Botanists Seek The First Flower

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SCHOLARS of vertebrate evolution may endlessly ponder why the dinosaurs died and how reptiles gave rise to mammals, but for botanists the most glorious mystery of all is the origin of the first flowering plants.

Today, flowering plants, or angiosperms, are the lords of the botanical kingdom, greatly outnumbering nonflowering plants and defining the contours of nearly every terrestrial habitat on earth, from the American plains to the Amazon rain forest.

But such preeminence was not always the case. Flowering plants descended from once-dominant species that lacked encased seeds and fruits, the hallmarks of angiosperms, and botanists have long wondered what the earliest floral specimen looked like, when it arose, and how its kind came to overwhelm the landscape.

Now, they are at last gaining clues into what Charles Darwin described as an "abominable mystery," the evolution of the most important plant group alive.

New research into early fossil flowers, along with more advanced techniques for exploring relationships among plant species both living and extinct, are tempting many paleobotanists to abandon long-cherished notions of angiosperm genealogy.
For the past half-century, scientists have believed that the first flowering plants were much like magnolias, shrubby plants with big, flamboyant flowers and all the male and female reproductive parts handily encased in every bloom. But the latest research suggests that the first flowering plants were members of a group called paleoherbs, with tiny, simple flowers and the male and female floral genitalia separated into different blossoms. Some scientists theorize that the earliest paleoherb was something like the black pepper plant, while others propose that it was more like a diminutive version of the water lily.

Still other scientists, basing their conclusions on the DNA sequences of hundreds of floral species, propose that the oldest living line of flowering plants is a bizarre type of aquatic plant, the hornwort, which lacks petals, sepals and many of the other parts associated with modern flowering plants.

Many of the recent findings will be presented at a major symposium on plant origins, to be held in early October at the Missouri Botanical Garden in St. Louis. Organizers of the conference said the meeting was already booked beyond capacity, so excited are botanists to hear the latest results and to squabble over the data.

Identifying the earliest flowering plant has enormous implications for understanding an array of evolutionary questions, including the development of the insects and other pollinators that helped spread the angiosperm seeds around. A magnolia-like plant, which thrives in the forest, would have been pollinated by a very different set of creatures than a flower afloat in a pond.

"The question has profound implications for understanding pollination and dispersal biology," said Dr. Peter R. Crane, a paleobotanist in the geology department of the Field Museum in Chicago, who favors the pepper plant as a contender for the earliest angiosperm. "If we knew which plant came first, it would force a radical rethinking of how the structure and function of flowers evolved."

Whatever they believe about the particulars of the first angiosperm, many botanists agree that it probably originated much earlier than previously suspected. By traditional dogma, angiosperms arose during the Cretaceous period, perhaps 130 million years ago. The new research pushes the roots much further back, to the Triassic period 200 million years ago or earlier.

Scientists also agree that the advent of flowering plants radically changed the look, smell and taste of nature, transforming it from a somber green expanse of ferns, conifers, cycads and other ancient plants called gymosperms into an explosion of color and flavor that came with fruits and blossoms.

"The world brightened up in a major way," said Dr. Michael J. Donaghue of the University of Arizona in Tucson, a proponent of the water lily version of genesis. "The introduction of angiosperms was revolutionary, and it absolutely changed the face of the earth."
One particularly radical feature of the angiosperm was the enclosure of its seed in a protective fruit or nut, an evolutionary advancement that helped protect the plant’s genetic legacy against shifts in the environment. In the more primitive gymnosperms, including those species that still exist, the seeds are naked: in a conifer, for example, the bare seeds can be seen lodged between the scales of a pine cone, while on a fern they are loosely attached to the undersides of the leaves.

The plant groups also differ in their standard method of pollination. Gymnosperm pollen is spread largely by the wind, the sperm-like dust of one plant blowing along until it reaches the egg-like ovule of another, thereby forming a new and fertile seed. Wind pollination requires that a plant live in a fairly dense stand of its own kind, to better increase its chances of a meeting between male and female gametes.

By contrast, angiosperms evolved a dazzling array of seductive traits like flowers and nectar to lure insects, birds and bats. That capacity to attract hardworking animal pollinators able to transfer the pollen of one plant to the female ovaries of another meant that angiosperms could colonize new territories and still have a chance of a pollinator’s bringing its genes to a mate of its kind. What is more, insect pollination increased the number of natural hybrids, plants that are a mixture of two slightly different species.

"Flowering plants are the best advertising agents ever developed in the world," said Dr. David Dilcher, a paleobotanist at the Florida Museum of Natural History in Gainesville. "They have organized the behavior of animal pollinators in such a way as to accomplish their own genetic exchange." For their part, the pollinators have benefited from the exploitation, and they evolved all sorts of methods for extracting as much nutrition as possible from their floral seducers.

Flowering plants fared brilliantly once they appeared on earth, and during the Cretaceous period they diversified wildly, to the point where there are now about 250,000 species of angiosperms, compared with fewer than 15,000 remaining varieties of fern, conifers and other gymnosperms.

Despite this impressive multiculturalism, angiosperms almost surely are all derived from one ancestral line. "They have too many complicated features in common for them to have developed those features independently," Dr. Donaghue said. The Magnolia Theory

The reason scientists have long assumed the first angiosperms were like magnolias is a mix of rational analysis and habit of mind. Magnolias possess many properties that seem quite primitive, including their method of conducting water; they share features with some extinct and very ancient gymnosperms, and a number of the indisputable fossil flowers from around 110 million years ago do look like magnolias.

Paleobotanists cannot yet dismiss the magnolia from its position as the earliest flower, but they are gathering enough evidence to cast extreme doubt. For one thing, after long bemoaning the scarcity of fossilized flowers, paleobotanists have lately been unearthing a wealth of such fossils, some of them older than the confirmed magnolia-like fossils.
Most of these whispery etchings in rockface display extremely tiny blooms, a millimeter or so across. Significantly, the flowers are simple and unisexual, the original wallflowers, rather than intricate and bisexual as the magnolias are.

For another reason, botanists have lately embraced the science of cladistics, a discipline that has forced a re-evaluation of many assumptions about how different plant groups are related. In cladistics, biologists cannot merely say two organisms look reasonably similar and therefore are likely to be related, as taxonomists have in the past; they must spell out precisely which features link one family to another.

For a cladistic analysis of plant origins, botanists must describe the outgroup: the particular type of nonflowering plant that is the closest relative of all to an angiosperm. They must say whether it is the gingko tree, the conifer, the fern, or whatever, that is most like the flowering plants, and they must say why.

"With cladistics you can't just say I think the primitive angiosperms looked like X," said Dr. P. Mick Richardson of the Missouri Botanical Garden, who is coordinating the symposium. "You have to say, I believe they looked like this because so-and-so is the outgroup. You put your money where your mouth is so others can see where you made your mistakes."

Using this type of analysis, paleobotanists have defined several possible outgroups, the closest gymnosperm cousins of the angiosperms. Most significant among them is the Gnetales (pronounced knee-TAIL-ees), a class of plants that has largely disappeared but that still claims some survivors, including ephedra, the plant that gives rise to the active ingredient in Sudafed, the antihistamine. Bad Times for Gnetales

During the mid-Cretaceous, the Gnetales were thriving right alongside the angiosperms; some even relied on insect pollinators, probably beetles. But as the environment worsened during the late Cretaceous, said Dr. Crane, the Gnetales began dying off while the angiosperms continued their relentless ascendance.

"Something made it bad to be a Gnetale, but we're not sure what that something was," he said.

Comparing angiosperms to these outgroups, researchers have surmised that the first flowering plants were more like today's herbs and grasses than like a bushy flower tree. Further detailed examination of fossilized and living plants has led to conjectures of either the black pepper or the water lily as possible models for the earliest angiosperm, although the founding plant would still have been significantly different from either of the modern descendants. The earliest pollinators of these plants were most likely small beetles, wasps or some type of aquatic insect, rather than the bees that might have feasted on magnolia pollen.

Molecular biologists have begun adding their perspective to the quandary. Dr. Elizabeth A. Zimmer of the Smithsonian Institution in Washington has examined a particular stretch of so-called ribosomal genetic material, comparing the sequences of that stretch in 75 angiosperm and gymnosperm species to see how much the sequence differs from one to
another. Her work also suggests the herbal family is the oldest, and that perhaps the water lily is the mother of all angiosperms.

But Dr. Mark Chase of the University of North Carolina in Chapel Hill and colleagues have examined another genetic sequence in 500 different species, and they believe that the ceratophyllum, or hornwort, is the most ancient line of angiosperms.

This plant is found in freshwater ponds and lakes, where it grows to 15 feet in length, lacks roots, has tiny, hooked leaves and produces spiny little fruits. It resembles no other living flowering plant, and Dr. Chase said that it had become so specialized over time for its watery niche that it did not reveal much about what it, as a progenitor angiosperm, might have looked like 200 million years ago or longer.

"It's a wonderful finding but it's an unsatisfactory finding," he said. "It doesn't necessarily tell us what the ancestral flowering plant looked like. To answer that one, I think we still need a bit more inspiration."
Although most species of plants on Earth have flowers, the evolutionary origin of flowers themselves are shrouded in mystery. Flowers are the sexual organs of more than 360,000 species of plants alive today, all derived from a single common ancestor in the distant past. This ancestral plant, alive sometime between 250m and 140m years ago, produced the first flowers at a time when the planet was warmer, and richer in oxygen and greenhouse gases than today. A time when dinosaurs roamed primeval landscapes.

But despite the fact dinosaurs went extinct 65m years ago we have a better idea of what an Iguanodon looked like than of how the ancestral flower was built.

The oldest flowering fossil, a 130m-year-old aquatic plant found in modern day Spain. This is partly because these first flowers left no traces. Flowers are fragile structures that only in the luckiest of circumstances can be transformed into fossils. And, as no fossil has been found dating back 140m or more years, scientists have only had a limited sense of what the ultimate ancestor would have looked like. Until now.

A major new study by an international team of botanists has achieved the best reconstruction to date of this ancestral flower. The research, published in Nature Communications, relies not so much on fossils as on studying the characteristics of 800 of its living descendant species.

By comparing the similarities and differences among related flowering plants, it is possible to infer the characteristics of their
recent ancestors. For example, because all orchid species have flowers in which one half is the mirror image of the other (bilateral symmetry), we can suppose that their ancestor must have had bilateral flowers. By comparing those recent ancestors to each other it is then possible to go a step further back in time, and so on, until eventually we reach the base of the flowering plants’ family tree.

Orchids are symmetrical. Joanna Dineva

**So what did it look like?**

In some respects, the original flower resembles a modern magnolia: it has multiple, undifferentiated “petals” (technically tepals), arranged in concentric rings. At its centre there are multiple rows of sexual organs including pollen-producing stamens and ovule-bearing ovaries. It is hard to resist the temptation to imagine ancient pollinators crawling in this flower, collecting pollen grains while unknowingly helping the plant to produce seeds.

The ancestor of magnolia. And oak trees, grass, tomatoes, daffodils, and much more. Hervé Sauquet & Jürg Schönenberger

**A controversial sex life**

The new study helps to settle the controversy about whether early flowers had separate sexes, or whether both male and female reproductive organs were combined in the same flower. Previous evidence pointed to different answers. On the one hand, one of the earliest diverging lineages of flowering plants, represented nowadays only by a rare shrub from the Pacific island of New Caledonia called *Amborella*, has flowers that are either male or female. On the other, most modern species combine both sexes in the same flower.
All living flowers ultimately derive from a single ancestor that lived about 140m years ago. Hervé Sauquet & Jürg Schönberger

The authors of the study settle the question and show that the ancestral flower was a hermaphrodite. This means that early flowering plants could reproduce both as a male and a female. Combined sexes can be advantageous when colonising new environments as a single individual can be its own mate, and indeed many plant species colonising remote oceanic islands tend to be hermaphrodite. Maybe the combination of sexes helped early flowering plants to outcompete their rivals.
The devil’s in the detail

Despite the apparent similarity with some modern flowers, their ultimate ancestor has a few surprises up its sleeve. For example, botanists have long thought that early flowers had floral parts arranged in a spiral around the center of the flower as can be seen in modern species such as the star anise.

The new reconstruction, though, strongly suggests that early flowers had their organs arranged not in a spiral, but in series of concentric circles or “whorls”, as in most modern plants. The early flower had more numerous whorls, however, suggesting flowers have become simpler over time. Paradoxically, this simpler architecture may have given modern plants a more stable base upon which to evolve and achieve more complex tasks such as sophisticated interaction with certain insects as in orchids, or the production of “flower heads” made of dozens or hundreds of simpler flowers as in the sunflower family.

Although now we have a good idea of what one of the earliest flowers may have looked like, we still know little about how that flower came to be. The detailed steps leading to its evolution are unknown. Perhaps we will have to wait for the discovery of new fossil flowers spanning the gap around 250m-140m years ago, before we can understand the very origin of what is the most diverse sexual structure on the planet.

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