DAVID MALCOLM RAUP

COURTESY OF ROCHESTER DEMOCRAT AND CHRONICLE

24 APRIL 1933 · 9 JULY 2015

In 1983, I delivered my first big lecture at a national meeting, a symposium on extinction at the Field Museum in Chicago. Job completed, I descended from the rostrum as the next speaker, David Raup, was ascending. Meeting me midway along the stairs, Dave smiled slightly and murmured, "Good show." To this day, I don't think I've ever appreciated a comment more. Why would two words mean so much? The answer is straightforward: to me and to many other young paleontologists of the time, Dave Raup was the standard to which we aspired.

Without question, David Raup was one of the most innovative and influential paleontologists of the twentieth century. As a young scientist, he entered a field driven almost exclusively by description and left it decades later a vibrant, quantitative discipline powered in no small part by models, numerical analysis, and hypothesis testing. Dave's research began, conventionally enough, with specimen-based studies of sea urchins and sand dollars. But even as a graduate student, he began to ask unconventional questions. While others focused on taxonomy and biostratigraphy, Dave asked instead how echinoids form the interlocking calcite plates that make up their skeletons (and so, their fossils). Meticulously completed and thoughtfully interpreted, Dave's studies anticipated important later developments in the emerging field of biomineralization, including the recognition of "vital effects" (biological processes that complicate environmental interpretation of shell chemistry; e.g., Weber and Raup 1966). The empirical focus on crystallography and geochemistry, however, only hinted at the conceptual leaps that would soon come to characterize Dave's research.

By the mid-1960s, Dave had discovered the power of computing, launching research that would change not only his own career trajectory but that of paleontology as a whole. To begin, he constructed a simple three-parameter model capable of generating the range of skeletal morphologies observed in fossil and living mollusks, as well as other animals that fashion coiled shells. Two aspects of this pioneering research stand out. First, because Dave's model generated the full range of morphologies possible for coiled shells, he could consider not only why different taxa have discrete morphological ranges but also why some shapes have never been realized (Raup 1966). Second, his theoretical morphologies were generated by computer, commonplace now but striking at the time (Raup and Michelson 1965).

As a new decade dawned, Dave turned his attention to another area of growing paleontological interest: the history of animal diversity in the oceans. Early tabulations of fossil ranges through time suggested broad and more or less persistent diversity increase over the last 541 million years, punctuated episodically by setbacks. Many asked why diversity should increase through time. Dave, instead, asked

whether the picture assembled from fossil compilations provides a faithful chronicle of evolution. Because older sedimentary rocks are more likely to have been eroded or metamorphosed, he reasoned, the fossil record might be biased toward younger time intervals. Indeed, a compilation of sedimentary rock volume for each period of the Phanerozoic Eon looks uncomfortably similar to then-current estimates of diversity through time (Raup 1972). And Dave's numerical simulations showed how various biases could impart an apparent trajectory of increasing diversity to an evolutionary history actually marked by constant taxonomic richness. This work challenged the notion that fossils provide an unbiased record of past life, while introducing null hypotheses and numerical analysis to paleontological research.

In the years that followed, Dave teamed with a handful of other Young Turks (Tom Schopf, Steve Gould, Dan Simberloff, and, in time, Jack Sepkoski) to mount continuing challenges to paleontological convention. In particular, Raup and colleagues asked to what extent observed temporal patterns of diversity and morphological change might be driven by stochastic processes. Computer simulations generated patterns of origination and extinction similar to those actually compiled from fossil occurrences, as well as seemingly meaningful trends in the morphology of nifty little *in silico* organisms called "triloboids" (Raup et al. 1973; Raup and Gould 1974). Natural selection, however, played no role in the simulations; all decisions of whether a lineage would branch, persist, or go extinct, and whether and how its traits would change through time, were generated randomly. It was not that Dave denied a role for natural selection in shaping evolution—he simply argued that confidence in conventional interpretation required that one be able to reject the null hypothesis of stochastic change. When Raup and colleagues compared their simulated clade histories with those of real taxa, they did find departures from stochastically generated patterns—fertile places, they suggested, to explore more deterministic hypotheses.

A conspicuous difference between stochastic simulations and the empirical fossil record lay in the tendency of real taxa to show episodes of unusually strong extinction, observed simultaneously across multiple groups. This distinction caught Raup's attention, and it moved to the forefront of his thinking after Alvarez et al. (1980) published their groundbreaking hypothesis that the dinosaurs and other, less evocative groups were extinguished by the impact of a large meteor. (Although a deadly serious scientist, Dave had a sense of humor about his work. I still have a copy Dave gave me of Will Cuppy's [1941] *How to Become Extinct,* which explains that "the Age of Reptiles ended because it had gone on long enough and it was all a mistake in the first place.") Dave

recognized earlier than most that mass extinction poses a challenge to the Neo-Darwinian narrative of competitive replacement through time, and he phrased the key question provocatively: Did extinction reflect "bad genes or bad luck" (Raup 1981, 1991)? Dave emphatically cast his vote for "bad luck," arguing that well-adapted species commonly disappear because of shifting environments rather than superior competitors, including the short sharp shocks that drive mass extinctions. Indeed, for a time, Raup thought that impacts large and small would provide a general explanation for extinction. That, alas, was not to gain traction; to this date, only the extinction that ended the age of dinosaurs is reliably associated with impact. Even the famous story that the Nakhla meteorite struck a dog as it landed in 1911 is probably apocryphal.

Nonetheless, Raup's interest in generality led him to some of his most stimulating and controversial research. With Jack Sepkoski, he revisited Sepkoski's database of marine fossil occurrences, now, however, seeing it afresh as a chronicle of extinction rather than diversification. First, Raup and Sepkoski (1982) recognized five intervals of unusual diversity decrease over that past 500 million years: the now canonical "Big Five" extinctions that frame discussions of an impending "Sixth Extinction," driven by human activities (e.g., Kolbert 2014). Then came the bombshell. Statistical analysis of the time series generated by all intervals of elevated extinction convinced Raup and Sepkoski (1984) that major extinctions occur periodically, recording a 26-million-year beat over the past 252 million years. The idea of extinction periodicity was anathema to many, but despite repeated reanalysis, the case for at least quasi-periodicity refuses to go away.

Trade books were not Dave's forte, but he did author two accessible volumes on extinction: *The Nemesis Affair: A Story of the Death of Dinosaurs and the Ways of Science* (Raup 1986) and *Extinction: Bad Genes or Bad Luck?* (Raup 1991). The former includes the quintessential and the much-quoted Raupism that in science "a new theory is guilty until proven innocent." More lasting was his textbook, *Principles of Paleontology*, written with Steven Stanley, which guided generations of students (including me) toward new ways of examining the past (Raup and Stanley 1971, 1978). A full bibliography of Raup's work can be found in Foote and Miller's (2016) eloquent tribute to their mentor and friend.

Throughout his career, David Raup was a teacher as well as a scholar. Most notably at the University of Chicago, where he retired as the Sewell L. Avery Distinguished Service Professor, Dave helped students and colleagues alike—a mentor to many and an example to all. Dave was widely recognized by his colleagues, earning membership in the National Academy of Sciences, the American Academy of Arts and Sciences, and

the American Philosophical Society. When the Paleontological Society created the Schuchert Award to honor excellence by young scientists, Dave was its first recipient (1973), and 24 years later, he received the society's highest honor, the Paleontological Society Medal, for his career-long contributions to the field.

Elected 2002

Andrew H. Knoll
Fisher Professor of Natural History
Harvard University

References

Alvarez, L. W., et al. 1980. "Extraterrestrial Cause for the Cretaceous-Tertiary Extinction: Experimental Results and Theoretical Interpretation." *Science* 208: 1095–108.

Cuppy, W. 1941. *How to Become Extinct*. New York: Farrar and Rinehart.

Foote, M., and A. I. Miller. 2016. "The Contributions of David Malcolm Raup (24 April 1933–9 July 2015) *in memoriam*." *Paleobiology* 42: 172–83.

Kolbert, E. 2014. *The Sixth Extinction*. New York: Holt.

Raup, D. M. 1966. "Geometric Analysis of Shell Coiling: General Problems." *Journal of Paleontology* 40: 1178–90.

———. 1972. "Taxonomic Diversity during the Phanerozoic." *Science* 177: 1065–71.

———. 1981. "Extinction: Bad Genes or Bad Luck?" *Acta Geologica Hispanica* 16: 25–33.

———. 1986. *The Nemesis Affair: A Story of the Death of Dinosaurs and the Ways of Science*. New York: W. W. Norton.

———. 1991. *Extinction: Bad Genes or Bad Luck?* New York: W. W. Norton.

Raup, D. M., et al. 1973. "Stochastic Models of Phylogeny and the Evolution of Diversity." *Journal of Geology* 81: 525–42.

Raup, D. M., and S. J. Gould. 1974. "Stochastic Simulation and Evolution of Morphology Towards a Nomothetic Paleontology." *Systematic Zoology* 23: 305–32.

Raup, D. M., and A. Michelson. 1965. "Theoretical Morphology of the Coiled Shell." *Science* 147: 1294–5.

Raup, D. M., and J. J. Sepkoski, Jr. 1982. "Mass Extinctions in the Marine Fossil Record." *Science* 215: 1501–3.

———. 1984. "Periodicity of Extinctions in the Geologic Past." *Proceedings of the National Academy of Sciences* 81: 801–5.

Raup, D. M., and S. M. Stanley. 1971 (1978, 2nd ed.). *Principles of Paleontology*. San Francisco: W. H. Freeman.

Weber, J. M., and D. M. Raup. 1966. "Fractionation of the Stable Isotopes of Carbon and Oxygen in Marine Calcareous Organisms—The Echinoidea. Part II. Environmental and Genetic Factors." *Geochimica et Cosmochimica Acta* 30: 705–36.