David M. Raup

1933–2015

BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
Michael Foote
and Arnold I. Miller

NATIONAL ACADEMY OF SCIENCES

DAVID MALCOLM **RAUP**

April 24, 1933–July 9, 2015

Elected to the NAS, 1979

By Michael Foote and Arnold I. Miller

David M. Raup, one of the most influential paleontologists of the second half of the 20th century, infused the field with concepts from modern biology and established several major lines of research that continue today:

Theoretical morphology. Why, despite eons of evolution, is the spectrum of realized biological forms such a tiny fraction of those that are theoretically possible?

First-order patterns in the geologic history of biodiversity. Has biodiversity increased steadily over time? What does the answer imply about the biosphere and the nature of the fossil record?

Mathematical modeling of evolution. What patterns result, for example, from the structure of evolutionary trees? And what is the apparent order that emerges from stochastic processes?

Biological extinction. What temporal patterns are evident in the history of life and what are their implications for the drivers of extinction and for Earth's place in the cosmos?

The pilot and the paleontologist

In *The Right Stuff* (1979), author Tom Wolfe observed that the calm West Virginia drawl of the renowned test pilot and World War II ace Chuck Yeager could still be heard in the voices of virtually all commercial pilots, decades after Yeager became the first to break the sound barrier. This inflection caught on in the late 1940s among a cadre of Yeager's disciples at an airfield in the high desert of California, and it spread from generation to generation, aided by the service of many of those disciples as astronauts. During the heyday of NASA's manned space program, the drawl could be heard regularly in televised exchanges between astronauts and mission control. Little did any of us know that the voice was really Chuck Yeager's. Wolfe's description of Yeager's influence on his peers reminds us that in any field there are a few people whose work is so transcendent that colleagues seek to emulate not only their methods but also how they carry themselves in the arena.

And so it was with Dave Raup. As is often true of people who become the best of the best, Dave did not actively seek the limelight. In fact, he tended to avoid it and was never particularly comfortable having attention focused on him in any forum. But his comportment—actively searching for holes in his own results; not dismissing someone else's work without first fully understanding it; letting one's work, rather than one's ego, do the talking; accommodating one's own self-doubts but not being defeated by them—profoundly influenced those who were lucky enough to spend time around him and, through this group, subsequent generations of students who have no idea that the "voice" they are really hearing and, in turn, are seeking to emulate is Dave Raup's.

Finding his bearings

Dave, age 3, observing lichens during a field season along the Athabasca River, summer, 1936.

Dave Raup was born in Boston, MA, in 1933 to biologists Hugh Raup, a botanist and Harvard professor, and the former Lucy Gibson, a lichenologist and teacher. Dave, his older brother Karl, and their parents spent summers in the field, mainly in remote areas of northwest Canada. The family lived an itinerant lifestyle, renting housing during the academic year—often near Harvard's Arnold Arboretum (in Boston), which Dave regarded as his backyard—and disappearing for field research in the summer. These early experiences did not preordain a life in science, however. Dave enjoyed hunting and photography, but showed little interest in natural history and in fact was discouraged by his parents from pursuing such a career.

When Dave was 15 years old, his father became director of the Harvard Forest in Petersham, MA, at which point Dave matriculated at the Loomis Institute, a college-prep school near Hartford, CT. At age 17 he began his undergraduate studies at Colby College (Waterville, ME), where by his own account he was not exactly a model student. He chose to major in geology,

At a railway station during an excursion to the Yukon, summer, 1943. Foreground, right to left: Dave, holding his camera; Hugh Raup; participant thought to be Charles Denny of the U. S. Geological Survey; Lucy Raup.

largely for social reasons. (Karl was already there as a geology major, and Dave developed an interest in the ski team, which was informally associated with the Department of Geology.) He sometimes chose courses based on whether the required texts were the same as those for courses he had already taken at Loomis. And he spent an inordinate amount of time playing poker, presumably benefiting from his gift for probabilistic thinking.

But after a couple of years, Dave felt it was time to try something else. Through an acquaintance of his father, he learned about the flexibility of the system at the University of Chicago, where students could earn college credit through high-school study and examinations, enabling them to start graduate work at a comparatively young age. Thus in the summer of 1952, Dave moved to Chicago with graduate-student status and was soon immersed in a research-intensive environment, surrounded by then- and future luminaries that included geochemist Heinz Lowenstam, vertebrate paleontologist Everett C. Olson, and paleoecologist Ralph Gordon Johnson. Though the atmosphere was exciting, Dave soon observed that the program lacked structure and that a graduate degree from Chicago would not be a useful credential. Ironically, in light of his later work, he was also turned off by the modeling and quantitative approaches exemplified by Olson and Robert L. Miller's research on morphological integration.

Dave on horseback in California, mid 1940s.

So a year later, Dave decided it was time to move on again. To enter a conventional Ph.D. program at most universities, he would need an undergraduate degree, which he lacked; and moreover his time at Colby and Chicago had included little formal study in geology. He somehow persuaded Chicago to grant him a bachelor's degree after doing a bit of coursework by correspondence, but it was stipulated that he could never return to the University—a stipulation that was obviously ignored when he later returned as professor and chair of the Department of the Geophysical Sciences.

Despite his mixed experiences at Chicago, Dave had developed a clear interest in paleontology. In 1953, he applied to the University of Michigan, where he hoped to study at the Museum of Paleontology. But his ersatz geology degree did not meet their standards, so he returned to Petersham, unsure what his next step would be. His mother suggested he consider working in sales, but his father instead directed him to Bernhard Kummel, a stratigrapher and paleontologist at Harvard. Kummel was impressed, and Dave entered the university's Ph.D. program.

In the summer of 1954, however, after only one year at Harvard, he again had itchy feet and took a job with Standard Oil of California, thinking he would eventually go into the petroleum-exploration business for himself. But Dave soon became disillusioned with what he regarded as low professional standards of many in the industry. In the meantime, he learned that he had been awarded a National Science Foundation graduate fellowship. Dave returned to Harvard in the fall, where he was influenced by Ernst Mayr's approach to evolutionary biology and by the infusion of biological principles into paleontology, as exemplified by the likes of Alfred Sherwood Romer and Harry B. Whittington.

It would be tempting but inaccurate to say that Dave never looked back. He often felt pulled by life's alternatives, and his visiting professorship at the College of the Virgin Islands—along with his love of the sea and of sailing—almost led him to abandon his academic career around 1970. It is sobering to imagine what a difference that would have made to our profession.

Early career

Dave's dissertation research–shaped in part by Mayr's interest in geographic variation in morphology and its relevance to the speciation process—concerned allometric, geographic, and environmental variation in the living sand dollar *Dendraster*. Among other results, he made a convincing case for the environmental basis of some among-population differences in shape, and he noted that many putative species-level differences among fossil populations are consistent with present-day variations that do not signify species status.

Dave followed the *Dendraster* work with a series of papers documenting the crystallographic axis orientations of plates in the echinoid test. This research demonstrated that: calcite c-axis orientations are largely fixed within species and at higher taxonomic levels; species show ontogenetic variation following a few general patterns; and groups of plates within a species often vary consistently from one another. He used the phylogenetic signal, evident in cases where higher taxonomic affinities are fairly well known, as a basis for suggesting solutions where affinities are less clear.

Toward the end of Dave's echinoid period, he and geochemist Jon N. Weber documented carbon- and oxygen-isotopic variation in echinoid plates. As with the crystallographic data, different components of the skeleton vary systematically, and the isotopes carry a phylogenetic signal—one that matches the signal in the c-axes and suggests solutions to taxonomic problems. Although oxygen isotopes are sensitive to temperature, Dave found that they show enough genetic variation to limit the use of echinoids for paleoenvironmental inference. Taxonomic variation in carbon isotopes suggested metabolic differences among clades, and the taxonomic diversification of echinoids since the mid-Paleozoic was found to correlate with increased variance in isotopic composition. This body of work represents one of the earliest demonstrations of vital effects in stable isotopic composition.

While Dave was engaged with echinoids, he began a long-term research program in theoretical morphology—a comparison between actual and theoretically possible biological forms, the latter in turn developed from generative models such as that for logarithmic coiling. By comparing the spectrum of possible forms to those that had actually evolved, Dave was able to use a combination of architectural, phylogenetic, and functional arguments to make sense of why brachiopods and various groups of mollusks—bivalves, gastropods, and ammonoids—occupy largely distinct regions of the coiling-parameter space. Among his other imaginative contributions were a soap-bubble model of echinoid plating.

Computer as a research tool

In 1961, Dave first simulated gastropod coiling mechanically by shrinking and enlarging the mathematical generating curve photographically. A year later he moved to a digital computer, with curves printed to a first-generation plotter; and a few years later, with electrical engineer Arnold Michelson, he showed that shells could be simulated more quickly using an analog computer with output piped to an oscilloscope. Thus began an exploration, which extended through the remainder of his career, using "the computer as a research tool." At the time, he was recognized as one of the few paleontologists who saw the potential for computers in Earth science, and he was invited to participate in a 1969 symposium, organized by Daniel F. Merriam, on that subject.

In computation as well as in other matters, Dave was a do-it-yourselfer and tinkerer, and he generally favored his own programming over canned solutions. In the 1980s, when many were discovering the utility of software such as Lotus 1-2-3, Dave wrote his own spreadsheet program, powered by BASIC. In retirement, he wrote programs for weaving design, some of which are still in wide use. And as a puzzle enthusiast and formidable Scrabble player, he also wrote programs to generate crosswords.

Dave's advocacy of computing was but one example of a lifelong dedication to improving the infrastructure of paleontology. Others include his collaboration with Bernie Kummel on the *Handbook of Paleontological Techniques*; his chairmanship of the National Research Council's Committee on Guidelines for Paleontological Collecting; the workshop on "species as particles" that he taught with Thomas J. M. Schopf at the Smithsonian Institution in 1978; and of course the first two editions of *Principles of Paleontology*, coauthored with Steven M. Stanley.

Biological diversity and the fossil record

James W. Valentine's depictions of Phanerozoic biodiversity and extinction patterns in the late 1960s and early '70s (e.g., Valentine 1969) sparked Dave's interest in possible biasing effects. Most importantly, Dave questioned the reality of the substantial Cenozoic diversity increase that was evident in raw-data compilations from the fossil record. He systematically laid out the time-dependent and -independent biases that were likely to be at play in general, including a secular increase in the amount of exposed fossiliferous rock and other factors—such as the taxonomic treatment of living taxa and the extension of stratigraphic ranges of extant taxa—which he collectively referred to as the "Pull of the Recent."

Dave also compiled an empirical tabulation of fossil species as an alternative to the indirect estimates of Valentine and others, which had suggested a 10-fold increase in species richness from the Mesozoic to the Recent. A compromise of sorts was struck in the 1981 "Consensus Paper," led by J. John ("Jack") Sepkoski, Jr., which argued that several different measures of diversity show similar trajectories over the Phanerozoic, and that these in turn reflect a true biological signal. But conversations with Dave over the years made it clear that he never fully embraced the consensus.

In the seminal papers of the "MBL Group" (so called because the authors began their collaboration at the Marine Biological Laboratory in Woods Hole, MA), Dave combined his penchant for questioning conventional views with another of his hallmarks—importing approaches and methods from other fields, in this case equilibrial demographic models. His contributions to the MBL Group included programmed simulations of the evolutionary branching process; he wanted to see how the history of diversity within higher taxa would appear if it behaved as if it were random—with all component lineages having the same inherent propensities to branch, persist, or become extinct in a given period of time. He also ferreted out the aspects of biodiversity that fell outside the boundaries of these simulations, such as rapid radiations and extinctions.

One of the principal lessons of the MBL work was that diversity patterns should not be taken as prima facie evidence of biologically meaningful differences among groups of organisms. An important conclusion of this research—that simulated higher taxa often become extinct even though they didn't do anything "wrong"—reflected a theme that would emerge in a number of Dave's papers. He likened the extinction of higher taxa to the stochastic disappearance of family surnames, a problem that had been treated mathematically during the 19th century (Watson and Galton 1875). In a paper that included an estimate of species-level extinction rates in the Late Permian, Dave came to the inescapable conclusion that an event so severe—up to 96 percent species extinction, by his estimate—simply must have a significant stochastic element regarding who survived. He called this phenomenon the "evolutionary founder effect."

The general theme that apparently strong nonrandom patterns could emerge from a stochastic system was repeated in Dave's collaboration with Stephen Jay Gould, which added morphological evolution to the MBL simulation model. The problem of phylogenetic structuring of biologic traits is now widely recognized in evolutionary biology, thanks to later work by Joe Felsenstein (1985) and many others. But in 1974, Dave showed that temporal trends, correlations between characters, and the correspondence between cladistic and phenetic patterns were among the features that resulted in the absence of directional selection. Other patterns, such as fine convergence of form, could not be simulated.

The theme of apparent order emerging from a stochastic system also figured in several papers on the random walk as a null model for phenotypic evolution, most notably Dave's collaboration with Rex E. Crick that reanalyzed Roland Brinkmann's classic biometric data on the ammonite *Kosmoceras*. Dave's work in this area prompted efforts, still ongoing, to infer evolutionary processes from temporal sequences of morphologic data by means of mathematical modeling (e.g., Hunt 2006, 2012).

Mathematical modeling of evolution

Although simulation studies could be effective for consciousness-raising, Dave considered analytical models to be more powerful in addressing evolutionary questions. We have already mentioned his application of branching models to the problems of higher taxonomic extinction and of the random walk model to evolutionary sequences. In a thought experiment with Valentine, Dave made the case that life on Earth could plausibly have originated multiple times; but if so, we would not know it because all but one of the "bioclades" drifted to extinction without leaving a fossil record.

Dave also demonstrated that the early *phylogenetic* origin of phylum- and class-level lineages—if not their profound morphological and ecological divergences—could be seen as an inevitable consequence of the geometry of evolutionary trees. This was because most pairs of living species share a common ancestor back in the Cambrian or Ordovician.

Starting in the mid-1970s, Dave considered the question of taxonomic survivorship in the context of Leigh Van Valen's "New Evolutionary Law"—the proposition that rates of extinction within ecological groups are stochastically constant (Van Valen 1973). To provide a rigorous test for constant survivorship, Dave imported a method of statistical analysis from the literature on the failure of manufactured parts.

Dave's consideration of taxonomic survivorship over geologic time raised the question of whether extinction could be episodic at all scales—from species over thousands of years to higher taxa over tens of millions of years. This question would become an integral part of his analyses, many of them with Sepkoski, of the Phanerozoic extinction record. Dave developed the idea of episodicity most thoroughly with the species-level "kill curve," a model of the average waiting times between species extinction events of a given magnitude. An important implication of the kill curve is that the major extinction events have accounted for a relatively small proportion of species extinctions in Earth's history. Although Dave studied patterns of major extinction episodes (see below), and used the terms "background" and "mass extinction," he remained skeptical of the notion of distinct classes of events, whether distinguished by cause or by magnitude.

The geological history of extinction

Dave and Jack Sepkoski discussing extinction at the University of Chicago, early 1980s. Note the photo of geologist J. Harlen Bretz in the background. (Photo courtesy University of Chicago.)

The Raup/Sepkoski analyses of extinction rates, mainly of marine animals, led to two novel results that are now common knowledge among paleontologists: that average rates of extinction have declined substantially over the course of the Phanerozoic; and that this decline has been punctuated by episodes of severely elevated extinction—including events that have come to be known as the "Big Five." Dave also demonstrated that major groups of marine animals show rather similar temporal patterns of extinction—albeit with different average levels of turnover. From the concordance among extinction profiles, Dave inferred that the groups must be "marching to the same drummer"—namely, widespread physical perturbations of the biosphere.

The foregoing summary of Dave's work on extinction omits one result on which paleontologists decidedly do not all agree: the finding that extinction events since the Late Permian were uniformly spaced with a periodicity, according to the initial estimate, of some 26 million years. Dave and Jack suggested that the driver was likely extraterrestrial, although to date no culprit has been found. Dave eventually stopped writing about periodicity, convinced that statistical analyses had taken it as far as it could go, and that future progress would depend on more highly resolved paleontological data and geochronology. Although he retained the hunch that extinctions are periodic, he realized that the case was not proven, and he viewed periodicity as a live enough hypothesis to merit continued consideration.

Dave had long maintained an interest in Earth and its biosphere as part of a "cosmic environment." In 1981 and 1982, he co-organized a series of NASA-sponsored workshops with the goal of furthering our understanding of the role of extraterrestrial events in the "evolution of complex and higher organisms" (affectionately known as ECHO). The interactions at these workshops were largely responsible for getting him and Sepkoski to test for periodicity of extinction in the first place. Dave's work and leadership were instrumental in helping to bring research on complex and higher organisms into the fold of NASA's program in exobiology. He was also a supporter of the Search for Extraterrestrial Intelligence (SETI), while questioning the common assumption that intelligent life elsewhere need be humanoid or even conscious.

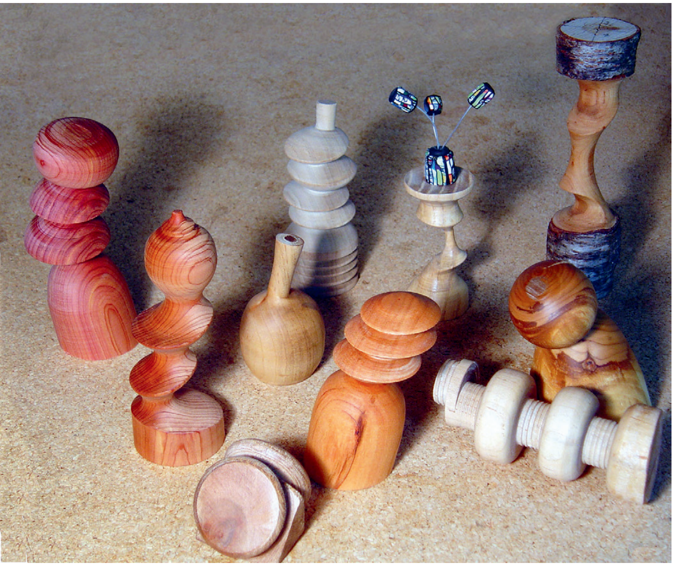
The possibility of an extraterrestrial driver of extinction of course meshed well with interest in the hypothesis that a major bolide impact may have triggered or at least contributed to the end-Cretaceous extinction event (Alvarez et al., 1980). Dave in fact modeled the possibility of mass extinction via bolide impacts before the work of Alvarez et al. was carried out. Dave had been motivated in part by Harold C. Urey's (1973) analysis of the timing of impacts and stratigraphic boundaries; and by Ernst J. Öpik's (1973) estimates of impact frequencies and the likely geographic extent of their effects. See Foote and Miller (2016).

The probable importance of extraterrestrial influences on terrestrial life led Dave to consider the possibility of impacts as a general cause of extinction. Combining the species kill curve mentioned earlier with what is known of the waiting-time distribution of impacts of given magnitudes, Dave argued that it is at least plausible that all but the smallest extinction events could be attributed to impacts. He also argued that other candidates for general causes of extinction, such as changes in climate or sea level, do not satisfy the requirements set by the distribution of waiting times.

As Dave often wrote, given that the vast majority of species that ever lived are extinct, to ignore extinction in evolution makes as little sense as to ignore mortality in demography. But was extinction "constructive" in the sense of shaping the evolution of the biosphere along some path that we might recognize as "improvement"? Dave contrasted three scenarios for extinction episodes both large and small: "field of bullets," or completely random extinction; "fair game," in which species survive because of differences in fitness that evolve over time (essentially the Darwinian model); and "wanton extinction," in which there is selectivity but with rules that differ from those operating in day-to-day natural selection, so that species are unlikely to be "prepared" to avert extinction. Our reading of Dave's work is that he found the evidence and logic in favor of wanton extinction most compelling, but also that paleontology and evolutionary biology still have much to learn about which models apply in which events and to which clades.

Dave Raup as a colleague

This account of Dave's research contributions touches on his scientific style, which was marked by: the broad scope and importance of questions he addressed; the importation



Examples of Dave's woodturnings and a polymer clay sculpture by Judie. (Photo by Dave Raup).

of ideas and methods from fields outside paleontology; his willingness to consider any idea, no matter how unlikely a priori; his respect for a diversity of scientific cultures and approaches; a skepticism regarding received wisdom as well as his own ideas; tight logic and analytical rigor; and concern for the health of paleontology as a discipline.

But Dave also had a personal style that his students and colleagues were fortunate to experience. He clearly had views about directions he thought were likely to be productive for paleontology, but we never knew him to bang a drum and tell the field what it should be doing. Rather, he led by example. He rarely gave explicit scientific advice to students (so that when he did so, one knew it had to be taken seriously!), and he never instructed them what to do. Dave evidently saw that we are who we are, and his role was not to mold students to his form but to help us reach our potential. Above all, Dave treated students as equals—as colleagues. This meant of course that he expected the highest-caliber work from us, but he demanded no more of others than of himself.

Despite his immense accomplishments, Dave was genuinely modest and avoided being the center of attention. He was one of the few established scientists we knew who was frank with us about the fact that academic life was full of ups and downs for nearly everyone, not only for students just setting out. So we felt we could trust him with our uncertainties and concerns.

Dave was a man of honesty and integrity. He called out evolutionists for misrepresenting the arguments of creationists, and he enjoyed receiving a private tour of the Creation Museum in northern Kentucky in December 2006, several months before the museum opened to the general public. He was pleased that the private library at the museum housed a copy of his book *The Nemesis Affair: A Story of the Death of Dinosaurs and the Ways of Science*, which he autographed during his visit. Dave was not a creationist, but he was respectful of different viewpoints, and it frustrated him that some of his colleagues did not even try to understand the basic tenets of young- or old-Earth creationism.

Finally, by transitioning resolutely at age 60 to a new phase of his life, Dave reminded us that fulfillment does not come from professional accomplishments alone. To be sure, his approaches to avocations pursued in retirement were often distinctly Raupian; for example, his appreciation for the geometry of organic form was evident in artistic works that included multi-axis woodturning. But he also remained available throughout his retirement years for visits from colleagues, to review manuscripts, and to provide professional or personal advice whenever it was sought. Clearly, though, he enjoyed the freedom, solitude, and beauty of Washington Island, and he enjoyed traveling the world with his wife, Judith T. (Judie) Yamamoto.

In summary, Dave Raup was a fine scientist and a true mensch.

Dave is survived by Judie and his son Mitchell, daughter-in-law Marian Raup, grandson Hugh Raup, stepson David Topaz, and first wife Susan Alexander.

ACKNOWLEDGMENTS

We thank D. C. Fisher, D. Jablonski, S. M. Kidwell, A. H. Knoll, M. D. Raup, F. M. Richter, J. D. Rummel, D. Sepkoski, and J. T. Yamamoto for discussing Dave Raup's life and work with us and for providing information on other scientists mentioned here. Parts of this memoir were repeated with permission from Foote (2015) and Foote and Miller (2016).

BRIEF BIOGRAPHY

April 24, 1933: Born, Boston, MA

1953: S.B., University of Chicago

1955: A.M., Harvard University

1957: Ph.D., Harvard University

1956–57: Instructor, California Institute of Technology

1957–62: Assistant Professor, Johns Hopkins University

1963–65: Associate Professor, Johns Hopkins University

1965–66: Associate Professor, University of Rochester

1966–78: Professor, University of Rochester (Chair, Geological Sciences, 1968–1971; Director, Center for Evolution and Paleobiology, 1977–1978)

1978–80: Chair, Geology, Field Museum of Natural History

1980–82: Dean of Science, Field Museum of Natural History

1982–2015: Professor, University of Chicago (Chair, Geophysical Sciences, 1982–1985; Sewell Avery Distinguished Service Professor, 1984–2015; Emeritus Professor, 1994–2015)

July 9, 2015: Died, Sturgeon Bay, WI

SELECTED HONORS AND AWARDS

1955–1957: Predoctoral Fellow, National Science Foundation

1973: Charles Schuchert Award, Paleontological Society

1979: Elected member of the National Academy of Sciences

1996: Elected fellow of the American Academy of Arts and Sciences

1997: Paleontological Society Medal

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