NATURAL HISTORY

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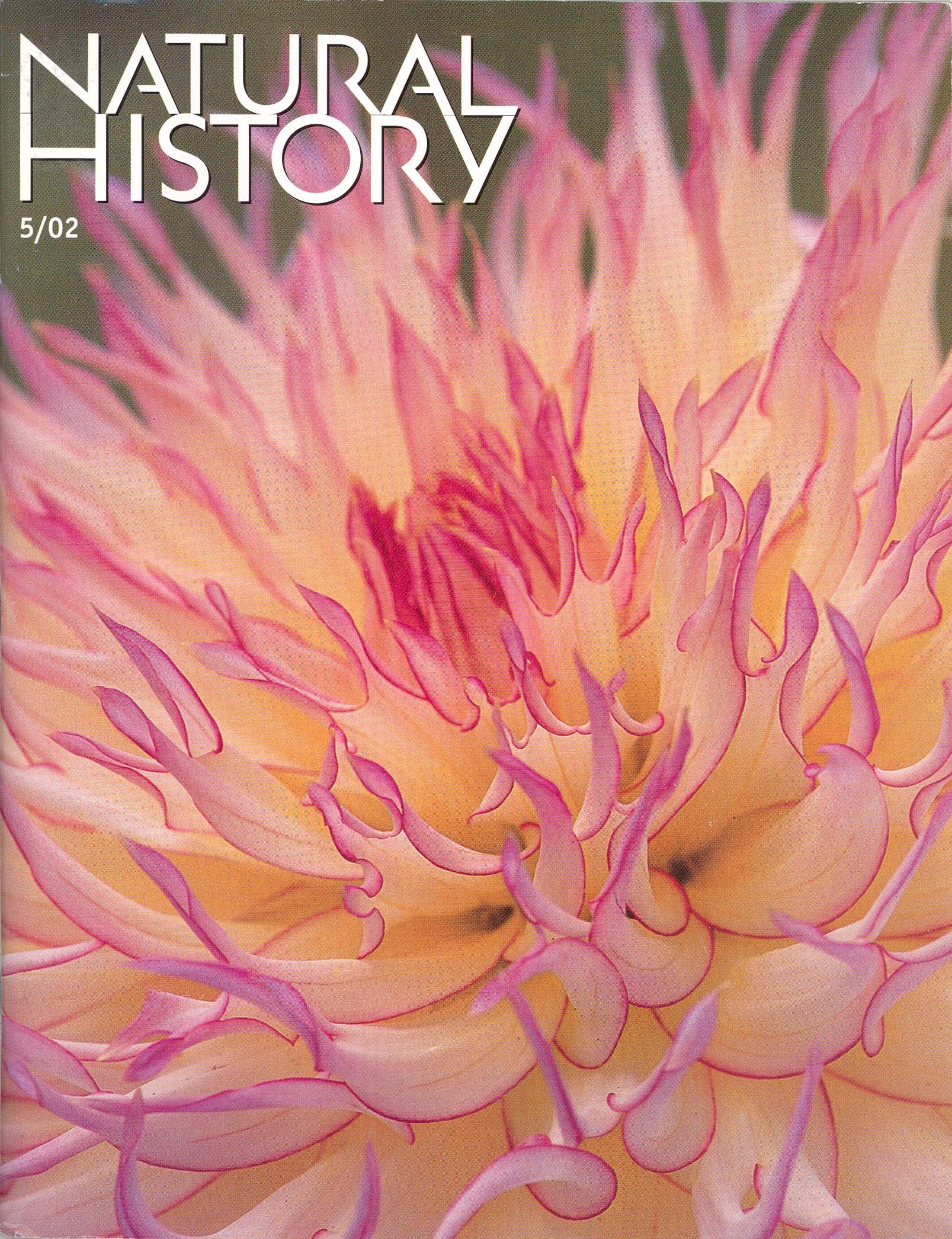


The Making of a Blossom

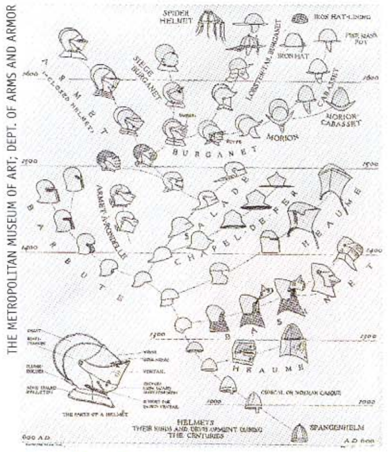
By Enrico Coen

A flower's evolutionary past may be read in the genes that influence its development.

The lower petals of a *Salvia* blossom are shaped quite differently from its upper petals. Flowers of this type provide a landing platform for flies and bees. Scientists believe that this kind of blossom probably evolved from a radially symmetrical ancestor millions of years ago, during the period when insects were becoming increasingly important pollinators.

NURIDSANY AND PÉRENNOU

Bashford Dean had two passions in life. One was studying the development and evolution of fishes, which led to his becoming a professor at Columbia University in 1891 and a curator at the American Museum of Natural History in 1903. The other was a fascination with arms and armor that was first roused in early childhood, when Dean saw a beautiful European helmet in the house of a family friend. He was so taken with the helmet that he sat with it on the porch, where he studied it inside and out for a long time. Dean's interest in armor grew over the years, and in 1906 he became honorary curator of arms and armor at New York's Metropolitan Museum of Art. Eventually he retired from active duty as a scientist and a teacher and devoted himself to making the Met's collection of arms and armor one of the finest in the world.



THE METROPOLITAN MUSEUM OF ART, DEPT. OF ARMS AND ARMOR

Bashford Dean's branching diagram of helmet "evolution" resembles charts illustrating relationships of species. At the bottom of the chart is an ancestral, radially symmetrical helmet, like the sixth-century Ostrogoth helmet below.

THE METROPOLITAN MUSEUM OF ART, GIFT OF STEPHEN V. GRANCSAY, 1942 (42.50.1)

Dean took his biological past with him, however. Diagrams he drew depicting the evolution of armaments such as helmets and shields have much the same branching pattern often used by scientists to illustrate the evolution of fishes or flowers. One diagram of helmets (at left) shows a simple, radially symmetrical ancestral helmet at the bottom. From this primitive form, various lineages emerge; some of them lead to highly elaborate, enclosed helmets with visors or chin guards, while others lead to dead ends or revert to simpler shapes.

Such diagrams are a good way to organize objects and to show how they are related. But insofar as they give the impression that one object is transformed directly into another—that one helmet, say, is directly modified to give rise to the next in the series—they are misleading. What evolve, of course, are not the helmets themselves but the ways people make them. Bashford Dean's diagram tells a story about changes in how people fashion helmets in response to changing circumstances, materials, and traditions.

A similar principle applies to biological evolution. Although we commonly portray evolution as a branching tree or bush along which one type of organism seems to transform into another, it is not organisms themselves that change but the way they develop. During the evolution of flowers, for example, blossoms of one type are not directly modified to produce blossoms of another type. What changes is the way flowers develop from seed in each generation. More precisely, changes come from the genes that influence development and that underlie the evolution of flowers, fishes, and every other complex biological structure.

DAN SUZIO

The way objects, whether flowers or helmets, change their shape over time can be understood only by paying attention to how they are made.

The earliest flowering plants are believed to have borne similar-shaped petals arranged around a center, as is the case with the poppy, above.

But how do evolutionary biologists unravel the history of developmental change when the ancestral organisms are no longer with us? Even when we are lucky enough to have a fossil record, we get only a few snapshots, not a dynamic view of how ancient plants and animals developed in each generation.

Recently, researchers have been approaching

DAVID LIEBMAN

The upper and lower petals of snapdragons are shaped differently because a particular gene, known as *cyc*, is active only in the upper region of the developing flower bud.

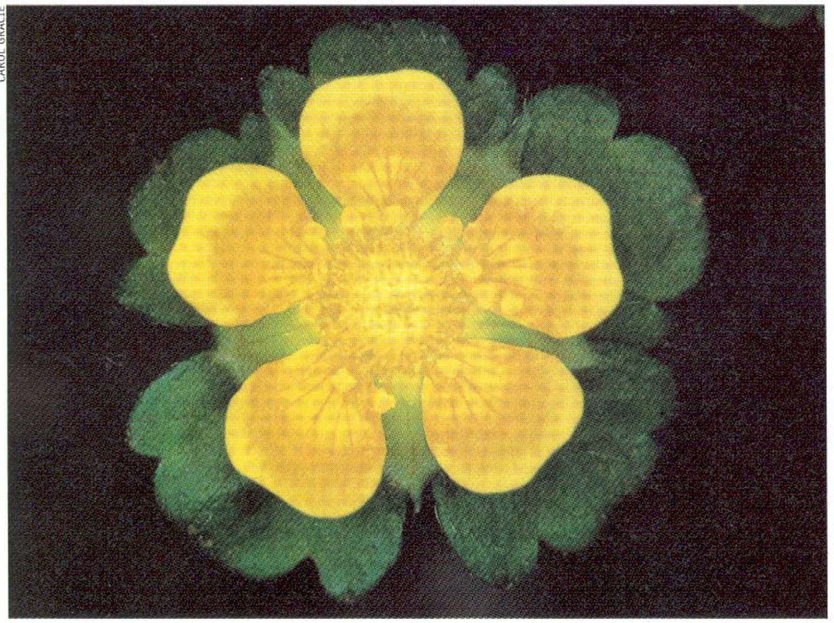
this problem from a new angle: studying how genes influence diverse organisms living today and then trying to infer what happened in the past. After all, genes, the units of heredity, are what connect us with our past. This approach, sometimes called evo-devo (short for evolution of development), became possible only in the last decade or so, when advances in our knowledge of genes allowed us to compare their roles in different types of organisms. Evo-devo has already yielded many surprises, prompting biologists to think afresh about some age-old problems, such as the evolution of the eye or the relationship between mammals and insects. In my own field—the evolution and genetics of flowering plants—I have been especially intrigued by how genes determine floral symmetry.

Flowers can be broadly divided into two types according to their symmetry. Radially symmetrical flowers, such as buttercups and tulips, have a single type of petal arranged the same way all around a center. There is more than one way to cut vertically through the center of these flowers to produce two halves that are mirror images. Bilaterally symmetrical flowers, such as snapdragons and sweet peas, have distinctive upper and lower petals and are therefore asymmetric from top to bottom. There is only one way you can cut one of these flowers to divide it into two mirror-image halves.

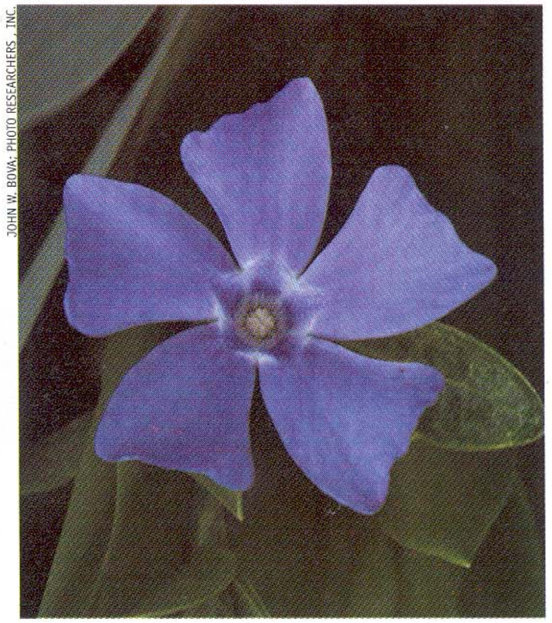
Like Bashford Dean's helmets, flowers are thought to have been radially symmetrical at first. Bilateral flowers evolved later in response to pollinators, the lower petals often providing a platform for insects to land on. Curiously, bilateral symmetry—and thus the developmental "trick" that makes it possible—seems to have evolved numerous times, independently. How was this possible?

One of the most familiar plants with bilateral symmetry is the snapdragon *(Antirrhinum majus)*. Highly regarded as reliable and colorful members of the summer garden, snapdragons hold a different attraction for geneticists. Some of the key genes controlling flower symmetry have been identified in this plant, and one gene, called *cycloidea*, or *cyc* (from the Greek *cyclo-*, meaning circular), plays a particularly important role. With *cyc*, snapdragons produce the double-lipped blossom popular with small children, who like to squeeze the sides together to make the "dragon" open its mouth. Some snapdragons, however, produce radially symmetrical blossoms; in such mutant plants, the *cyc* gene is inactive.

A few years ago, my colleagues Da Luo and Rosemary Carpenter and I isolated the *cyc* gene. Then we began to look at when and where it first becomes active in the developing flower bud. (All of a plant's genes, of course, are present in all of its cells, but only if a gene is activated, if it turns on, can it have an effect.) We showed that in normal snapdragons, *cyc* turns on at a very early stage of flower development, when the bud is just a tiny bulge, less than one-tenth of a millimeter across. At this stage, viewed through a scanning electron microscope, the bud still appears symmetrical from the outside. But when we stained a section of the developing bud to reveal where the *cyc* gene was active and then looked through a light microscope, we saw something striking: the *cyc* gene was active only in the upper part of the bud, visible as a region that stained dark blue. This early internal asymmetry in gene activity is what leads to the distinctive upper and lower petals that develop later on.



CAROL GRACIE



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The Indian strawberry, above left, is radially symmetrical, while the periwinkle, above right, is an example of a "left-handed" flower. Its petals are tilted like the blades of a fan turning counterclockwise; as a result, it is not symmetrical on any one plane.

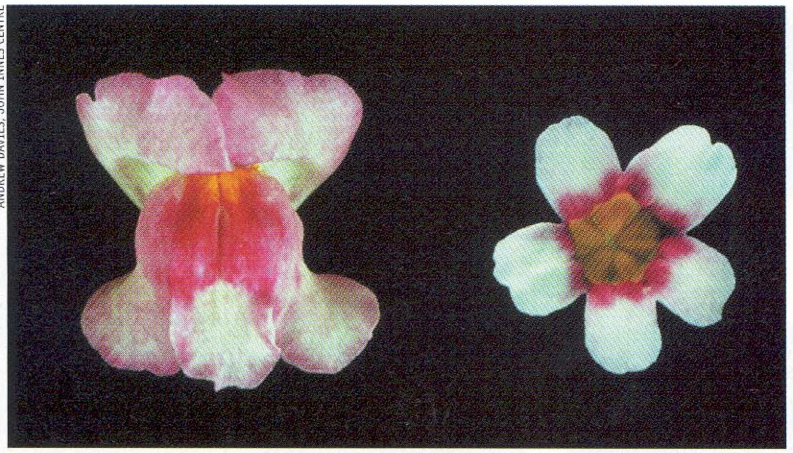
Cyc is a regulatory gene, which means it influences the activity of other genes. Regulatory genes produce particular types of proteins (sometimes called master proteins) that are able to bind to other genes and switch them on or off. In the snapdragon, *cyc* influences a specific set of genes in the upper part of the bud, leading the upper petals to develop characteristics that differ from those of the lower petals.

How could this be? We can gain some insight into this question by thinking about how certain letters of the Latin alphabet are used in the English language. Some words contain letters that aren't pronounced when we speak. The letter *k*, for example, is silent in the word "knight." The *k* is not useless, however; in written text, it distinguishes "knight" from "night"—words with very different meanings. Similarly, a pattern of gene activity may not always manifest itself in the most obvious way in an organism. In *Arabidopsis*, for example, the asymmetric pattern of *cyc* activity is there in the early bud but is of no consequence to the symmetry of the mature flower that develops from it. This is probably because the genes that respond to *cyc* in *Arabidopsis* are different from those that get switched on or off by *cyc* activity in snapdragons. Rather than influencing the way the petals grow, these genes might have to do with orienting the flower or with ensuring that the petals develop in regular positions. Researchers in various laboratories are currently working to pin down *cyc*'s role in *Arabidopsis*.

Some of the key genes regulating the development of flower symmetry have been identified in Antirrhinum majus, *the snapdragon.*

What happens in plants such as buttercups, in which radially symmetrical flowers are the norm? In these cases the upper and lower petals look the same, so you might think there would be no gene like *cyc* present. Right? Wrong. In 2001, scientists sequenced the genome of a plant named *Arabidopsis thaliana*. Bearing tiny, white, radially symmetrical flowers, this small member of the mustard family is the workhorse of gene research in plants. A computer scan of all this genome-sequencing information revealed that among its 25,000 or so genes, *Arabidopsis* has one that is, in fact, very similar to *cyc*. The real surprise came when my colleague Pilar Cubas, working at the Universidad Autónoma de Madrid, discovered that the *cyc* gene was active in *Arabidopsis* only in the upper part of developing flower buds—just as we had found for the snapdragon.

Even without revealing just what that role may be, however, the *cyc* research to date has provided an important clue as to why bilateral asymmetry in flowers has evolved so many times. Since the asymmetric pattern of *cyc* activity is found in both snapdragons and *Arabidopsis*, it was presumably also pre-



ANDREW DAVIES, JOHN INNES CENTRE

Above: A snapdragon with a functional *cyc* gene will develop the typical double-lipped blossom (left). In a mutant snapdragon (right) with similar petals radiating around the center, *cyc* is inactive. Opposite: This dahlia blossom contains two types of flowers. The eight pink rays belong to eight bilaterally symmetrical flowers, whose structure cannot be fully seen without dissecting the blossom.

sent in their most recent common ancestor, a plant that would have lived about 100 million years ago. This ancestral plant probably had radially symmetrical flowers, and thus, as in *Arabidopsis,* the *cyc* gene must have had a different role to play. Whatever its role, the asymmetric pattern of *cyc* activity meant that, in terms of gene activity, the ancestor's flowers were already asymmetric from top to bottom. This may have made it relatively easy for differences between upper and lower petals to evolve numerous times in the descendants of the ancestral plant, through minor modifications in *cyc* or in the genes that respond to *cyc.*

Much of what seems novel in an organism's appearance stems from ancient patterns of gene activity manifesting themselves in new ways.

The key point here is that much of what seems novel in the appearance of an organism stems from ancient patterns of gene activity manifesting themselves in new ways, rather than from the invention of something completely new. And we do not have to go back millions of years to find evidence of the importance of changes involving regulatory genes. A more recent example is the domestication of maize (corn) by the prehistoric peoples of Mexico. The maize we cultivate today has one main stem, from which grow large cobs with lots of accessible, nutritious seeds (the kernels). Teosinte—maize's nearest living wild relative—looks very different; it is a highly branched plant with relatively small cobs, each of which bears a few seeds that have a hard, inedible covering.

About ten years ago, John Doebley, then at the University of Minnesota, and colleagues, building on earlier work by George Wells Beadle, showed that changes in as few as five genes could convert teosinte into a useful food plant like maize. Recently, Doebley's group went on to isolate one of these genes. Called *teosinte-branched,* or *tb1,* this gene is largely responsible for the difference in branching patterns between maize and teosinte. As might have been expected from the appearance of the plant, *tb1* was found to be most active in the developing side buds. Quite unexpectedly, however, the DNA sequence of *tb1* turned out to be very similar to that of the *cyc* gene of *Antirrhinum,* and like *cyc, tb1* seems to be a regulatory gene.

In the process of domesticating maize, the ancient peoples of Mexico seem to have chosen a plant with a mutant form of the *tb1* gene that was particularly effective at preventing side buds from developing into long branches. They were unwittingly playing with regulatory genes, much as may have happened naturally in the evolution of bilateral symmetry. And the evolution of maize has another parallel with that of floral asymmetry: both enabled plants to establish new associations with animals—humans in one instance, insects in the other. By studying these genes, we are revealing not only the history of changes in plant development but also something of the habits and predilections of the animals that interacted with them.

During one of Bashford Dean's trips to Europe, he came across an ancient box in the corner of an attic in Dijon, France. The box had belonged to an armor maker some 600 years earlier and contained parts of unfinished gauntlets. Dean remembered: "It gave me a curious feeling to take in my hands these ancient objects which seemed only yesterday to have been put in the box by their maker. I had the strong impression that if I should go through the old door near by, I would by some 'Alice in Wonderland' wizardry, pass into the sixteenth century and find in the next room a veritable armorer at his table by the low window."

The study of genes can also help transport us into the past to contemplate previous acts of making. But as with all cases of imaginary time travel, the fascination does not lie simply with re-creating the past, for the past is intrinsically no more or less interesting than the present. Rather, the deepest satisfaction comes from viewing the past through the eyes of the present and contemplating how they are related through time. □