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Sex among the Flowers

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Abstract: The recent breakthroughs in reconstructing early angiosperm evolution and diversification have come from work in three interconnected fields of evolutionary biology: paleontology, phylogenetics (the analysis of the genealogical relationships of life), and morphology (the study of the development and structure of organisms). All in all, those paleontological findings are remarkable, particularly in light of the assumption, which prevailed through most of the twentieth century, that the first flowering plants had moderately large, multipart flowers with a conspicuous perianth-the one morphology consistently absent from the earliest fossil record of flowers.

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A bouquet of botanical breakthroughs is shedding light on the exuberant evolution of the earliest flowering plants and their mysterious sexual history.

In an oft-quoted letter written in 1879, Charles Darwin confessed, with his usual candor, that the "rapid development as tar as we can judge ot [flowering plants] within recent geological times is an abominable mystery." In fact, through much of Darwin's later life, he was keenly interested in and vexed by the evolutionary origin of flowering plants, or angiosperms. In 1875, for instance, Darwin confided to a colleague that the "sudden appearance of so many [angiosperms] in the [Cretaceous period] appears to me a most perplexing phenomenon to all who believe in any form of evolution, especially to those who believe in extremely gradual evolution." Even just months before his death in 1882, Darwin continued to maintain that "nothing is more extraordinary in the history of the Vegetable Kingdom .. . than the apparently very sudden or abrupt development of the [flowering plants]."

Darwin's frustration stemmed, in large part, from the remarkably rapid origin and diversification (as shown by the fossil record) of flowering plants within a brief period of earth's history-and bis own strong views that evolutionary change was typically a slow and gradual process. Darwin was convinced that the origin of angiosperms was one of the great challenges in the effort to decipher the evolutionary history of life.

What so impressed him remains impressive today: how some 250,000 species of flowering plants have, come to dominate the earth's vegetation.They flourish in the tropics and in the arctic, in alpine terrain, as well as in deserts and lakes. They range from mighty oak trees to woody and herbaceous vines, from underground parasites to carnivores that prey on insects, from floating aquatics to epiphytes (plants that live on other plants), such as orchids and bromeliads. Darwin was also astute enough to recognize the importance of a question that intrigues evolutionary biologists today: how to square such diversity with the fact that flowering plants are tar and away the youngest major lineage ot plants.Their evolutionary origin can be traced in the fossil record to the Early Cretaceous, some 130 million years ago. In contrast, conifers had a head start of more than 170 million years. By all measures, angiosperms have diversified to a greater extent and in a shorter time than any other group of plants.

What were the progenitors of angiosperms? What did the first ones look like? How did their many unique biological features evolve? Why did the origin and early diversification of flowering plants proceed so rapidly? To shed light on such questions, I have studied extant plant species belonging to the same ancient flowering plant lineages that flourished in the days of dinosaurs. My findings, together with the recent work of other botanists, indicate that many of the century-old assumptions about the biological features of the first flowering plants and the subsequent diversification of early angiosperms are fundamentally wrong.

Like gymnosperms, angiosperms propagate via seeds, which house and nourish the developing embryo. Hut unlike gymnosperms, whose seeds are exposed to the environment (in cones, for instance) angiosperms envelop their future seeds in one or more protective structures called carpels. The word "angiosperm," the botanical name for flowering plant, comes from the Greek words tor "vessel" and "seed."

The recent breakthroughs in reconstructing early angiosperm evolution and diversification have come from work in three interconnected fields of evolutionary biology: paleontology, phylogenetics (the analysis of the genealogical relationships of life), and morphology (the study of the development and structure of organisms).

The fossil record remains silent about the ancestors of flowering plants, just as it was in Darwin's day. Such a lack of data has been an important obstacle to understanding the origins of flowering plants, fortunately, in the past decade, paleontologists-by digging, hammering, and sifting through layers of Early Cretaceous fossils-have radically expanded knowledge of how the earliest flowering plants diversified. Armed with soil sieves and microscopes (or hand lenses), paleobotanists have discovered thousands of fossil flowers, seeds, and fruits, exquisitely preserved in all three dimensions at sites around the world. Those primeval forms were fossilized nearly instantaneously through a process ot charcoalitication. In essence, they were toasted to a hard consistency by proximity to a tire and dropped into sediments that still cling to the banks of rivers.

It is now evident that within just a few million years of their origin, an astonishing array of floral and vegetative morphologies had evolved among flowering plants. Paleobotanists have discovered early flowers resembling those of water lilies, star anise, members of the Chloranthaceae, the magnolia order, the buttercup order, monocots and more. Other early angiosperm flowers are sufficiently different from those of extant lineages to represent groups now long extinct.

Most people think of a flouer as having four basic parts or organs: sepals and petals (the sterile parts of the flower that together make up the "perianth"), stamens (the pollen-producing "male" organs), and carpels (the seed-producing "female" organs). Although we rend to be drawn to flowers because of their often showy petals, the earliest fossil flowers either lacked a perianth or had an inconspicuous perianth made up of morphologically similar parts culled tepals. All of the earliest fossil flowers were small, on the order of a few millimeters, and rather undistinguished. Those fossil discoveries confirm the recent hypothesis made by the floral morphologist Peter K. Endress of the University of Zurich: that sepals and petals evolved after angiosperms began to diversify.

Although most Early Cretaceous flowers were hermaphroditic (with both stamens and carpels), some species had individual flowers that included only stamens (male function) or only carpels (female function). In some cases a single stamen constituted the entire flower-definitely not corsage material!

All in all, those paleontological findings are remarkable, particularly in light of the assumption, which prevailed through most of the twentieth century, that the first flowering plants had moderately large, multipart flowers with a conspicuous perianth-the one morphology consistently absent from the earliest fossil record of flowers.

Following on the heels of that wealth of newfound fossil data, advances in phylogenetic theory and data analysis have opened a second major front in the effort to decipher the early evolution of angiospcrnis.

Throughout most of the twentieth century, a broad consensus emerged that angiosperms evolved from magnolia-like plants. Then in the late 1990s. DNA analyses dethroned them, and crowned two other lineages as the most ancient living exemplars of angiosperms: the amhorella family (with a single species of small trees endemic to New Caledonia, Amborella trichopoda) and the Nymphaeales (water lilies, numbering about seventy species). Both or those lineages began to evolve before the origin of the three groups of flowering plants that dominate today: the nionocots. the eudkots, and the eumagnoliids.

Once botanists realized their studies of the earliest flowering plants had been rbcusing on the wrong groups, plant morphologists intensified their studies of the poorly known biological features or A. trichopoda and the water lilies. But in interpreting their findings, a note or caution must be sounded. Can one make valid inferences about the flowering plants or the distant past from studies of extant members of ancient flowering plant lineages? Can the modern plants really he regarded as "living fossils?" The answer to both questions is yes, and no. All organisms, ourselves included, are an amalgam ot ancient and more recently evolved biology. So only some of the biological features ofAinhorcllti and water lilies can help clarity the early evolutionary history of flowering plants.The A. trichopoda plants growing in New Caledonia today are 130 million years removed from the earliest angiosperms, as are the water lilies that grace lakes worldwide.The key to the study of so-called "ancient lineages" of flowering plants is to identity those biological features of the extant members of the lineage that have been inherited from the earliest flowering plants themselves.

Even the two most ancient lineages of flowering plants have undergone substantial changes in their evolutionary history. The best current evidence is that the earliest angiosperms were small, tropical understory trees that produced small hermaphroditic flowers. In other words,although today's water lilies are aquatic, their ancestors were not. And although today's A. trichopoda are dioecious, that is, their male and female parts are borne on different plants, their precursor plants have parts of both sexes.

In particular, in the case of the amborella lineage, unisexual plants evolved at some point between its divergence from all other flowering plants 130 million years ago and the origin of the sole extant species, A. trichopoda (which may even be a relatively young species). Despite that change, A. trichopoda retains "primitive" characteristics in that it lacks differentiated petals and sepals (it has tepals).

In my laboratory in the late 1990s-practically before the ink was dry on the new phylogenics-my colleagues and I began to investigate the reproductive features of Amborella, water lilies, and members of other extant ancient angiosperm lineages. One of the biggest questions about the origin and early evolution of flowering plants arises from the unique way they nourish their progeny. Inside the seed of every flowering plant are two closely integrated partners in the reproductive process: an embryo that will develop into the next generation of plant, and an entity called the endosperm. Endosperm is a tissue that forms alongside the embryo, acquires nutrients from the maternal plant, and subsequently passes the nutrients along to the developing embryo.

Although endosperm may seem tar removed from people's day-to-day lives, nothing could be further from the truth.Two-thirds of human caloric intake worldwide is endosperm. Endosperm accounts tor most of what is the edible grain of rice and wheat, most of the kernel of corn, even the milk and meat of a coconut.

It is no wonder that many kinds of endosperm taste good and are nutritious; endosperm is tilled with nutrients that, barring human intervention, would have nourished a plant embryo. Without endosperm, human evolution might have proceeded very differently-or not at all. The diet of early humans on the savannas of Africa probably included many kinds of grains that were, essentially, endosperm. The initial cultivations of maize in the New World and wheat in Eurasia were central to the development of human agricultural practices thousands of years ago.

Angiosperms are the only plants to nourish their embryos with endosperm. What makes endosperm so unusual and distinct from the embryo-nourishing tissues of any other plants is that it, like the embryo. develops only after being fertilized [see illustration on page 53]. The fertilization event takes place at the same time as the egg is fertilized. Hence the process is known as "double fertilization." and it is unique to flowering plants.Typically, endosperm begins growing when one of the two sperm carried by a pollen grain fuses with two "polar nuclei" within the future seed.The other sperm fertilizes the egg. The result is that each endosperm nucleus typically carries three sets of chromosomes (hence it is "tnploid") and is genetically biparental.

By contrast, in all other plants the tissue that nourishes the embryo carries only one set of chromosomes (hence it is"haploid") and is derived solely from the maternal plant. Evolutionary biologists regard the biparental genetic endowment of endosperm nuclei as a potential major advantage because an extra set of genes from a second parent confers hybrid vigor on the tissue. That hybrid vigor may have been a critical factor in enabling flowering plants to reproduce more quickly than their ancestors, which in turn may have enabled angiospenns to move into ecological niches not already occupied by other plants.

But bow did plants shift from embryo-nourishing tissue that was haploid and genetically maternal to the more vigorous tissue that is triploid and genetically biparental? For more than a century, that question has remained unanswered. About twenty-five years ago, a few geneticists suggested that the endosperm of flowering plants had evolved through a diploid stage. Hut there was no evidence: almost all flowering plants have triploid endosperms. Of course, it was possible that an ancient lineage of flowering plants bearing a diploid intermediary stage had gone extinct.

Armed with the new phylogenics, Joseph H. Williams, a botanist now at the University of Tennessee in Knoxville, several of my students, and I began an intensive study of fertilization and endosperm in Nymphaeales (water lilies) and members of other ancient angiospenn lineages such as Illicium (star anise) and Austrobaileyales. To our surprise, we found that endosperm begins to form after the fusion of a sperm with a single haploid female nucleus in members of the Nymphaealesand Austrobaileyales. The result is diploid, genetically bipareutal endosperm. It looked as though we had discovered a missing link-a diploid intermediate step-between the haploid, genetically maternal, embryo-nourishing tissues in the ancestors of flowering plants and the triploid, genetically biparental endosperms of most flowering plants.

If only we had left well enough alone!

Two years ago I finally began to explore the reproductive biology of amborella.There had been hints in the past that its endosperm might be triploid, like that of most other flowering plants. My work confirmed that it was, in contrast with the diploid star anise. Because Amborella represents a lineage more ancient than Nymphaeales or the Austrobaileyales, the conceptually satisfying identification of a potential missing link in the two younger groups was called into question. Two equally plausible scenarios emerged from that research. Perhaps endosperm was originally diploid, and the amborella lineage and most other angiosperms separately became triploid. Or perhaps endosperm started oft triploid, at least in the common ancestor of all extant angiosperms. If the latter was the case, the diploid endosperms of water lilies and the relatives of star anise evolved by eliminating one of the two sets of chromosomes from the mother plant. Sometimes, more data lead from a clear-cut hypothesis to several alternative evolutionary explanations, none of which is provably better than the others. Such is the life of an evolutionary biologist.

Another line of investigations has led to similarly intriguing complications. As I was examining the reproductive process in A. trichopoda, I discovered that the species differs from all other flowering plants in the way it forms an egg cell. The feature was extremely subtle, and it took nearly two years of data collection and analysis to become certain of the details.

The way gametes (eggcells and sperm cells) form in plants is highly conservative; evolutionary innovation is rare. In all plants except the angiosperms the formation of an egg cell is "indirect": the egg is one of the daughter cells from a cell division of the so-called egg-mother cell, (for unknown reasons the other daughter cell eventually degenerates.) In contrast, all flowering plants form egg cells directly. There is no egg-mother cell or final cell division.

All flowering plants, that is, except A. trichopoda. When it comes to making an egg cell, A. trichopoda behaves like all nonflowering plants: it first forms an egg-mother cell that divides to produce an egg and a sister cell that eventually degenerates. Here. then, is a potential missing link between flowering plants and their nonflowering ancestors.

Or is it? It is also possible that the first flowering plants formed their egg cells directly, and that sometime along the 130-million-year-long path to A. trichopoda, this lineage reverted to (or convergently evolved) indirect egg-cell formation. Each explanation is A good fit with the known data. For now. there is nothing to rule out any of these hypotheses.

The two recent embryological discoveries-diploid endosperm in Nymphaeales and Austrobaileyales, and indirect egg-cell formation in Amborella-may one day gain satisfactory evolutionary explanations. Yet, no matter what the explanations, one thing is certain: these findings demonstrate that the reproductive biology of ancient angiosperm lineages is tar more diverse than botanists had ever dreamed.

Taken together, the discoveries strongly suggest that within the first 15 million years of angiosperm history more structural and developmental innovations evolved than during the preceding 230 million years of seed-plant evolution. In essence, angiosperms broke the mold.

And so, to return to the question I asked at the beginning of this article, what accounts tor this biological revolution? Why, nearly 230 million years after the establishment of slowly evolving seed-bearing plants, did so many biological innovations appear among angiosperms in such a brief period of time?

Many ideas have been put forward over the years. The French paleobotanist Gaston de Saporta, in his correspondence with Darwin, first suggested that the rapid pace of angiosperm diversification was a result of the co-evolution of showy flowers and insect pollinators. Many biologists have pointed to the potential advantages of a genetically biparental endosperm, as I mentioned earlier.

Recently botanists have discovered evidence of n "whole-genome duplication" among the inimediate ancestors of flowering plants. It the first angiosperms had an extra, redundant genome, it would have provided an entire set of genes that were no longer constrained to perform their previously necessary biological roles. Instead, they could have served as raw materials for evolutionary experimentation at the molecular level, significantly enhancing the potential for biochemical and structural innovations.

In the final analysis, modern biologists must still live with Darwin's assessment: the rapid and extraordinary diversification of flowering plants within recent geological times is "perplexing" and "mysterious." In spite of recent breakthroughs, it remains difficult, if not impossible, to fathom the myriad causes for such rare periods of rapid evolutionary diversification and innovation during the history of life.

Is that a problem? Hardly. It is a fair reminder that reconstructing evolutionary history is not always simple or straightforward. It is, however, always enjoyable-a statement with which Darwin, vexed as he was by the angiosperms, would surely agree.

Sidebar

Claude Monet, Water Lilies: Green Reflections (detail), ca. 1914-26. The painting celebrates one of the world's most familiar flowers. Water lilies are also among the most ancient flowering plant lineages on earth, having thrived since the age of the dinosaurs.

Sidebar

Evolutionary "family tree" depicts the relations among the lineages of flowering plants, reconstructed on the basis of recent DNA analysis. Amborella and its ancestors have now supplanted a magnolia-like group as the lineage thought to be the most ancient among flowering plants.

Sidebar

Hypothetical flower of the ancestral angiosperm (at right, top) looked quite different from the flowers most people think of today. It lacked petals and was just a few millimeters across. Its coloring is unknown. The distinction between sepals and petals characteristic of most modern flowers evolved after angiosperms began to diversify (near right). Like most modern flowers, the archetypal flower was probably a hermaphrodite: it possessed both female parts (carpels) and male parts (stamens). Yet the flowers of modern Amborella, the only living member of the most ancient extant lineage of angiosperms, are unisexual (far right). The flowers are not all drawn to the same scale.

Sidebar

Amborella plants living in New Caledonia today may bear the closest resemblance among modern plants to the first angiosperms-though which features of the modern plant are ancient and which developed more recently is often hard to tell. The flowers are just a few millimeters across; the ones in the photograph are magnified 20X.

Sidebar

Shifts in fertilization among three plant groups may hold a key to understanding the evolution of flowering plants. In nonflowering seed plants such as the conifers (top row), one of two sperm released by a pollen tube fertilizes an egg cell in what will become the seed and forms an embryo. The conifer's embryo-nourishing tissue is haploid, that is, each of its cells has one set of chromosomes. What makes most angiosperms unique in the plant world is double fertilization (bottom row). Once the tip of the pollen tube reaches a helper cell called a synergid, one sperm from the tube fertilizes an egg cell, and a second sperm fertilizes two female "polar nuclei" near the egg cell. That second fertilization initiates the growth of the embryo-nourishing tissue, known as endosperm. Endosperm in most angiosperms is triploid, that is, each of its nuclei has three sets of chromosomes. Nuphar (middle row), a member of the ancient angiosperm lineage of water lilies, may be a missing link between seed plants such as conifers and most angiosperms. Its endosperm is diploid (each of its nuclei has two sets of chromosomes), the result of the fusion of a sperm with one rather than two female polar nuclei.

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WILLIAM E. FRIEDMAN ("Sex among the Flowers," page 48) has spent twenty-five years pondering Darwin's "abominable mystery"-the broad and rapid diversification of flowering plants since they appeared 130 million years ago. Friedman earned his Ph.D. in botany at the University of California, Berkeley, and he teaches ecology and evolutionary biology at the University of Colorado, Boulder. He is also the principal investigator of a National Science Foundation Research Coordination Network called MORPH (Molecular and Organisinic Research in Plant History). Friedman has lectured worldwide on topics ranging from the evolutionary history of photosynthetic life to the history of evolutionary thought before Charles Darwin.

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