

Prehistoric GM Corn

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Corn (maize) is arguably man's first, and perhaps his greatest, feat of genetic engineering. Its huge ears—each packed with firmly attached kernels filled with starch, protein, and oil—make it a food staple. Contemporary corn, unlike its wild grassy ancestor teosinte, can't survive without people because it can't disperse its own seeds. The origins of maize have long intrigued geneticists, but only recently have new molecular methods enabled evolutionary sleuths to pinpoint its origins and identify the genetic modifications (GMs) that enabled the radical transformation of teosinte into contemporary maize. On page 1206 of this issue, Jaenicke-Després, Doebley, and their colleagues (1) provide the latest chapter in this detective story and suggest that prehistoric people were quick to adopt GM corn.

Teosinte and corn (*Zea mays*) don't look much alike, but they are interfertile. Teosinte-corn hybrids arise in the wild but look so different from either parent that they were originally classified as a different species (*Zea canina*). In the 1920s, Beadle examined chromosomes in teosinte-corn hybrids and concluded that the two plants belonged to the same species, and even shared the same chromosomal order of genes. That should have resolved the question of corn's origins, but it didn't.

In 1938, the eminent maize geneticist Mangelsdorf proposed that maize evolved from an extinct South American maize species and that teosinte originated from a cross between another grass, *Tripsacum*, and maize (2). Although cumbersome, this hypothesis was widely accepted, and Mangelsdorf and Beadle sparred publicly for years. Upon retirement, Beadle organized an expedition to Mexico to look for more wild maize relatives, returning with seeds that proved invaluable to the next generation of molecular archaeologists. The *Tripsacum* hypothesis was briefly resurrected in the mid-1990s, but by then molecular evidence overwhelmingly favored the notion that teosinte was the ancestor of modern maize (3).

So how, when, and where was teosinte transformed into maize? Beadle gave his mentor, Emerson, credit for the idea that just



Primitive popcorn. Teosinte (left) and primitive maize (right). Primitive maize was "reconstructed" by crossing teosinte with Argentinian corn.

a few mutations changed teosinte into maize (4). Analyzing backcrossed maize-teosinte hybrids with molecular probes, Doebley's group came to a startlingly similar conclusion: The differences between maize and teosinte could be traced to just five genomic regions (5). In two of these regions, the differences were attributable to alternative alleles of just one gene: *teosinte glume architecture (tga1)* and *teosinte branched (tb1)*, which affect kernel structure and plant architecture.

The *tga1* gene controls glume hardness, size, and curvature (6). Teosinte kernels are surrounded by a stone-like fruitcase, assuring their unscathed passage through an animal's digestive tract, which is required for seed dispersal. But the plant's reproductive success is the consumer's nutritional failure. Not surprisingly, one of the major differences between maize and teosinte kernels lies in the structures (cupule and outer glume) enclosing the kernel. Maize kernels don't develop a fruitcase because the glume is thinner and shorter and the cupule is collapsed. The hardness of teosinte kernels comes from silica deposits in the glume's epidermal cells and from impregnation of glume cells with the polymer lignin. The maize *tga1* allele supports slower glume growth and less silica deposition and lignification than does the teosinte *tga1* allele.

The *tb1* locus is largely responsible for the different architecture of the two plants. Teosinte produces many long side branches, each topped by a male flower (tassel), and

its female flowers (ears) are produced by secondary branches growing off the main branches. Modern corn has one main stalk with a tassel at the top. Its lateral branches are short and bear its large ears. Much of the difference is attributable to the *tb1* gene, originally identified in a teosinte-like maize mutant. Mutations generally abrogate gene function, indicating that the maize allele acts by suppressing lateral shoot development, converting grassy teosinte into slim, single-stalked modern corn and male into female reproductive structures (7).

Knowing that this cluster of traits is controlled by just two genes makes it less surprising that genetic differences in these genes could render teosinte a much better food plant. Yet however useful to people, a *tga1* mutation would have been detrimental to teosinte, making it more vulnerable to destruction in the digestive tract of the consumer and so less able to disperse its seeds. Thus, the only way this mutation could have persisted is if our ancestors propagated the seeds themselves. This implies that people were not only harvesting—and likely grinding and cooking—teosinte seeds before these mutations came along, but also were selecting for favorable features such as kernel quality and cob size. In turn, this suggests a "bottleneck" in corn evolution: Several useful GMs were brought together in a single plant and then the seeds from this plant were propagated, giving rise to all contemporary maize varieties. Such a prediction can be tested by calculating the number of generations and individuals it would take to account for the molecular variability present in contemporary maize. The results of such a test suggest a bottleneck for maize domestication of just 10 generations and a founding population of only 20 individuals (8). Did this happen once or many times? Because genetic differences arise at a fairly constant rate, this question can be answered by constructing family trees using similar sequences from different varieties of teosinte and contemporary maize. The results are unequivocal: All contemporary maize varieties belong to a single family, pointing to a single domestication event.

Knowing how quickly differences arise, how many there are today, and where the family of origin survives, it is possible to determine when—and where—it all started. The answer is that maize most probably arose from teosinte of the subspecies *parviglumis* in the Balsas River basin of southern Mexico roughly 9000 years ago (9). Recent redating of cobs from the Guilá Naquitz cave (about 500 km from the Balsas River basin) demonstrated that they were more than 6200 years old, providing archae-

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ological support for the molecular findings (10, 11). These earliest corn cobs don't look much like those of modern corn, but they look even less like teosinte cobs (see the figure). They are tough and have several rows of tightly attached kernels, implying that the plants wouldn't have survived without people to detach and plant the seeds. By contrast, teosinte's reproductive structure, the rachis, falls apart when mature to release its hard seeds. Thus, even 6000 years ago, ancient maize cobs were already corn-like.

The GM corn spread far—and fast. Maize appears in the archaeological record of the southwestern United States more than 3000 years ago (12), and it is evident that cob size had already increased under selection. The Jaenicke-Després *et al.* study (1) examines the selection of traits that can't be observed in fossilized cobs. Taking tiny samples of fossil cobs from the Ocampo Caves in northeastern Mexico (2300 to 4400 years old) and the Tularosa Cave in the Mogollon highlands in New Mexico (650 to 1900 years old), the authors extracted DNA and amplified, cloned, and sequenced small DNA fragments of the *tb1* gene, the *pbf* gene that controls the amount of storage protein, and the

sul gene encoding a starch-debranching enzyme whose activity affects the texture of corn tortillas. They compared their ancient DNA sequences with those of 66 maize landraces (the corn grown by indigenous farmers) from South, Central, and North America and 23 lines of teosinte *parviglumis*.

They report that alleles of these genes typical of modern corn were already present more than 4000 years ago, implying that plant architecture and kernel nutritive properties were selected early, long before corn reached North America. All 11 ancient cobs carried the *tb1* allele present in modern corn, but fewer than half of the 23 teosinte varieties carried this allele. Similarly, all ancient samples contained a *pbf* allele that is common in corn but rare in teosinte. The predominant modern *sul* allele was found in all of the older Mexican cobs, but the younger New Mexican cobs had several different alleles, suggesting that this gene was still undergoing selection when maize reached North America.

The authors conclude that "... by 4400 years ago, early farmers had already had a substantial homogenizing effect on allelic diversity at three genes associated with maize

morphology and biochemical properties of the corn cob." This suggests that once this special combination of GMs was assembled, the plants proved so superior as a food crop that they were carefully propagated and widely adopted, perhaps causing something of a prehistoric Green Revolution. It also implies that the apparent loss of genetic diversity following the introduction of high-yielding Green Revolution wheat and rice varieties in the 1960s and 1970s, and attending the rapid adoption of superior GM crops today, is far from a new phenomenon.

References

1. V. Jaenicke-Després *et al.*, *Science* **302**, 1206 (2003).
2. P. C. Mangelsdorf, R. G. Reeves, *Proc. Natl. Acad. Sci. U.S.A.* **24**, 303 (1938).
3. J. Bennetzen *et al.*, *Lat. Am. Antiq.* **12**, 84 (2001).
4. G. W. Beadle, *Sci. Am.* **242**, 112 (January, 1980).
5. J. Doebley, *Trends Genet.* **8**, 302 (1992).
6. S. White, J. Doebley, *Trends Genet.* **14**, 327 (1998).
7. J. Doebley *et al.*, *Nature* **386**, 485 (1997).
8. A. Eyre-Walker *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 4441 (1998).
9. Y. Matsuoka *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 6080 (2002).
10. B. F. Benz, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 2104 (2001).
11. D. R. Piperno, K. V. Flannery, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 2101 (2001).
12. B. B. Huckell, *J. World Prehist.* **10**, 305 (1996).

PHYSICS

Flux Quanta on the Move

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Most superconductors are penetrated by flux vortices when exposed to magnetic fields. The dissipative motion of these "Abrikosov vortices"—first predicted by Alexei Abrikosov, one of

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the recipients of this year's Nobel prize in physics—can be good or bad for practical applications.

In applications involving large superconducting currents, vortex motion is best avoided altogether, whereas controlled vortex motion can be useful in superconducting electronic devices.

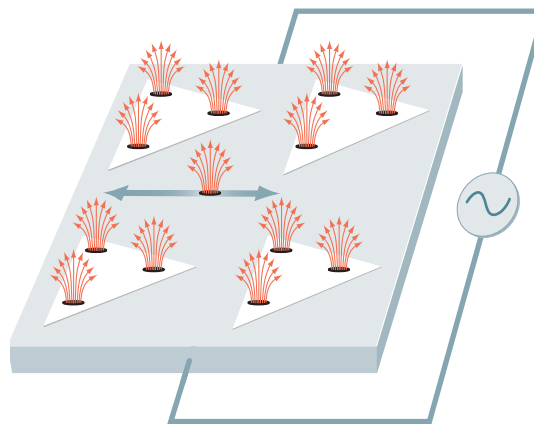
On page 1188 of this issue, Villegas *et al.* show how vortex motion may be controlled in superconducting electronic devices (1). They have realized a rectifier that

converts a zero-averaged ac supercurrent into a dc voltage. In the device, the vortex motion in superconductors is guided with asymmetric vortex-pinning sites. For certain values of applied current and magnetic field, an inversion in the direction of the vortex flow, and thus in the sign of the dc voltage signal, occurs.

The Abrikosov vortices in superconductors are kept in place by a pinning force. However, under the influence of electrical currents they also experience a Lorentz force. When the Lorentz force exceeds the pinning

force, the vortices start to move. This motion produces a voltage over the superconductor. The resulting energy dissipation is unwanted for large-current applications, such as magnets, and hence many groups have tried to create strong pinning sites.

Because the core of an Abrikosov vortex is in a normal conducting state, it is energetically favorable for the vortex to be located in regions of reduced superconductivity. Furthermore, the vortex can be "pinned" by magnetic dots within, or on top of, the superconductor. This pinning is further enhanced by the local suppression of superconductivity near magnetic dots. For strong magnetic fields, the vortex density becomes so large that the vortices start to feel each other. The repulsive interaction between them gives rise to an ordered vor-



Directed vortex motion. For large applied magnetic fields, the triangular pinning sites are completely saturated with three pinned vortices each. Due to the interaction with these pinned vortices, the interstitial sites experience a ratchet potential, resulting in net motion to the left when an ac-bias current is applied. For smaller magnetic fields, the vortex motion is in the opposite direction, from triangle to triangle. In that case the asymmetric shape of the triangles forms the basis for the ratchet behavior.

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