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The Abominable Mystery of The First Flowers: Clues from Nebraska and Kansas

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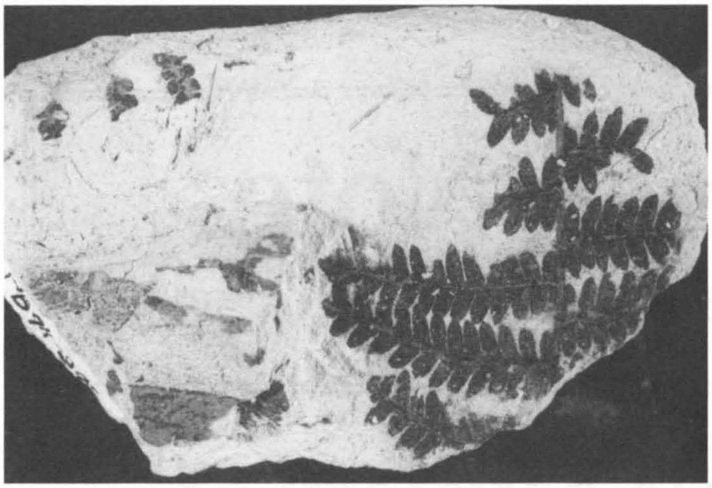
The plant fossils found in shales and sandstones of the late Cretaceous age Dakota Group in Nebraska and Kansas figure prominently in the "dramatis plantae" of the long-running and still unsolved mystery of the origin of flowering plants (angiosperms). This mystery has many fans because almost all of the plants that humans depend on for food and shelter are angiosperms; half of the calories in the world's diet come from the grass family alone. The Dakota fossils were discovered by western science more than one hundred years ago during the early stages of geological exploration of the western territories. The discovery of 100 million year old, late-Cretaceous leaves that had the shapes, sizes, and outlines of modern trees such as sassafras (*Sassafras*), magnolia (*Magnolia*), rubber tree (*Ficus*), and willow (*Salix*) astounded nineteenth century scientists. Although they had some reservations about the identifications, these early paleobotanists assigned many of the leaves to modern genera. These almost modern flowering plant leaves seemed to appear suddenly in the mid-Cretaceous and, with amazing geological rapidity (10 - 20 million years), preempted the leading role in the world's flora. All reports of flowering plant fossils at or before the beginning of the Cretaceous, 138 million years ago, are doubtful. However, by the end of the Cretaceous, 9 out of every 10 vascular plants were angiosperms. (Now there are 250 species of flowering plants for every species of gymnosperm.) There was no geological warning of this change in the cast of vegetational players, no prominent understudy (or understory) roles that signaled that flowering plants were to be the stars of the future. These upstarts replaced the cast of conifers, ginkgoes, seed ferns, cycads, cycadeoids (all gymnosperms), and ferns that had composed the floristic company for the previous 150 million years. Charles Darwin called the questions of when and where flowering plants arose and why and how they so quickly stole the limelight in the plant part of

Collection manager Charles Messenger excavating plant fossils at Rose Creek.



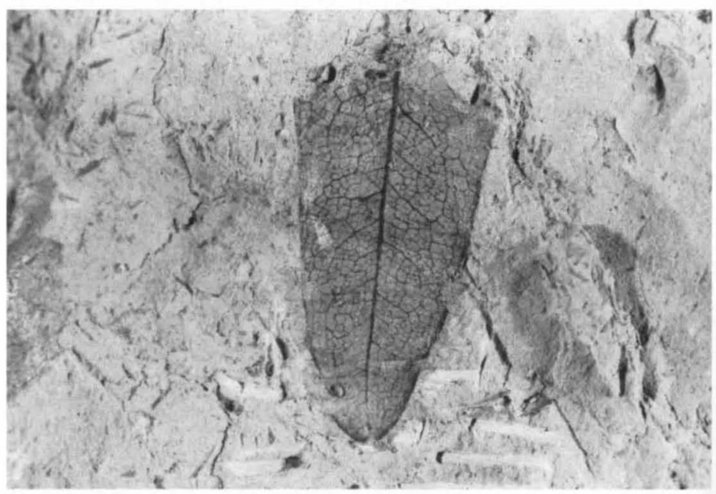
Ferns dominated the swampy areas during most of the Cretaceous.

the evolutionary stage an "abominable mystery." The leaf fossils of the Dakota Group in Nebraska and Kansas figured prominently in this mystery because they provided one of the oldest records of a flora in which flowering plants out-numbered the ferns, conifers, and cycads.

The mystery of the origin of flowering plants was and still is complicated by the lack of any obvious candidates for next-of-kin for the group. The immense variation within angiosperms makes it difficult to find characters that are common to all angiosperms but that are lacking in any other seed plants. Perhaps the best character, the nature and developmental origin of the nutritive tissue that feeds the embryo seed (the endosperm), is extremely unlikely to leave fossil traces. As a result, no one has been able to find a living or extinct group of seed plants that shares enough of the features that best describe angiosperms to be generally accepted as the missing link.

Several theories have been proposed to explain the apparent lack of flowering plant ancestors and their sudden appearance in nearly modern form. For many years the most popular theory explained the lack of fossil intermediates between gymnosperms and angiosperms by hypothesizing that angiosperms evolved in regions where fossilization was unlikely and/or that the group of ancestral angiosperms underwent a burst of evolution that was so astoundingly rapid that no fossils were left behind. After the super-speed evolution of the new stars of the plant kingdom, they sprang forth almost fully developed to assume the leading role on the vegetational stage and to receive rave reviews from the great evolutionary critic. Luckily for us, the flowering plants have yet to receive their final curtain call. The favorite staging area for these why-we-don't-find-early-fossils scenarios was mountain uplands; one can almost see an army of stout flowering shrubs (MacBeth's Burnham Woods?) marching down highland slopes to take on the unwary but entrenched ferns and gymnosperms.

The idea that the mid-Cretaceous flowering plants were fully developed and closely related to contemporary angiosperms began to change in the early 1970s because of new results from more intensive studies of fossil pollen and of the details of leaf structure. A reexamination of the early Cretaceous fossil record of Maryland and Virginia showed that the first angiosperm pollen appeared there about 125 million years ago. Over the next 25 to 30 million years the number of different angiosperm pollen types increased steadily as did the structural complexity of these various pollen grains. Similarly, a more complete and extensive comparison of the early Cretaceous fossil leaves and their putative modern counterparts revealed differences in the complexity of the vein organization. The earliest leaves had veins that were more simple and less regularly organized than younger fossil forms or than modern leaves. Significantly, the increase in complexity of the venation of the leaves parallels the increase in complexity and diversity of the pollen. Now, very few early or mid-Cretaceous leaves or pollen types are thought to show a definite relationship with a single modern family, much less any modern genera.

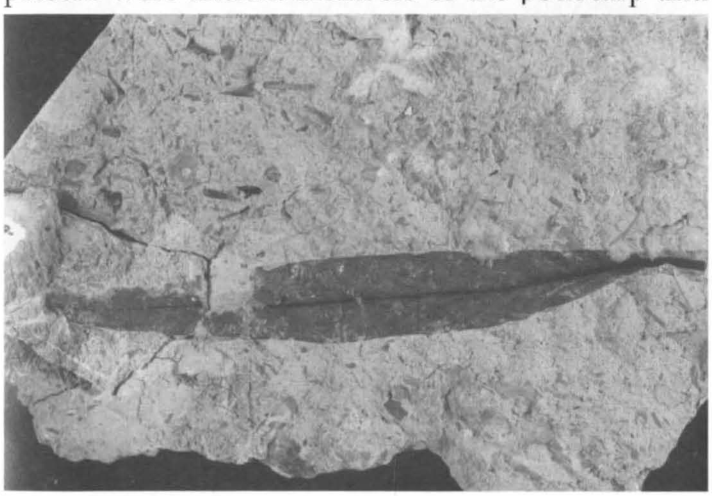


Today, identifications of fossil leaves are based on the details of the vein, tooth, and cuticle structure rather than the shape, size, and outline.

What do the new methods of studying plant fossils tell us about the vegetation of the Dakota Group? What were eastern Nebraska and Kansas like 100 million years ago? In the Central Plains, the Dakota rocks run in a band from southwestern Minnesota, southeastern South Dakota, northwestern Iowa, and eastern Nebraska (Dakota City to Lincoln and Fairbury) to central Kansas, northwestern Oklahoma and northeastern New Mexico.

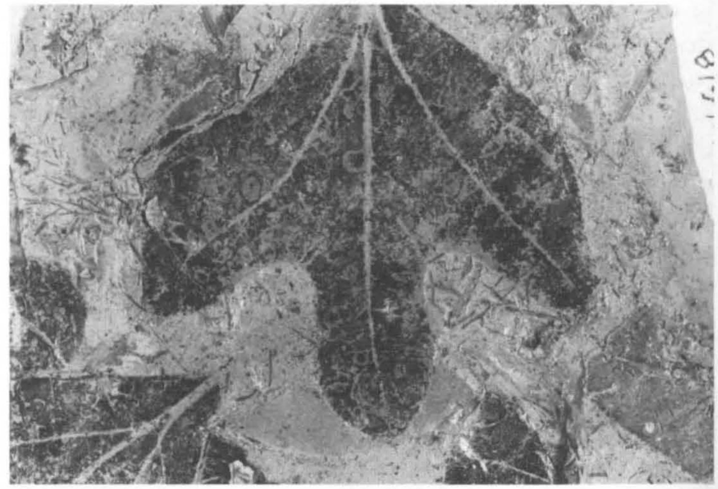
The sediments that became the rocks of the Dakota Group were eroded from Precambrian rocks to the north and east and from Paleozoic rocks to the south. They were deposited in the channels and on the banks of streams that flowed into the lagoons, swamps, estuaries and beaches of an ancient inland sea. This sea, at its greatest extension, reached from the Gulf of Mexico to the Arctic Ocean; it covered most of central to western Nebraska and Kansas during the mid-Cretaceous. This enormous version of the Gulf of Mexico was also the home of the Loch Ness monster-like sea reptiles (plesiosaurs) whose bones are the Central Plains substitute for dinosaurs. Because the late Cretaceous climate was much warmer than that of today, the closest modern analog for the habitat of the Dakota Group is probably the low-lying areas of tropical regions. It seems that rather than charging down from the highlands (enter stage left), the first flowering plants literally had an uphill battle (staggering entrance from stage right) in their campaign to upstage the other plant types.

The kinds of plants in the act that preceded the angiosperms' entrance in what is now North America are fairly well known. The scene that emerges is one of a complex vegetation where each of the major groups of plants seemed to have its own turf (pun intended). In what is now North America, the well-drained and well-developed upland soils were the province of some types of ferns and of the conifers, particularly the ancestors of the pine and redwood families. Other conifers present were ancient members of the podocarp and



Long, narrow leaves of *Crassidenticulum* and *Pandemophyllum* look superficially like modern willows.

Norfolk Island pine families, groups that are now largely restricted to the Southern Hemisphere. The lowlands were the province of other kinds of gymnosperms — the cycads, the vegetatively similar cycadeoids, and the ginkgoes. The swampy and marshy areas were dominated by ferns (not the same ones that grew in uplands), lycopods, and horsetails, and by members of an extinct group of juniper-leaved conifers called the Cheirolepidiaceae. In the 10 million year time span preceding the deposition of the Dakota Group, the percentages of fern, cycad, seed-fern, ginkgo, and conifer leaves in fossil floras drop while the percentage of angiosperm leaves rises from 0% to 50%. However, because the fossil leaf record is more likely to preserve plants that grew

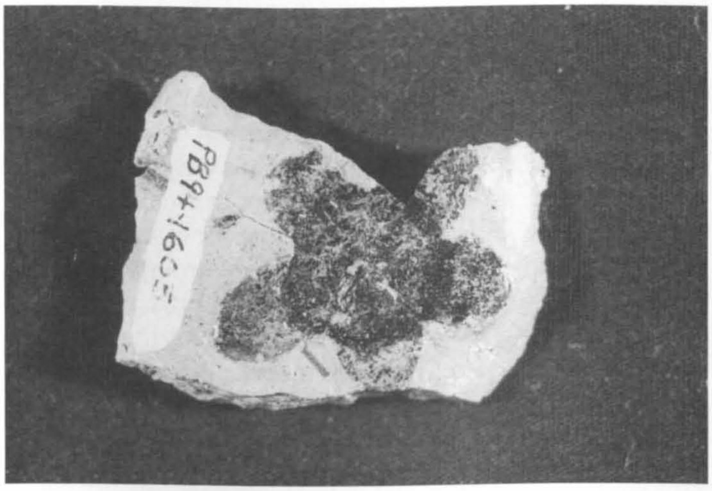


Pabiana, a common leaf at Rose Creek, was first called *Sassafras*.

on stream banks and flood plains, this probably overestimates the numbers of flowering plants. The fossil pollen record for roughly the same time shows that the upland conifers and ferns were holding up well against the first appearances of flowering plants even as the ginkgoes, cycads, cycadeoids, and cheirolepids were left like silent film stars in the age of talkies; some were able to persist in minor roles but most were never to be seen or heard again.

Darwin's "abominable mystery" asked how did the world's flora go from no flowering plants at the beginning of the Cretaceous to modern ones by the time of the Dakota Group, 40 million years later. Current studies on the Dakota Group plants helped solve Darwin's mystery by showing that these fossils are only distantly related to the plants of today. In addition, the Nebraska and Kansas fossils provide clues to the whys and hows of the angiosperm take-over. (Unlike some of their colleagues in vertebrate paleontology and the ancient Greek dramatists, paleobotanists are not as fond of heavenly [deus ex machina] exits for their characters. In general, the flowering plants not only survived but flourished after the "terminal Cretaceous event" [asteroid impact] that some think caused the extinction of the dinosaurs.) The clues come from the fossil plants (pollen, flowers, fruits, and leaves), the fossil animals, and from the geology of the rocks.

One of the Dakota Group localities that has been the focus of several recent studies is in Jefferson County,



The Rose Creek flower has five sepals and petals; only the sepals remain here.

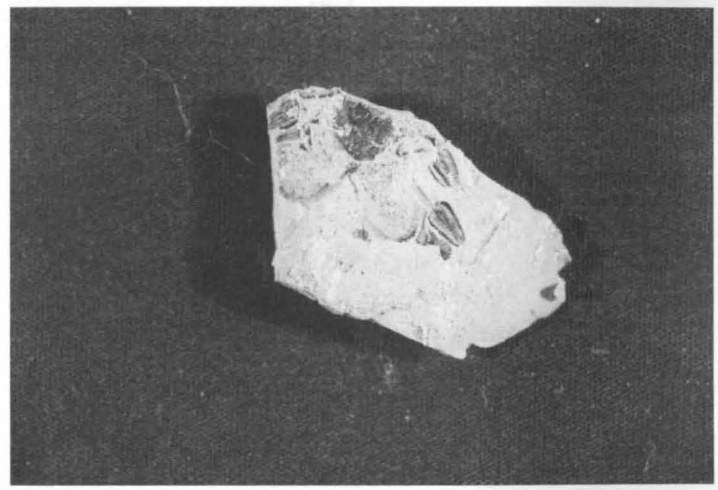
Nebraska. This quarry, called the Rose Creek Quarry because of its proximity to the creek of the same name, has become world-renowned for the abundance of five-petaled fossil flowers that look superficially like those of a wild rose. The floral characters of these fossils can be found, among modern plants, in three orders of the subclass Rosidae. However, none of the three orders (they include plants like roses, spireas, saxifrages, gooseberries, buckthorns, and grapes) share all of the features of the fossil. Other reproductive structures found at Rose Creek include seed cones of a distant relative of modern redwoods and two kinds of small (about 1/4 inch long) seeds or fruits attached to 1 or 2 inch long stems.

The leaves from the Rose Creek Quarry are among the first to receive a thorough study using the new techniques for detailed analysis of the vein patterns, the structure of the teeth on the leaf margins, and the waxy cuticle coating on the leaf surface. This careful work by paleobotanists Garland Upchurch, Jr. and David Dilcher provided more accurate information on how the fossils might fit into classifications based on modern plants. About half of the Rose Creek leaves fit best in the subclass that contains the most primitive modern plants, the magnolias and their relatives (the Magnoliidae).

The easiest way to describe most of the Rose Creek fossil leaves is to compare their shape and outline to those of more familiar trees and shrubs as did the nineteenth century botanists. However, we now know that these superficial shape and size comparisons are contradicted by the details of the vein and cuticle structures, and the names do not imply any ancestor-descendent relationships. Long (1 - 6 inches), narrow, willow-like leaves are one of the more common fossils at Rose Creek; they are grouped under *Crassidenticulum* and *Pandemophyllum*. Other variations within *Pandemophyllum* look like bay leaves, magnolias, or persimmons. A second common leaf is three-lobed like that of the modern sassafras trees; Upchurch and Dilcher named this one *Pabiana* in honor of Prof. Pabian. These leaves range in size from barely an inch long to about 4 inches in length and width. Other fossil leaves look like common house plants; *Landonia* has moderately sized leaves shaped like those of rubber plants or ficus. Another species has leaves that are toothed and palmately 5-lobed resembles aralias; it is placed in the fossil genus *Dicotylophyllum*. *Reynoldsiophyllum* leaves look something like those of holly or myrtle.

Two leaf types from Rose Creek show more similarities with the rosid subclass (the Rosidae) than the magnolids. *Anisodendromum* has compound leaves with long, narrow leaflets like some modern sumacs or buckthorns. *Citrophyllum*, as the name suggests, has simple oval leaves like those of orange or lemon trees.

Important cues and clues to the main plot of the Rose Creek story come from studies of how the floral actors made their exit from this particular stage and from which kinds of animals comprised the supporting cast. Land animals and fish did not make the playbill at Rose Creek; there are no bones from small vertebrates such as mammals, birds, or fish nor fossil imprints of insects.

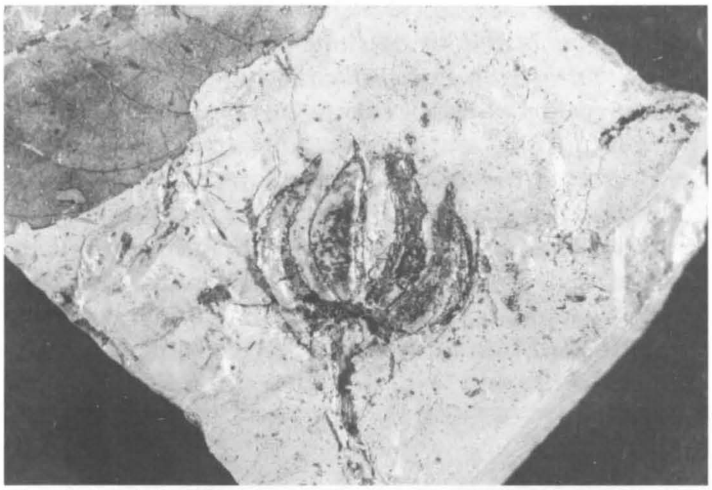


Another Rose Creek flower shows the petals and the stamens.

The only animals that did fit the script were two kinds of thin-shelled aquatic invertebrates, brachidontid clams and vivipared snails. The fact that the shells are thin and the lack of fish fossils suggest that the aquatic background scenery (water) at the site was low in oxygen (dysaerobic).

The stage directions for the exit of the leaves and flowers can be figured out from the positions of the fossils and their state of preservation. The leaves and flowers left the scene on land without the escort of their stems and branches; this suggests that their exit cue was a storm or the changing of the seasons. In their final frame they are flat and well preserved, suggesting that their exit scene was short; they did not travel long distances nor spend much time in the water before they were immortalized in stone. (The Cretaceous was short on Hollywood sidewalks.)

Flowers and fruits found elsewhere in the Dakota Group, in northeast Kansas, include a large magnolia-like flower that develops into clusters of dry, elongated pod-like structures (follicles) with 100 or more seeds (*Archaeanthus*). The leaves of this species looked something like those of tulip trees. Another Kansas magnolia relative is represented by a compact head of more



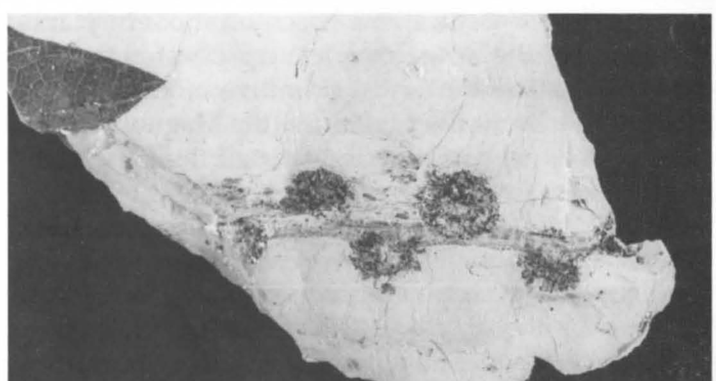
The fruit of the Rose Creek flower is a circle of pod-like follicles.

than 175 small, dry fruits with a split tip (*Lesqueria*). Flowers and leaves from a third subclass of flowering plants, the Hamameliidae which includes trees like oaks, elms, and walnuts, are also found in Kansas. Both the flowers and the leaves show similarities to modern sycamores.

Many theories on why the flowering plants were/ are so successful have been proposed and just about every difference between angiosperms and gymnosperms has been cited as an advantage for flowers. One set of theories emphasizes the evolution of interactions with animals. Most gymnosperms are wind pollinated, a very inefficient way get the pollen from one plant to another. Thousands of grains are lost for every one that lands in the right place and fertilizes an egg. In contrast, angiosperms are often more efficiently pollinated by animals. The flowers and inflorescences that we find so beautiful came about to lure insects, birds, and mammals first to the pollen sources and then on to the pistil and ovules. The seeds of flowering plants encased in their often delicious fruits attract animals who then carry their bounty off and spread the next crop of seedlings. Although some gymnosperms use animals to disperse their seeds (think of the junipers along fence rows where birds have relieved themselves), plants like conifers are amateurs compared to the many and varied contrivances used by flowering plants. For example, birds steal cherries, squirrels bury acorns, cats and dogs carry cockleburs, and humans save the seeds from particularly sweet watermelons.

Other ideas on why the angiosperms came to dominate the world's vegetation emphasize the differences in life cycle, physiology, and anatomy between them and gymnosperms. Flowering plants have the most streamlined life cycle of any land plants; at one extreme they can go from seed to flower to new seed in a few weeks. All other seed plants need years instead of weeks or months to produce a seed crop.

Another major difference is seen in the plant's vascular system, the "plumbing" that carries water from the roots to the leaves and that also forms the plant's skeleton or structural support. The double duties of support and transport for the vascular system require different structures for maximum efficiency. Pipe-like cells with large, empty cross-sections are better for car-



Relatives of the sycamores were among the first angiosperm trees to appear; both leaves and flowers are found in the Dakota Group.

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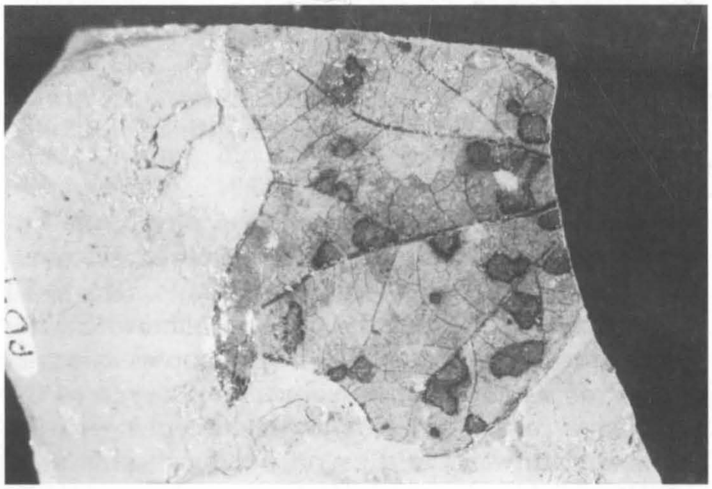
rying water but they are not particularly strong. Thick-walled cells with little or no interior openings provide the best support but they don't carry much water. Flowering plants use a separate kind of cell for each function; they have hollow, thin-walled vessels for efficient plumbing and very strong, thick-walled fibers for support. However, in gymnosperms only one kind of cell is used for both support and water transport. This double duty means that it is not as effective for either purpose. (The thick-walled fibers in the wood of flowering plants make it stronger and harder than the wood of other seed plants; this is why gymnosperm trees are often called softwoods and angiosperm trees are called hardwoods.) With more available water, flowering plants can collect the sun's energy during photosynthesis at a much faster rate for a given leaf surface than can gymnosperms. This is especially important at the seedling stage. Older conifers with several years' growth of needles can be very productive by having many needles; however, young conifers with only one or two year's crop of needles, cannot. In most circumstances, these gymnosperm seedlings will not be able to compete with flowering plants because the angiosperm seedlings have higher rates of energy capture for a given leaf surface. (One botanist has called flowering plants the hares of the flora and gymnosperms the tortoises.)



Like their modern counterparts, the ancient leaves were damaged by fungi and insects.

The accelerated growth and life cycle of angiosperms is enhanced by another anatomical difference: the location of the growing points (meristems), the areas where new cells are formed. Most flowering plants have growth areas that allow them to space their leaves on relatively long stems to gather more light while the leaves of conifers and ginkgoes remain in much tighter clusters on very short stems. Angiosperms have a second growth area for widening the leaves that is lacking in gymnosperms. These additional meristems give flowering plants the ability to generate more leaf surface per year, enough that many angiosperms can afford to throw away the old leaf crop at the end of the growing season.

Together, the accelerated growth and enhanced energy capture of angiosperms allowed the first flowers to invade areas that were frequently disturbed. In particular, they first became abundant on stream banks and flood plains where getting out a seed crop before the sand and mud shifted or the next flood washed the ground out from under the roots was critical. Their success in such areas explains why they are so common in the Dakota rocks that were deposited in exactly these conditions. The fossil record also shows that it was only in rocks younger than the Dakota Group that flowering plants were able to begin their invasion of the parts of the land where foundations were firmer. Yet even where the sands were less likely to shift, the ability of flowering plants to grow quickly would have been an advantage in recovering from other types of disturbances such as being lunched on by a dinosaur, singed by a fire, covered by volcanic ash, or even chilled out by an asteroid impact. Increasingly, evidence from the fossil record suggests that the rapid growth rate of flowering plants was the determining factor in their initial success. However, the evolution of interactions with animals for pollination and seed dispersal became an important factor by the end of the Cretaceous. There is little doubt that these interactions helped the flowering plants diversify in shape, size, and form which, in turn, allowed them to dominate most of the terrestrial plant world.

The new Mesozoic gallery in Morrill Hall will include a video of Museum staff and students from Lincoln and Seward digging up Dakota Group fossils. The filming was done by a crew from Nebraska Educational TV.