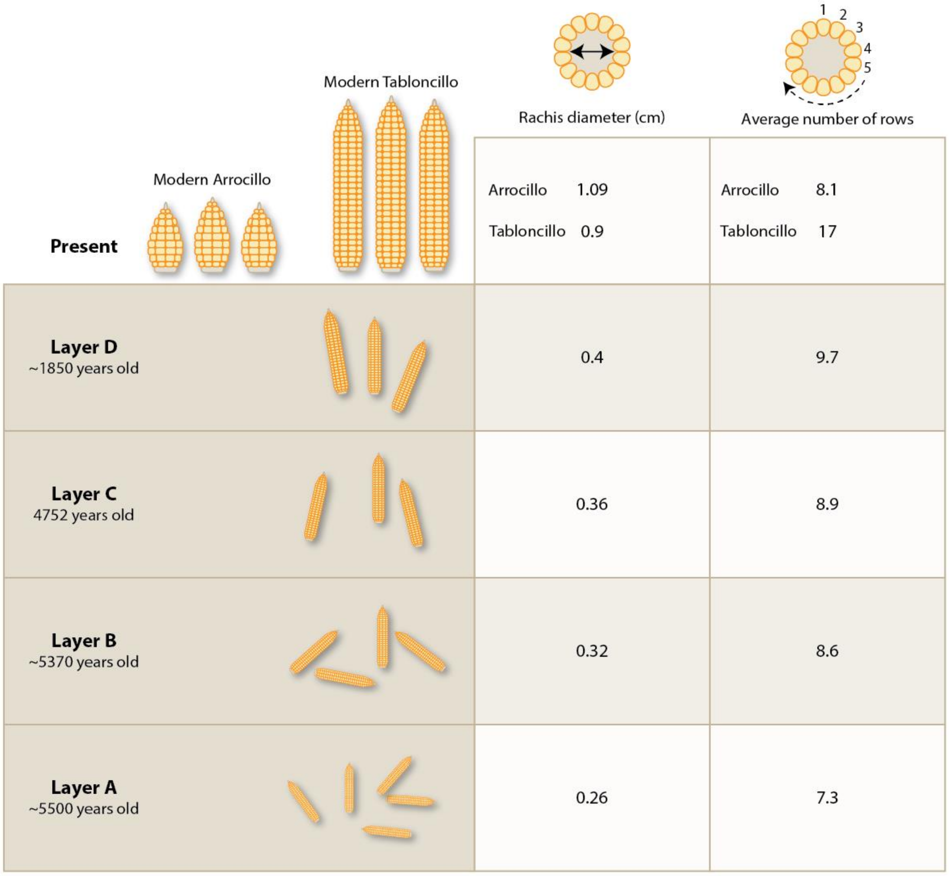

Figure 3. (Figure 1 in Student Handout) Corn cob fossils discovered in different layers of the Tehuacán cave in Mexico. The age of each layer is indicated. Present-day corn consists of two different varieties. For each corn sample, the average rachis diameter and row number are noted.

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