David M. Raup, 1933–2015

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David M. Raup was one of the most influential paleontologists of the second half of the 20th century, infusing the field with concepts from modern biology and laying the foundation for several major lines of research that continue today: theoretical morphology, which addresses why, despite eons of evolution, the spectrum of realized biological forms is such a tiny fraction of those that are theoretically possible (1); first-order patterns in the geologic history of biodiversity, in particular whether it has increased steadily over time and what the answer implies about the biosphere and the nature of the fossil record (2, 3); mathematical modeling of evolution: for example, patterns that result from the very structure of evolutionary trees and the apparent order that emerges from stochastic processes (4); and temporal patterns of biological extinction in the history of life and their implications for the drivers of extinction and the place of Earth in the Cosmos (5–7). Despite his many accomplishments, Dave was modest and not known to seek attention or proselytize. He preferred to let his research do the talking.

In his research, Dave Raup was respectful of traditional approaches but routinely questioned received wisdom and pioneered alternative ways of looking at the world. In the 1960s, for example, he brought theoretical morphology to a new level by improving mathematical models of form and by introducing modern computational methods to this endeavor (8). However, he modestly described his efforts initially as mainly a way of describing form, and was always careful to point out limitations in his models. More broadly, he downplayed the novelty of much of his work, stating for example, that the stochastic simulation of evolution was similar to approaches already being taken in other fields, and that the highly quantitative, model- and data-rich studies he and others pursued were really addressing the same questions that had long interested paleontologists and evolutionary biologists, differing mainly in emphasis. Nevertheless, his scientific colleagues evidently felt otherwise, and an unusually high proportion of his work was seminal.

David Raup (*Right*) and Jack Sepkoski discussing analyses of extinction rates in the early 1980s. Image courtesy of the University of Chicago.

Dave had remarkable intuition and strong hunches, but was always careful to distinguish what he thought was true from what was actually demonstrated. Perhaps his two most controversial and far-reaching findings were: first, that the apparent increase in species diversity over the past 500 million years may be an artifact of biases in the geologic record (2, 3); and second, that mass extinction events over the past 250 million years appear to be periodic, with a return time of some 26 million years (5). Dave was careful, however, to point out that the available data allow the possibility of constant diversity rather than demonstrating it conclusively; and, although confident that extinctions were periodic, that additional, perhaps more definitive tests were still needed. One of my favorite examples of the power of Dave's hunches is that he explored the feasibility of large-body impact as a general mechanism of extinction a few years before the Alvarez group published their paper on the end-Cretaceous impact hypothesis (9, 10).

Dave is rightly recognized for bringing a highly quantitative, computational, and analytical approach to paleontology. Equally important, however, were his skepticism, especially toward his own work, and his open-mindedness and desire to understand fully the ideas of others (11). Although Dave, through his example, taught many of us to question our own results and try to "kill" them with alternative ways of modeling and analyzing data before believing them, he also realized that excessive caution would stifle scientific progress. About 20 years ago, Dave and I independently developed a model for estimating extinction and sampling rates of fossil species (12). I then tested the approach with the first three appropriate datasets I could find, and the agreement between model and data were nearly perfect. "Better stop there!" was his instant reaction.

In an age when active mentoring is often an institutional obsession, it is worth remembering the benefits of a hands-off approach. I was fortunate to start graduate school in 1985 amid a few successive student

Author contributions: M.F. wrote the paper.

The author declares no conflict of interest.

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cohorts who would go on to successful, influential careers. One of my fellow students, early in his time at Chicago, mentioned to Dave that he must change his work habits now that he was no longer an undergraduate. Dave's simple response was, "Why? Obviously whatever you've been doing has worked well so far." Dave had an amazing gift for fostering the progress of students by giving them room to develop their ideas, and leading by example rather than supervising. I once pursued a research project that turned out to lead me down a blind alley. In hindsight it was clear that Dave knew this idea would probably go nowhere, but he evidently thought it was important for me to discover that on my own. A complementary interpretation is that he thought it highly unlikely that anything would come of it, but that real progress mainly comes from taking risks—this experience was during the thickest days of periodic extinction—and clearly Dave was no stranger to taking risks.

Dave rarely gave explicit scientific advice, but he was famously astute, so we quickly learned—sometimes the hard way—that on those rare occasions that he did volunteer advice, one would do well to heed him. In my case, an enlightening example came at the time of my comprehensive examinations. A couple of weeks before that I had asked Dave if there was anything in particular I should do to prepare. "Not really," he replied, then thought about it a bit, and added, "You might brush up on your stratigraphy." I ignored the suggestion and later imploded when questioned at my oral examination on some routine stratigraphic matters that I should have had down cold. I never ignored him again.

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