David M. Raup

(1933–2015)

Palaeobiologist who pioneered mathematical modelling of mass extinctions.

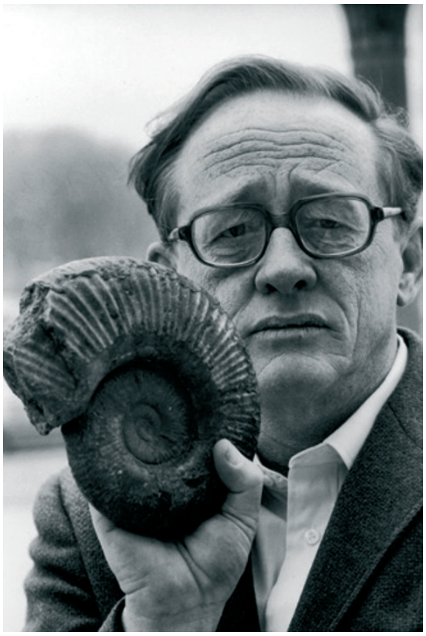
In the early 1960s, few palaeontologists favoured the mathematical over the morphological. But by introducing an analytical approach to the fossil record, David M. Raup changed how we understand patterns and processes in the history of life. Through his championing of 'species as particles in time and space' Raup pioneered computer modelling and increasingly quantitative explorations of the fossil record.

His landmark 1984 study with Jack Sepkoski, a colleague at the University of Chicago in Illinois, proposed a strikingly periodic pattern to mass extinctions over the past 250 million years.

Raup, who was born in Cambridge, Massachusetts in 1933, died on 9 July. His sceptical bent may have come from his father, Hugh, a professor of botany at Harvard University in Cambridge, Massachusetts, and a longtime head of the ecological research facility Harvard Forest. His mother Lucy was a teacher who studied lichens.

Raup graduated with a degree in geology from the University of Chicago in 1953. Following graduate studies in geology and palaeontology with Bernard Kummel at Harvard, focusing on sea urchins, Raup taught palaeontology at the California Institute of Technology, Johns Hopkins University in Baltimore, Maryland, and the University of Rochester in New York. He moved to the Field Museum in Chicago in 1978 as chair of geology and became dean of science in 1980. A few months later he realized his mistake in moving to a position with little active engagement in research. It took two years to engineer a move back to the University of Chicago, where Raup established a vibrant palaeobiological community that still exists today.

The motivating question behind much of Raup's work was how much of the history of life, as captured by the fossil record, requires an adaptive explanation, or any causal explanation at all. The earliest expression of this question came in the 1960s through simulations of coiling in organisms using early analogue graphics computers. Clams, snails, some nautiloids, fossil ammonoids and brachiopods grow in a logarithmic spiral. Such growth can be described by a few parameters, which Raup defined in several influential papers in *Science* and the *Journal of Paleontology*. By exploring the morphological space occupied (and not) by ammonoids, he challenged adaptive explanations of morphological diversity.



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In the 1970s, Raup was a key figure in a project exploring the importance of random events in the diversity of life. Working at the Marine Biological Laboratory in Woods Hole, Massachusetts, with Daniel Simberloff, Stephen Jay Gould, Thomas Schopf and later Sepkoski, he probed stochastic models of patterns in clade diversity — the number of taxa within a group of related organisms.

In contrast to the common view that adaptive selection was responsible for evolutionary trends, the group's results suggested that no adaptive explanation was required for the waxing and waning of different organism groups through time. These models pushed the limits of available computers and were highly influential at the time. The results were subsequently faulted for failing to take into consideration the differences in scale between the models and the fossil record, and have since been superseded by other approaches.

The most significant work of Raup's career began in the 1980s. He and Sepkoski analysed Sepkoski's laboriously compiled record of the first and last occurrences of marine families (later expanded to genera). They identified a 26-million-year cycle in extinction peaks. Their 1984 paper (D. M. Raup & J. J. Sepkoski Jr *Proc. Natl Acad. Sci. USA* **81,** 801–805; 1984) generated widespread speculation about potential extraterrestrial causes for the pattern, unsurprising in the wake of the 1980 discovery of the Chicxulub asteroid-impact crater in Mexico, which is associated with the Cretaceous–Palaeogene mass extinction 66 million years ago. The status of the provocative periodic-extinction hypothesis remains unproven, although Raup remained convinced that it was basically correct

Students were never far from Raup's mind. In 1971, he and palaeontologist Steven Stanley published *Principles of Paleontology* (W. H. Freeman), a textbook so different from existing palaeontology works that he told me that he was unsure sure if anyone would adopt it for classroom use. But the best textbooks help to codify emerging fields, and the two editions by the pair (the second in 1978) taught several generations. Characteristically, when I was considering writing a textbook in the mid-1990s, Raup told me that the field needed a new approach, something as different from Raup and Stanley as it had been from its predecessors.

Raup wrote two popular books, *The Nemesis Affair* (W. W. Norton, 1986) and *Extinction* (W. W. Norton, 1991) in which he described the importance of mass extinctions to evolutionary change, and advanced his ideas that mass extinctions could be the result of bad luck rather than bad genes. His accomplishments were recognized by numerous honours.

By asking questions that no one else thought we could answer, Raup challenged comfortable adaptive explanations for the diversity of life with intuitive mathematical models. Although he admitted to friends that his mathematical skills were limited, his intuition could be profound. Yet he insisted that simulation studies required testing against empirical data. The elegant arguments and spare prose of his papers reflected his rigorous mind, and his high expectations for students and colleagues. His legacy is a much richer and more sceptical palaeobiology. ■

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