WHERE DID ALL THE FLOWERS COME FROM?

Throughout his life, Charles Darwin surrounded himself with flowers. When he was 10, he wrote down each time a peony bloomed in his father's garden. When he bought a house to raise his own family, he turned the grounds into a botanical field station where he experimented on flowers until his death. But despite his intimate familiarity with flowers, Darwin once wrote that their evolution was "an abominable mystery."

Darwin could see for himself how successful flowering plants had become. They make up the majority of living plant species, and they dominate many of the world's ecosystems, from rain forests to grasslands. They also dominate our farms. Out of flowers come most of the calories humans consume, in the form of foods like corn, rice and wheat. Flowers are also impressive in their sheer diversity of forms and colors, from lush, full-bodied roses to spiderlike orchids to calla lilies shaped like urns.

The fossil record, however, offered Darwin little enlightenment about the early evolution of flowers. At the time, the oldest fossils of flowering plants came from rocks that had formed from 100 million to 66 million years ago during the Cretaceous period. Paleontologists found a diversity of forms, not a few primitive forerunners.

Long after Darwin's death in 1882, the history of flowers continued to vex scientists. But talk to experts today, and there is a note of guarded optimism. "There's an energy that I haven't seen in my lifetime," said William Friedman, an evolutionary biologist at the University of Colorado, Boulder.

The discovery of new fossils is one source of that new excitement. But scientists are also finding a wealth of clues in living flowers and their genes. They are teasing apart the recipes encoded in plant DNA for building different kinds of flowers. Their research indicates that flowers evolved into their marvelous diversity in much the same way as eyes and limbs have: through the recycling of old genes for new jobs.

Until recently, scientists were divided over how flowers were related to other plants. Thanks to studies on plant

RARE PLANT Amborella trichopoda, a small shrub found only on the island of New Caledonia in the South Pacific, represents the oldest living lineage of flowering plants

DNA, their kinship is clearer. "There was every kind of idea out there, and a lot of them have been refuted," said James A. Doyle, a paleobotanist at the University of California, Davis.

It is now clear, for example, that the closest living relatives to flowers are flowerless species that produce seeds, a group that includes pine trees and gingkos. Unfortunately, the plants are all closely related to one another, and none is more closely related to flowers than any of the others.

The plants that might document the early stages in the emergence of the flower apparently became extinct millions of years ago. "The only way to find them is through the fossils," Dr. Doyle said.

In the past few years scientists have pushed back the fossil record of flowers to about 136 million years ago. They have also found a number of fossils of mysterious extinct seed plants, some of which produce seeds in structures that look faintly like flowers. But the most intriguing fossils are also the most fragmentary, leaving paleobotanists deeply divided over which of them might be closely related to flowers. "There's no consensus," Dr. Doyle said.

But there is a consensus when it comes to the early evolution of flowers themselves. By studying the DNA of many flowering plants, scientists have found that a handful of species represent the oldest lineages alive today. The oldest branch of all is represented by just one species: a shrub called Amborella that is found only on the island of New Caledonia in the South Pacific. Water lilies and star anise represent the two next-oldest lineages alive today.

If you could travel back to 130 million years ago, you might not be impressed with the earliest flowers. "They didn't look like they were going anywhere," Dr. Doyle said.

Those early flowers were small and rare, living in the shadows of far more successful nonflowering plants. It took many millions of years for flowers to hit their stride. Around 120 million years ago, a new branch of flowers evolved that came to dominate many forests and explode in diversity. That lineage includes 99 percent of all species of flowering plants on Earth today, ranging from magnolias to dandelions to pumpkins. That explosion in diversity also produced the burst of flower fossils that so puzzled Darwin.

All flowers, from Amborella on, have the same basic anatomy. Just about all of them have petals or petal-like structures that surround male and female organs. The first flowers were probably small and simple, like modern Amborella flowers.

Later, in six lineages, flowers became more complicated. They evolved an inner ring of petals that became big and showy, and an outer ring of usually green, leaflike growths called sepals, which protect young flowers as they bud.
It would seem, based on this recent discovery, that a petal is not a petal is not a petal. The flowers of, say, the paw-paw tree grow petals that evolved independently from the petals on a rose. But the genes that build flowers hint that there is more to the story.

In the late 1980s, scientists discovered the first genes that guide the development of flowers. They were studying a small plant called Arabidopsis, a botanical lab rat, when they observed that mutations could set off grotesque changes. Some mutations caused petals to grow where there should have been stamens, the flower's male organs. Other mutations transformed the inner circle of petals into sepals. And still other mutations turned sepals into leaves.

The discovery was a remarkable echo of ideas first put forward by the German poet Goethe, who not only wrote "Faust" but was also a careful observer of plants.

In 1790, Goethe wrote a visionary essay called *The Morphology of Plants*, in which he argued that all plant organs, including flowers, started out as leaves. "From first to last," he wrote, "the plant is nothing but a leaf."

Two centuries later, scientists discovered that mutations to genes could cause radical transformations like those Goethe envisioned. In the past two decades, scientists have investigated how the genes revealed through such mutations work in normal flowers. The genes encode proteins that can switch on other genes, which in turn can turn other genes on or off. Together, the genes can set off the development of a petal or any other part of an Arabidopsis flower.

Scientists are studying those genes to figure out how new flowers evolved. They have found versions of the genes that build Arabidopsis flowers in other species, including Amborella. In many cases, the genes have been accidentally duplicated in different lineages.

Finding those flower-building genes, however, does not automatically tell scientists what their function is in a growing flower. To answer that question, scientists need to tinker with plant genes. Unfortunately, no plant is as easy to tinker with as Arabidopsis, so answers are only beginning to emerge.

Vivian Irish, an evolutionary biologist at Yale, and her colleagues are learning how to manipulate poppies because, Dr. Irish points out, "poppies evolved petals independently."

She and her colleagues have identified flower-building genes by shutting some of them down and producing monstrous flowers as a result.

The genes, it turns out, are related to the genes that build Arabidopsis flowers. In Arabidopsis, for example, a gene called AP3 is required to build petals and stamens. Poppies have two copies of a related version of the gene, called paleoAP3.

But Dr. Irish and her colleagues found that the two genes produced different effects. Shutting down one gene transforms petals. The other transforms stamens.

The results, Dr. Irish said, show that early flowers evolved a basic tool kit of genes that marked off different regions of a stem. Those geography genes made proteins that could then switch on other genes involved in making different structures. Over time, the genes could switch control from one set of genes to another, giving rise to new flowers.

Thus, the petals on a poppy evolved independently from the petals on Arabidopsis, but both flowers use the same kinds of genes to control their growth.

If Dr. Irish is right, flowers have evolved in much the same way our own anatomy evolved. Our legs, for example, evolved independently from the legs of flies, but many of the same ancient appendage-building genes were enlisted to build those different limbs.

"I think it is pretty cool that animals and plants have used similar strategies," Dr. Irish said, "albeit with different genes."

Dr. Irish said, however, that her studies of petals were only part of the story. "Lots of things happened when the flower arose," she said. Flowers evolved a new arrangement of sex organs, for example. "A pine tree has male cones and female cones," she said, "but flowers have male and female organs on the same axis."

Once the sex organs were gathered together, they underwent a change invisible to the naked eye that might have driven flowers to their dominant place in the plant world.

When a pollen grain fertilizes an egg, it provides two sets of DNA. While one set fertilizes the egg, the other is destined for the sac that surrounds the egg. The sac fills with endosperm, a starchy material that fuels the growth of an egg into a seed. It also fuels our own growth when we eat corn, rice or other grains.

In the first flowers, the endosperm ended up with one set of genes from the male parent and another set from the female parent. But after early lineages like Amborella and water lilies branched off, flowers bulked up their endosperm with two sets of genes from the mother and one from the father.

Dr. Friedman, of the University of Colorado, Boulder, has documented the transition and does not think it was a coincidence that flowering plants underwent an evolutionary explosion after gaining an extra set of genes in their endosperm.

It is possible, for example, that with extra genes, the endosperm could make more proteins.

"It's like having a bigger engine," Dr. Friedman said.

Other experts agree that the transition took place, but they are not sure it is the secret to flowers' success. "I don't know why it should be so great," Dr. Doyle said.
As Dr. Friedman has studied how the extra set of genes evolved in flowers, he has once again been drawn to Goethe's vision of simple sources and complex results.

Flowers with a single set of female DNA in their endosperm, like water lilies, start out with a single nucleus at one end of the embryo sac. It divides, and one nucleus moves to the middle of the sac to become part of the endosperm.

Later, a variation evolved. In a rose or a poppy, a single nucleus starts out at one end of the sac. But when the nucleus divides, one nucleus makes its way to the other end of the sac. The two nuclei each divide, and then one of the nuclei from each end of the sac moves to the middle.

Duplication, a simple process, led to greater complexity and a major change in flowers.

"Nature just doesn't invent things out of whole cloth," Dr. Friedman said. "It creates novelty in very simple ways. They're not radical or mysterious. Goethe already had this figured out." ●

CARL ZIMMER
THE NEW YORK TIMES