The Multi-Stranded Career of Leo J. Hickey

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Introduction

Leo J. Hickey was born in Philadelphia on 26 April 1940. He attended a minor seminary in Indiana for high school, then earned a B.S. from Villanova University in 1962. Leo went to Princeton University to work on his Ph.D. in geology under the supervision of Erling Dorf, receiving his degree in 1967. After completing his doctorate, Leo was a postdoctoral fellow at the Smithsonian Institution's Museum of Natural History until 1969 when he was hired as a curator in the Department of Paleobiology. In 1982 he left the Smithsonian for Yale University, becoming director of the Peabody Museum of Natural History and professor in the Department of Geology and Geophysics and the Department of Biology. Leo was director of the Peabody for five years, and then returned to research, teaching and work on the Peabody Museum's collections and exhibits. He served as chair of the Department of Geology and Geophysics from 2003 to 2006. Leo remained active in research, teaching and exhibits until shortly before his death on 9 February 2013.

Leo Hickey was an imaginative and iconoclastic scholar whose ideas had wide influence across many areas of biology and geology. In botany, he made fundamental contributions to understanding the morphology, systematics, phylogeny and evolution of flowering plants. In paleontology he carried out groundbreaking studies in paleoecology, paleoclimate, biostratigraphy and the study of mass extinctions. Throughout his 45-year scientific career Leo's most important insights reflected his twin interests in geology and botany, as well as his remarkable depth of knowledge in both fields. Below we outline some of Leo's major contributions, emphasizing a few case studies of his best-known work, including leaf architecture, angiosperm evolution and radiation, early Paleogene plant communities and the extinction and response of plants to the Cretaceous–Paleogene boundary mass extinction event.

Leaf Architecture and Angiosperm Systematics

Angiosperm leaf fossils are abundant in terrestrial rocks of Cretaceous and Cenozoic age, and as a result they were studied early in the development of paleobotany. From the 1820s to the 1940s, leaves were a major basis for interpreting terrestrial paleoenvironments and biostratigraphy. Unfortunately, most fossil leaves were identified by superficial matching of their general form with living genera, which led to inconsistent recognition of morphotaxa and rampant botanical misidentification. As a consequence of this flawed approach, paleoclimate had been misinterpreted, trends in angiosperm phylogeny had been misrepresented and biostratigraphic patterns had been obscured. By the 1960s, the field suffered from a nearly complete loss of credibility.

When Leo entered paleobotany in the 1960s he saw great potential in the fossil record of angiosperm leaves—if they could be recognized consistently and identified successfully. He was writing up his Ph.D. thesis on the Paleocene–Eocene flora of the Golden Valley Formation of North Dakota when it became clear that many of the names that had traditionally been applied to the fossils were botanically incorrect. He later described the horrible sinking feeling that came from realizing he had been building castles on a

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sand foundation. Not given to despair, he devoted himself to what he called a "herbarium crawl" at the New York Botanical Garden, and realized that before the potential of leaf fossils could be tapped he would need to regularize and improve on existing terms for describing leaf morphology, as well as store the vein features of thousands of living angiosperm species in his remarkable visual memory. This survey resulted in his new system of leaf architectural terminology and in the two papers with the largest number of citations recorded on his Google Scholar page (Hickey 1973, 1979).

While working for the Smithsonian Leo recognized that in order to study the leaf architecture of the enormous diversity of angiosperms properly, he had to create a collection of cleared and stained leaves representing the group as broadly as possible, and so he began the National Collection of Cleared Leaves at the Smithsonian Institution. Collaborating with Jack Wolfe of the US Geological Survey, who was amassing a similar collection of cleared leaves, Leo compiled information on leaf architecture for all dicotyledons, which then included magnoliids, water lilies and other basal angiosperms. By mapping vein architectural characters onto the then-current understanding of angiosperm phylogeny, Hickey and Wolfe were able to show that many high-level phylogenetic relationships in angiosperms were supported by characteristic vein patterns. Vegetative morphology, specifically leaf venation and particularly characters of the leaf margin and teeth, did contain systematically informative features—flowers were not the only route to understanding the relationships among flowering plants. The resulting paper (Hickey and Wolfe 1975) is now Leo's third-most-cited publication. In addition to providing new characters supporting some traditional systematic relationships, Hickey and Wolfe also suggested new relationships that had not been inferred from analyses of floral characters alone. They argued for a close relationship between Juglandaceae and rosids because of similarities in tooth venation and leaf organization, a then-controversial idea later confirmed by molecular systematic studies (e.g., Stevens 2001). They also recognized two major subgroups within asterids, though the orders assigned to these subgroups do not correspond exactly to those currently assigned to the two major subclades of asterids. Through much of his career Leo and his colleagues integrated observations of the leaves of living and fossil plants, and used cladistic methods to arrive at phylogenetic conclusions (e.g., Li and Hickey 1988; Hickey and Taylor 1991; Fuller and Hickey 2005; Jud and Hickey 2014).

Geology, Sedimentology and Plant Fossils

Even as Leo was developing leaf architectural terminology and investigating the systematic distribution of leaf features, he was also working on improving the interpretation of the sedimentary environments in which fossil leaves were preserved. This work began in earnest during his Ph.D. project on the Golden Valley Formation, where he completed scores of meticulous stratigraphic sections and a map of the formation that is still the bible today for anyone working on these rocks (Hickey 1977). As part of that study he documented the large variations in floral composition that can occur in different local sedimentary environments of the same age, a point he returned to strongly with his work on Paleocene floras of the Clark's Fork Basin in Wyoming (Hickey 1980). He realized that such local variation recorded real habitat heterogeneity along an ancient landscape, in addition to the influence of deposition and preservation. Leo's ability to read sedimentary facies and reconstruct the environmental mosaic of ancient landscapes was key to understanding the habitats in which ancient plants lived, but also to making robust biostratigraphic zonations that represented real change through time rather than the vagaries of shifting local habitats. During subsequent work in the Paleogene of Montana (Hickey 1980) and the Canadian Arctic (Hickey et al. 1983), Leo continued to break new ground by integrating angiosperm paleobotany with sedimentary facies analysis, magnetostratigraphy and vertebrate biostratigraphy. In so doing he provided some of the first terrestrial climate curves that were temporally well calibrated, and could thus be compared with the rapidly developing marine paleoclimate record.

The integration of paleobotany with sedimentary geology had its most influential expression in Leo's studies with James A. Doyle on the Early

Cretaceous fossil record of angiosperm diversification in the Potomac Group (Doyle and Hickey 1976; Hickey and Doyle 1977). This work provided not only a description of early angiosperm evolution, but also a view of its environmental and ecological context. Collections were made in carefully described sedimentological context, showing that angiosperms were initially very rare and first became abundant in environments with clear signs of frequent disturbance—fluvial pointbars or sites with abundant fossil charcoal or both. Not until the late Early Cretaceous did angiosperms become highly abundant in most stable Potomac Group environments. Leo also interpreted the morphology of early angiosperm leaves in a functional context, showing that regardless of their systematic affinities, they had features similar to living early-successional plants. These observations, integrated with Jim Doyle's palynological work, led the two to develop the "riparian weed" model of the early angiosperm radiation, the idea that early angiosperms were relatively small plants with rapid growth and reproduction that preferentially occupied disturbed habitats with abundant light. This idea has heavily influenced all subsequent work in the field.

Hickey and Doyle's papers on the Potomac Group were influential among botanists from the start, but they have become classic paleoecological works in a broader sense because of their masterful integration of data from so many sources—sedimentology, stratigraphy, biostratigraphy, functional morphology, systematics and evolution. The Potomac Group papers of 1976 and 1977 provided strong evidence to the scientific world that the fossil record held extraordinary insights about plant evolution, if it were only studied seriously and in a modern way. Together these papers have now been cited more than 650 times.

Case Study: Paleogene of the Clark's Fork Basin and the Arctic

Upon moving from Princeton to the Smithsonian in 1967, Leo began to work in the Clark's Fork Basin of northern Wyoming, using the geology field camp in Red Lodge, Montana, as a base. Vertebrate paleontologist Glenn Jepsen, a mentor of Leo's from Princeton, had been collecting Paleocene mammals in this area since the late 1930s and had developed a zonation of the Paleocene strata using mammalian fossils. Phil Gingerich at the University of Michigan had added much greater detail and statistical rigor to the mammalian biostratigraphy, and Leo realized that the maturing mammal zonation gave him the potential to subdivide the 10 million years of the Paleocene into four evolutionary stages.

Interacting with geologists at the Red Lodge camp, Leo saw that the Paleocene sedimentary rocks in the Clark's Fork Basin offered more than just a refined time scale. The rocks had been deposited as the adjacent Beartooth Mountains were being uplifted, and Leo recognized that these synorogenic sediments recorded a diversity of landscapes and facies with distinct fossil floras (Hickey 1980; Yuretich and Hickey 1984; Hickey and Yuretich 1997). The rocks and fossil leaves preserved much greater landscape heterogeneity than he had encountered in the Potomac Group or the Golden Valley Formation. The fossils of the Clark's Fork Basin offered the chance to study both change through time (with age control from the vertebrate fossils) and varied depositional settings that recorded vegetation at the landscape scale. Between 1967 and 1979, Leo discovered and quarried more than 60 fossil plant sites and published an overview that discussed the biostratigraphic, paleoecological and paleoclimatic implications of Paleocene floras from the Clark's Fork Basin (Hickey 1980).

By this time, Mary Dawson at the Carnegie Museum had discovered the first Paleocene–Eocene vertebrate fossils in the Canadian Arctic, and she invited Leo to join her project to document the plants that she had seen. Leo made his first trip to Ellesmere Island in 1979 and quickly caught the Arctic bug. The Eureka Sound Formation is tremendously thick and contains fossil plants at many levels. Leo realized that work in the Arctic would add latitudinal range to his developing understanding of Paleocene floras and landscapes, and also that Paleocene polar forests were a unique and extinct biome. As the work in the Arctic developed it began to appear that species occurred earlier in the polar region than they did at middle latitudes in the Rocky Mountains, suggesting the possibility that the Arctic might have been a center of origin for some lineages that appeared only later in middle latitudes. Leo collaborated with magnetostratigraphers from the University of Wisconsin–Milwaukee to test this hypothesis, and they published their interpretation in *Science* (Hickey et al. 1983). The article caused considerable controversy, and ultimately the magnetostratigraphy was revealed to be faulty. Leo spent three more field seasons rectifying the results and correcting the errors. Even though the idea of the Arctic as a center of origin in the Paleogene turned out to be incorrect, Leo's collections, stratigraphic sections and field observations are a unique resource, and modern scientific interest in warm Arctic ecosystems was spurred by his work.

Leo worked in the High Arctic for six field seasons, documenting Paleocene–Eocene floras and exploring more than a dozen different field areas on Ellesmere, Axel Heiberg and Devon Island. On Devon Island, the team discovered fossil vertebrates and plants in the sediments that filled the Miocene Haughton asteroid impact crater and recovered a nearly complete rhinoceros skeleton (Omar et al. 1987; Hickey et al. 1988). Recognizing that a large river flowing through the crater had no name, Leo worked with the Canadian Geographic Names board and formally named Canada's first and only Rhinoceros River.

Case Study: Plant Extinction at the Cretaceous–Paleogene Boundary

In 1980, Leo's graduate school friend Walter Alvarez led a team that proposed the revolutionary idea that the Cretaceous–Paleogene (K-Pg) mass extinction was the result of a bolide impact. Alvarez's paleontologist colleagues at Berkeley rejected the idea as too simple and in opposition to the vertebrate fossil record that had been developed in eastern Montana. Both Leo and Walter had studied geology at Princeton with paleobotanist Erling Dorf, who had evaluated plant extinction at the K-Pg boundary in Wyoming in the 1940s. Familiar with this work, Leo surveyed the paleobotanical literature, concluding that land plants experienced gradual rather than catastrophic extinction at the end of the Cretaceous (Clemens et al. 1981; Hickey 1981). Leo's careful analysis of the floral record across the K-Pg boundary also showed that terminal Cretaceous floras were poorly known and that Dorf's earlier work lacked the stratigraphic resolution necessary to resolve an essentially instantaneous event.

In 1983, Leo invited prospective student Kirk Johnson to join him on a field trip to Jordan, Montana, where Alvarez and his supporters had recently discovered evidence of the K-Pg bolide smack in the middle of the Berkeley paleontology field area. Alvarez and his paleontologist opponents agreed to bring the debate to the outcrop.

During this trip, it became clear that it might be possible to combine the microstratigraphy of the K-Pg boundary pollen record with studies of plant macrofossils to test the Alvarez hypothesis. Leo encouraged Kirk to tackle this problem and allowed him the use of his field equipment and field vehicle. Over the next five years, Kirk applied Leo's methodology to the K-Pg boundary problem, paying strict attention to stratigraphic control, depositional setting and sample sizes. Eventually these data showed that plants did undergo a local extinction at the K-Pg boundary, documenting the extinction better than any other group of terrestrial organisms (Johnson and Hickey 1991). When the data came in Leo changed his initial opinion on the suddenness of the K-Pg extinction, a move that was unusual among paleontologists, and therefore highly influential.

Teaching and Exhibits

Leo's scientific accomplishments are notable for their breadth and for the way they are rooted in a deep understanding of quite distinct areas of knowledge: geology and botany. However, his joy in thinking, analyzing and knowing was accompanied by a desire to share his ideas with others, and this he did from the start to the finish of his career. Leo found inspiration in fieldwork and in reading the history of the earth from rocks and landscapes. At Yale he was famed for his stratigraphy class, which more than one student described as the most difficult but most interesting class taken in four years of college. He also shared his enthusiasm through longer research trips with graduate and undergraduate students, mostly to the northern Rocky Mountains. There are many stories of Leo in the field, where he cut a distinctive figure. Even during the roughest field conditions, amid perils from rattlesnakes to polar bears, he maintained certain formalities: a morning shave, a clean khaki shirt, a brimmed field hat, cold chocolate cookies at lunch and a glass of bourbon in the evening. These field excursions were conducted with a wonderful combination of personal warmth and scientific rigor. Field trips were also nonstop learning opportunities in topics far from geology and botany. Leo had command of a truly remarkable diversity of knowledge ranging from early Christian history, through Celtic culture and frontier lore, to formal logic and classical languages. Following the International Organization of Palaeobotany Convention in Bonn, Germany, in 2008, he took a short side trip with two former students to the cathedral in Cologne. There he gave an impromptu tour replete with detailed information on iconography, architecture, Roman history and Latin, to the point where he began to attract a small following of tourists, convinced he was an official guide.

During his career Leo contributed to science education not only through graduate and undergraduate teaching, but also by developing museum exhibits that reached a younger and broader audience. At the Smithsonian he was chair of the Exhibits Committee from 1973 until almost the time of his departure, and developed a plan for renovating the paleontology halls in a phased fashion that allowed different but interlocking sets of curators to apply their expertise in separate areas of a coordinated overall exhibit. He himself worked hardest on exhibits about the Ice Age, the Conquest of Land, the Origin of Flowering Plants, and Fossils and Industry. These exhibits entranced and educated literally tens of millions of visitors for more than 30 years until they closed in the spring of 2014.

Leo's favorite part of the Smithsonian fossil halls was a walk-through diorama representing the Early Cretaceous environment of the Washington, DC, area, where so many important early angiosperm fossils had been found in the Potomac Group, and where he and Jim Doyle had done seminal work on early flowering plant evolution, ecology and environment. The display consisted of a bridge across a reconstruction of the ancient landscape, with the wet, conifer-dominated backswamp habitat on one side and a scraggly, leggy thicket of *Sapindopsis* plants clambering over the point bar on the other. On recordings archived at the Smithsonian one can hear Leo instructing the artists in exhaustive (and no doubt exhausting) detail about how things needed to look. The "water" at the edge of the diorama's swamp had to be the color of strong tea to reflect the dissolved tannins, somewhat translucent to a depth of a few inches, but opaque where deeper. The "north" side of a log had to be painted darker than the dry, sun-bleached "south" side. The attention to detail must have been maddening to the artists, but it delighted generations of museumgoers and fanned the imaginations of more than one future paleobotanist. Another unique perspective was the minor and distant role for dinosaurs in Leo's Cretaceous landscape—the plants were the stars of the show.

During his decades at Yale, Leo continued to be extremely active in public education as well as teaching, helping develop seven exhibits at the Peabody Museum, including enhancements to the "Age of Reptiles" mural in the Great Hall. Leo's love for the murals and museums was on display when he announced the publication of the then-oldest evidence of flowers, the Koonwarra plant (Taylor and Hickey 1990). He took care to make sure the correct age was represented in the background mural of the Peabody's Great Hall, and his careful staging of the press conference ensured coverage of the event by national and international print, television and radio press. A relatively recent addition to the museum is an outdoor bronze statue of the ceratopsian dinosaur *Torosaurus*, which looms over passersby on the Whitney Avenue side. Anyone who pays attention to the landscaping surrounding *Torosaurus* will see Leo's hand in the choice of plants for the Cretaceous Garden, an exhibit he delighted in working on during his last few years, and that will continue to represent his paleobotanical perspective on the past as it grows along the side of the Peabody in years to come.

Closing

This volume demonstrates how Leo's students and postdocs have continued to push the boundaries of areas that Leo himself pioneered. In a symmetry he would have enjoyed, it includes contributions with coauthors from his first (Scott Wing) and last (Dan Peppe) students, and first (Jim Doyle) and last (David Winship Taylor) postdocs, as well as other students, students of students and postdocs of postdocs. Little et al. (2014) refine one of Leo's leaf architectural methods called leaf ranking. Taylor and Gee (2014) apply leaf architectural characters to the evolution of water lilies. The contribution by Doyle and Upchurch (2014) revisits early angiosperm diversification in the Potomac Group, while Jud (2014) applies leaf architectural methods to a previously undescribed Potomac Group collection that includes early angiosperms. Hu and Taylor (2014) examine the paleoecology of an Albian flora from Jordan. Peppe and Hickey (2014) detail plant biostratigraphy and paleoecology in the early Paleocene of the Great Plains, and Green (2014) examines the functional morphology of arborescent lycopsids.

In 2008, while working on a project with his last student, Dan Peppe, Leo reflected on his career and his contributions to paleobotany. Leo felt that his research contributed in two major ways. First, by developing and applying leaf architectural analysis to angiosperm fossil leaves, he showed how to identify and in many cases classify fossil species represented by dispersed leaves alone. These rigorous descriptive methods were a significant improvement over early paleobotanical reliance on superficial similarities between fossils and modern plant taxa. Second, by making large, quantitative collections of fossil leaves in the context of sedimentary environments and stratigraphic sections, he had shown it was possible to reconstruct ecosystems and how they changed through time. Further, because these environmentally and geochronologically well-constrained floral collections were carefully described, identified and taxonomically classified (when possible) on the basis of leaf architectural analyses of floras, it has become possible to assess patterns of plant evolution, plant phylogeny and the response of plants to climate change and major extinction events more rigorously. The impact of these types of integrative studies is evident in the work being done by many paleobotanists today, and by the many citations to Leo's work (documented on his Google Scholar page [http://scholar.google.com/citations?user=_nGJ5YQAAAAJ&hl=en, accessed 16 June 2014]).

In 2009 Leo was awarded the Moore Medal by the Society for Sedimentary Geology for his major insights into plant ecology and evolution, achieved by integrating geological and biological approaches to the plant fossil record. The award recognized his exceptional capacity to bring together sedimentology and stratigraphy and couple them with his deep understanding of angiosperm morphology and evolution. There are few who ever master such disparate fields. Leo's diverse base of knowledge and his acutely logical mind are reasons his work has been so innovative and influential. By the end of his life Leo had played a major role in reinvigorating paleobotany, the discredited discipline he found as a youth, and his insights had already been expanded and extended by two generations of botanists and paleobotanists, including many of his own students and postdocs, and their students.

In his last few years Leo returned to his roots in plant systematics and descriptive paleobotany, working on a series of Cretaceous floras with current and former students (e.g., Peppe et al. 2008; Miller and Hickey 2008, 2010). He loved the process of chasing down the oldest valid name for the taxon he was working on. Surrounded by fossils, herbarium sheets, and 19th-century taxonomic monographs, he said he felt as though he was writing a symphony. Leo's work continued literally until the last weeks of his life. In an e-mail to a former student sent from his hospital room prior to brain surgery in December 2012, Leo wrote: "Here are the two specimens that I asked about this morning: *Sequoia longifolia* Lesquereux, 1878, Plate 61, figures 28 and 29... They have come to take me away now so there is no time for further comment." A few weeks later, in early January 2013, Leo said he was regretful that it did not appear he would be able to complete the project he was working on—a Late Cretaceous flora from the Meeteetse Formation—which is still being worked on by his coauthors. It seemed that his inability to bring more of the former world to human attention was almost of greater concern to him than his own departure.

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