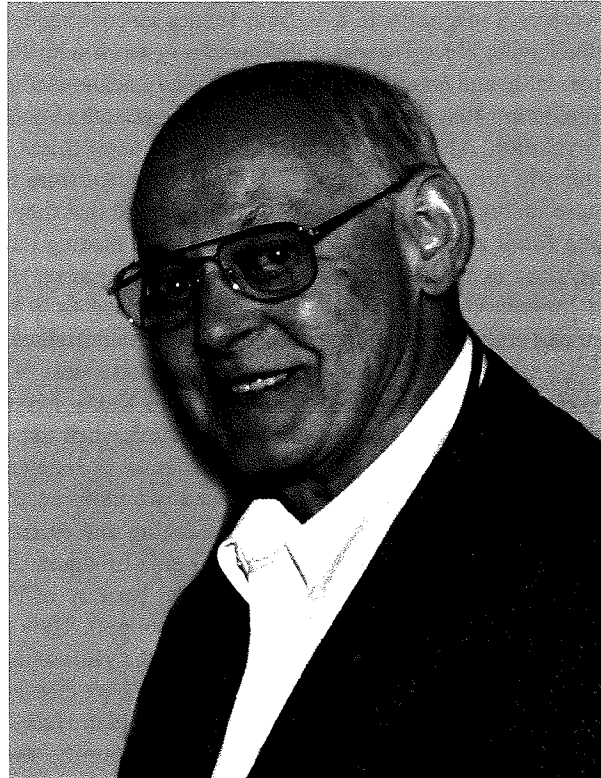


## David Dilcher: An Appreciation



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Gregory J. RETALLACK, Steven R. MANCHESTER & Garland R. UPCHURCH, Jr.

Professor David Leonard DILCHER is renowned for bringing renewed rigor to the paleobotanical study of angiosperm evolution through an emphasis on cuticular anatomy and reproductive morphology. He has gained fundamental insights into the evolutionary biology of flowering plants by focusing on the smallest of details in fossil plants, one species at a time. His originality is striking when viewed within the context of the 1950s and 1960s, a time when the study of fossil angiosperms in North America was dominated by the California school

of paleobotany. The California school documented entire leaf floras and considered their paleoecological, biogeographic, and paleoclimatic implications, but deemphasized the importance of evolution and extinction within individual plant lineages. David DILCHER was also one of the first paleobotanists to challenge the widely held notion that flowers are too rarely preserved in the fossil record to contribute significantly to an understanding of angiosperm evolution. DILCHER's discovery of rare but well-preserved fossil flowers from the Eocene of Ten-

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nessee was followed by continued discoveries of increasingly older fossil flowers from the Cretaceous of Kansas, Nebraska, and northeastern China. This pioneering work has led to the recognition that flowers are, in some instances, abundantly preserved in the geologic record and are treasure troves of information about the evolution and ecology of ancient angiosperms.

David DILCHER was born in Cedar Falls, Iowa, on July 10, 1936. He moved at the age of five to Anoka, Minnesota, where his father found work as a machinist in a factory that supplied cannons to the Pacific Fleet. He was raised with a conservative Christian faith, and entered the University of Minnesota with trepidation that he might be corrupted by the teaching of evolution. Although the subject of evolution was not explicitly presented in his university coursework, he became increasingly aware of its importance to understanding fossil plants and the world around him. Ironically, the class in Evolutionary Biology that David initiated at Indiana University in 1980 was among his most popular and enduring teaching legacies.

When he began his college education at the University of Minnesota in 1954, David DILCHER was unsure of his major. He recalls a personal epiphany, brought on by the observation of sublimating ice, which persuaded him that his future was not in medicine, the ministry nor the military, but rather in the study of natural history. He soon fell under the spell of Professor John HALL, who employed him as a work-study student to make acetate peels from Paleozoic coal balls and prepare pollen from sediment. The name of John HALL often comes up in conversation with David DILCHER; Professor HALL's style of teaching and research was very influential in DILCHER's personal mentoring style with his own students.

David DILCHER made his first visit to the famous Eocene fossil site of Puryear clay pit near Paris, Tennessee in 1959, and was fascinated by the abundance and quality of the well-preserved fossil plants embedded in the clay. These Eocene angiosperm leaves, along with associated pollen and epiphyllous fungi, became the subjects of his master's degree papers on fossil cuticles and pollen at the University of Minnesota in 1960, and later served as the basis for his PhD dissertation at Yale University.

David DILCHER began his PhD work at the University of Illinois in 1961, but when his adviser, Ted DELEVORYAS, secured a new position at Yale University, David accompanied him and was admitted to the PhD program at Yale. Also in 1961, David married his high school sweetheart, Katherine SWANSON. Marrying the class valedictorian turned out to be a very smart move when time came to write, revise and type his PhD thesis. When Professor DELEVORYAS suggested that Kathy should share in the authorship of a publication she replied "I think I will keep publishing under the name I have already been using," by which she meant David DILCHER. Epiphyllous fungi from Puryear, the topic of David's dissertation research, graced the cover of *Science* magazine in 1963. This was

the first of four covers that he has contributed to this prestigious journal over the course of his career. David had a missionary zeal to enlighten the scientific community that paleobotany was real science, requiring more than just a magnifying glass and walking stick. His numerous publications in high-profile journals have done much to raise the profile of paleobotany within the scientific community as a whole.

David's research on the well-preserved fossil leaves from Tennessee continued in 1964 through a postdoctoral fellowship to work with Professor Richard KRÄUSEL, an internationally acknowledged expert in cuticular studies of angiosperms, at the Senckenberg Museum in Frankfurt am Main, Germany. Some of the compressed leaves that David had collected from the Claiborne Formation were so well preserved that they could easily be isolated from the clay matrix, making them prime candidates for maceration in the laboratory. He would sometimes carry one or more of these leaves in his wallet, producing them like business cards to introduce himself and the nature of his research at conferences.

David and Kathy DILCHER moved to Bloomington, Indiana in 1965 when David accepted a position as Assistant Professor at Indiana University. In Bloomington they raised two children, Peter and Ann, as David's career in teaching and research gained momentum. Their life in this small Indiana University town was idyllic, in no small part because of Kathy's quiet competence and unwavering support. They entertained many visitors and students over the years at their two-story home in Bloomington only a short distance by walking from David's laboratory in Jordan Hall. Always welcoming the wider paleobotanical family, the DILCHERS remodeled their basement to include a guest room. In their home they hosted countless students and colleagues from across the country and around the world who came to visit and work in David DILCHER's laboratory. Through their many years in Bloomington, Indiana, and later Gainesville, Florida, David and Kathy were gracious hosts who would regularly invite his students and their families to join them for Holiday dinners and other social occasions, featuring home-cooked meals prepared by Kathy and served family-style around their large dining room table. During such gatherings, David kept the conversation lively and especially enjoyed learning and discussing cultural differences when meeting with students and colleagues from other countries.

For many years the fossils from the Eocene clay pits of Tennessee and Kentucky figured prominently in David's research, and he led many collecting trips there with students and colleagues. Much to the annoyance of his departmental chairman, the paleobotanical collections grew at a rapid pace. Before long cabinets of fossil plants were lining the corridors of Jordan Hall, advertising the need for adequate collection space as well as laboratory facilities to facilitate his expanding research program. David also led student trips to the open cast coal mines

of southern Indiana and developed an excellent collection of Pennsylvanian plants useful both for teaching and research. After 14 years of collecting, the Tennessee clay pits had yielded thousands of fossil leaves as well as a few hundred fossil flowers. These were the subject of a number of papers by David DILCHER and his graduate students on the systematics of Eocene angiosperm leaves.

David DILCHER's leaves from the Eocene clay pits of Tennessee and Kentucky figured prominently in the revolution in angiosperm leaf systematics in the 1970s. Rather than using the 'gestalt' approach that had been the mainstay of earlier research, the new approach emphasized careful description of fossil material and detailed phenetic comparisons with living taxa. In contrast to his contemporaries, Jack WOLFE and Leo HICKEY, who focused on architectural features of the leaf margin and venation as tools for leaf identification, DILCHER emphasized the added value of epidermal anatomy. Leaf cuticles provided a ready source of information on epidermal features that were known to have systematic significance at the level of genus, family, and order in seed plants, including stomatal complex, trichomes, trichome bases, and glands. David estimated that up to 60% of the earlier identifications of Eocene angiosperm leaves from the southeastern US were either incorrect or could not be substantiated. Studies by David DILCHER and his students on the systematics of Eocene leaf megafossils and dispersed leaf cuticles were important stand-alone works that helped point the way towards new approaches to the study of past plant diversity. One approach indebted to this work is the integrated analysis of leaf megafossils and dispersed leaf cuticles across the Cretaceous-Tertiary boundary by WOLFE and UPCHURCH.

Studies on the reproductive biology of angiosperm fossils, previously considered impractical for lack of material, began in earnest in 1973 and were first published in *Science* in 1975. These were conducted with Bill CREPET, David's first "postdoc", who was initially employed as Teaching Coordinator for the Introductory Botany Laboratories at Indiana University. Bill was a big city boy, maladapted to small town living, but he survived and thrived in Bloomington. Studies of the Tennessee fossil flowers soon dispelled the prevailing notion that such fossils were too rare or poorly preserved to be scientifically definitive. The "needles in the haystack" of leaves could be found with time and patience. The study of fossil flowers generated excitement within the field of botany because flowers form the basis for classification in modern angiosperms. In addition, the functional morphology of modern flowers could be used to infer the pollination biology of fossil flowers and, hence, the evolution of reproductive biology in fossil plants. For the Eocene, studies of fossil flowers have yielded new insights into tropical vegetation of the southeastern US, including the abundance and diversity of woody legumes and the high frequency of taxa with wind pollination. For the Cretaceous, studies of fossil flowers have become a

mainstay of systematic paleobotany and document a pattern of rapid diversification and increasing specialization in flower-pollinator interactions.

Another major research initiative that began in 1973 was the evolution of Cretaceous angiosperms. The announcement by Howard REYNOLDS of fossil cuticles blowing in the wind from excavations in the Dakota Formation of Kansas caught the attention of more than one paleobotanist, in large part because that famous fossil flora had previously been known only from unpromising ferruginous impressions. It is a credit to David's diplomacy and persistence that these remarkable fossils found a home in his laboratory. Interest in early angiosperm evolution already had been stirred by the studies of Jim DOYLE and Leo HICKEY on fossil leaves and pollen from the mid-Cretaceous Potomac Group near Washington DC; however, it was the parade of fossil flowers from the mid-Cretaceous of Kansas and Nebraska that became iconic images in textbooks and popular articles. David's interest in reassembling whole plants by bringing together isolated fossil leaves, fruits, flowers, and pollen resulted in popular artistic reconstructions of several different Cretaceous plants as they are thought to have appeared when living, prior to fossilization.

David's success with National Science Foundation funding was already well established, but the five-year grant for study of Cretaceous flowers beginning in 1978 set a new level of funding. Administrators at Indiana University took note as well, and the large teaching lab adjacent to his original office and laboratory was converted entirely to research and student offices. This was a heady time for research, as the expanded facilities drew together a motivated group of postdocs and graduate students. Greg RETALLACK, a brash Australian, Jim BASINGER, a reserved Canadian, and Peter CRANE, a diplomatic Englishman, were postdocs followed in quick succession by Mike ZAVADA and Gary UPCHURCH. Frank POTTER, John ROTH, Steve MANCHESTER, Jay JONES, Ray PFEIFER, Paul GROTE and Pat HERENDEEN were among the PhD students who conducted their dissertation work in the DILCHER laboratory during these "Bloomington years" of the 1970s and 80s. In 1989, David's contributions were formally recognized with his election to the prestigious National Academy of Science. In 1990, David and Kathy DILCHER, David's collection of about 100,000 fossils, his students and assistants, moved en masse to Gainesville Florida, where David became Graduate Research Professor in the Florida Museum of Natural History, at the University of Florida. Attractive features of the new Florida position were the option to continue his work as long as desired, without the threat of mandatory retirement, and the security that it would bring to the fossil collections that he had worked so diligently to build. There had been no assurance of a future for the collections at Indiana University, but the collections of the Florida Museum are considered a permanent archive and resource promoted with funding by the state.

Aside from his professional life, David has had a long-time love of nature that keeps him busy with his home garden and various properties that he purchased including patches of forest and farmland in Indiana, a swamp in Minnesota, and a natural area just east of Gainesville. He delights in touring these properties with students and guests, providing them with highlights of the local flora and ecology (and letting them experience mosquitoes, ticks, chiggers, snakes and alligators, as well!). His Gainesville tract has figured importantly in published research, being used as a sample site for foliar physiognomic transects, coring of recent pond sediments for the investigation of CO<sub>2</sub> changes, and studies of modern pine resin accumulations as an analog for interpreting the microecology of inclusions found in Tertiary amber. David's career has been marked by continuing international outreach, reflected not only in his collaborative publications with authors from many countries, but by the diverse sources of specimens he has contributed to the FLMNH paleobotanical collection. He traveled extensively in Europe, India, Afghanistan, had sabbaticals in Germany, London and Adelaide, and gave lectures in China sponsored by the National Academy of Science. Chinese connections proved especially fruitful with discovery and description with Ge SUN of the very ancient angiosperm *Archaeofructus*, which turned out to beat all expectations as an apetalous emergent aquatic plant. A cooperative arrangement with the University of Utrecht brought greater collaboration between David DILCHER's and Henk VISSCHER's very active laboratories. This collaboration included studies of the Permo-Triassic mass extinction, where abundant fungal spores provide evidence for mass mortality of vegetation. Other collaborative work utilized paleobotanical techniques to assess CO<sub>2</sub> changes as reflected in sub-fossil Recent sediments in Florida. Those following David's career from afar have come to expect the unexpected with each new batch of reprints.

David thoroughly enjoys his role as educator as well as researcher, and makes a point of being accessible to his students. A trademark feature of the DILCHER laboratory is its informality and the feeling that one is part of a large extended family. Despite his busy schedule, David has made it part of his daily routine to exit his office at lunch time and take a seat in the laboratory to eat in the company of his students, post docs, and visiting scholars. There he invites informal discussion on any topic imaginable, ranging from academics and research to the world of politics (e.g. his opposition to the REAGAN and BUSH administrations). Also a bibliophile, he has acquired a magnificent library of books and reprints in paleobotany,

geology, biology, natural history and other topics which he shares freely with students and colleagues. David takes a genuine concern in the well-being of his students. This support is not limited to his own students but extends to other situations where he sees the chance to make a positive contribution; for example by providing personal financial assistance to enable students to attend college who would otherwise not have had the chance.

And as if that were not enough, David DILCHER has tirelessly worked to serve the field of paleobotany and the greater botanical community. He has held a variety of posts within the Botanical Society of America, including President and Program Director. He served as President of the International Association of Angiosperm Paleobotany and Vice President of the International Organization of Paleobotany. David is perhaps the world's best known paleobotanist, serving as an important scientific and cultural ambassador. During the days of the Iron Curtain, he was an important liaison between paleobotanists of the Eastern bloc countries and those of the non-communist world. David has served on a number of panels for the US National Science Foundation and on the editorial boards of several journals, including the American Journal of Botany and Review of Palaeobotany and Palynology. Recently David DILCHER was showcased (along with other paleobotanists) in a television documentary entitled, "First Flower", which examines Darwin's "abominable mystery" of the origin of flowering plants and the search for the oldest fossil flowers.

The occasion of David DILCHER's 70th birthday, which he shared with another great North American paleobotanist Jack WOLFE, was honored by a memorable meeting in Gainesville, Florida. Each participant was presented with a full-color, book-length autobiographical sketch "A curious life" (Shanghai Scientific and Technological Education publishing House, China, 2006), which gives a more detailed account of this remarkable scientist than is possible here. It was a chance to reminisce with many old friends, and relive perhaps the greatest legacy of David DILCHER's career, that we are in a sense family, united by a love of fossil plants.

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