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Invited Essay

IN MEMORIAM

The Contributions of David Malcolm Raup (24 April 1933–9 July 2015)

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In recounting the exploits of the renowned test pilot and World War II ace Chuck Yeager, Tom Wolfe (1979) observed that Yeager's calm, West Virginian drawl can 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, who sought to emulate the "ace of aces," and it spread further, from generation to generation, aided by the participation of many of those disciples as astronauts in NASA's manned space program. During the heady days of the Mercury, Gemini, and Apollo programs, the drawl and demeanor 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, by dint of the examples they set, colleagues seek to emulate not only their methods, but also how they carry themselves in the arena. And so it was with Dave Raup, one of the most influential paleontologists of the past half-century, who died this past summer after a brief illness. 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 as the center of attention in any forum. But the way he carried himself—actively seeking out 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 appreciable 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.

Dave's earliest work, influenced in part by Ernst 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* (bibliog. 1–2). Among other results, he made a convincing case for the ecophenotypic basis of some among-population differences in shape, and noted that many putative species-level differences among fossil populations are consistent with non-genetic variation in living populations. This work already exemplified the careful analysis, logic, and attention to modern ecology and evolutionary biology that would come to characterize Dave's subsequent contributions.

The *Dendraster* work was followed by a series of papers documenting the crystallographic axis orientations of plates in the echinoid test (bibliog. 3–4, 6–8, 13, 18–19). These demonstrated that c-axis orientations are largely fixed within echinoid species and at higher taxonomic levels; that species show ontogenetic variation following a few general patterns; and that groups of plates within a species often vary consistently from one another. Dave used the phylogenetic signal evident in cases where higher taxonomic affinities are fairly well known as a basis for

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suggesting solutions where affinities are less clear. He also tackled the functional significance of axis orientations, ultimately arguing for the relevance of light penetration, in view of the among-species covariation in light sensitivity and axis orientation, and suggesting that light penetration in the apical plates might even play a role in navigation. He also argued that c-axes orthogonal to the plate surface facilitated the ontogenetic development of plate curvature. A study of teratologies in *Strongylocentrotus* demonstrated that crystallography was inverted when plate position was inverted, and that the missing plates in tetraradiate specimens could be identified.

Toward the end of Dave's echinoid period, he and geochemist Jon N. Weber documented carbon- and oxygen-isotopic variation in echinoid plates (bibliog. 14, 16–17, 24). 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 somewhat sensitive to temperature, they show enough genetic variation to limit the use of echinoids for paleoenvironmental inference. Taxonomic variation in carbon isotopes suggests metabolic differences among clades, and the taxonomic diversification of echinoids since the mid Paleozoic correlates with increased variance in isotopic composition. This body of work represents one of the earliest demonstrations of vital effects in stable isotopic composition.

Judging from citations to his publications, the work discussed so far seems to have been of interest mainly to students of echinoids, and even then the application and extension of Dave's findings to phylogenetic problems has been limited (for echinoid examples, see Emlet 1988 and Kroh and Smith 2010). However, a few paleontologists, notably Dan Fisher and his students, have gone on to apply crystallography to the systematics of other echinoderm groups, including stylophorans, crinoids, and blastozoans (Fisher and Cox 1988; Bodenbender 1996; Bodenbender and Ausich 2000; Bodenbender and Hiemstra 2004).

While Dave was engaged with echinoids, he began a long-term research program in theoretical morphology—a comparison between actual and theoretically possible 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 bivalves, gastropods, brachiopods, and ammonoids occupy largely distinct regions of the coiling-parameter space (bibliog. 20). He also demonstrated that the concentration of ammonoids in certain regions of the coiling space is unlikely to reflect optimization of a single functional demand such as stability or shell efficiency, and therefore probably reflects a tradeoff resulting from multiple demands (bibliog. 21).

Dave started with a consideration of gastropod coiling (bibliog. 5, 9), but eventually modified and extended the model to other coiled forms (bibliog. 12, 20–22, 35–36) and even developed a soap-bubble model of echinoid plating (bibliog. 25), a model for helical bryozoans such as *Archimedes* (bibliog. 69, 133), and an algorithm for generating grazing traces from a few simple rules with an added stochastic element (bibliog. 28). In the last example, his simulation program occasionally generated "mistakes"—traces that looked like no ichnofossils ever found. He thought the algorithm might not be working, but his collaborator Dolf Seilacher found sense in the mistakes by noting that they mimicked suboptimal plowing patterns that he had seen in rural Swabia, when farmers didn't plan properly and ended up crossing their own furrows!

Although Dave evidently realized the great potential of theoretical morphology from the start, laying out possible applications to ontogeny, phylogeny, ecology, and adaptation, his treatment in his earliest papers seems somewhat cautious, referring to the coiling model mainly as an objective way to *describe* gastropod form, in lieu of terms such as "turbiniform" or "turriculate," and stating that, "the objectives are practical rather than theoretical" (bibliog. 5: p. 603). Likewise, he commented that his insightful analysis of ammonoid coiling, "is primitive in many regards" (bibliog. 21: p. 65). Downplaying the innovative aspects of his

work is something that would characterize Dave's papers for his entire career; understatement and claims that his approaches were rather similar to what others had already done, differing only in emphasis, were to become recognizable aspects of his style. (Even mundane titles often belied clever and groundbreaking analyses; see [bibliog. 62], for example.) A common theme that emerges in the echinoid soap-bubble work and the simulation of grazing traces is that, even though we do not know whether the model is biologically realistic, its ability to generate forms so similar to what we see argues that the "rules" an organism follows *need not* exceed the complexity of the model. Such statements of parsimony and a willingness to entertain unconventional ideas would emerge in later work as well; for example, his conclusion that the available data *allow the possibility* that species richness has not increased since the early Paleozoic (bibliog. 33, 45, 49), a topic to which we return below.

In the first coiling paper (bibliog. 5), Dave reproduced gastropod form mechanically, shrinking and enlarging the generating curve photographically. A year later (bibliog. 9), he moved to a digital computer with curves printed to a first-generation plotter, and, a few years later, with electrical engineer Arnold Michelson (bibliog. 12), he found that shells could be simulated much more quickly using an analog computer with output piped to an oscilloscope. Thus began an exploration that 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; he was invited to participate in a 1969 symposium organized by D. F. Merriam (bibliog. 27), and he himself organized a symposium at the first NAPC (bibliog. 31). (An amusing side-note: Dave was compelled to add to the figure legends for bivariate plots in the echinoid modeling paper that "illustrations were drafted by computer.") At this time, he envisioned an important role for computers in many areas of paleontology, such as morphometrics and image recognition; a follow-up paper in 1981 (bibliog. 60) conveyed that computational approaches had failed to live up to their potential in many areas, such as image analysis and biostratigraphy, but that they had clearly succeeded in the areas of mathematical modeling and simulation, and were likely in the coming years to enable "increasingly ambitious analyses of large data sets having to do with distribution of fossil taxa in time and space" (bibliog. 60: p. 269). His 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 *Handbook of Paleontological Techniques* (bibliog. 15); his chairmanship of the National Research Council's Committee on Guidelines for Paleontological Collecting (bibliog. 103); the workshop on "species as particles" that he taught with Tom Schopf at the Smithsonian in 1978; and, of course, the two editions of *Principles of Paleontology*, co-authored with Steve Stanley (bibliog. 32, 52).

In computation and other matters, Dave was a do-it-yourselfer and tinkerer, and generally favored his own programming over canned solutions. In the 1980s, when many were discovering the utility of software like 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. (His wife, Judie Yamamoto, is an accomplished artist whose many talents include weaving.) As a crossword enthusiast and a formidable Scrabble player, he also wrote programs to generate crossword puzzles.

In the late 1960s and early 1970s, Jim Valentine's depictions of Phanerozoic biodiversity and extinction patterns (e.g., Valentine 1969) sparked Dave's interest in possible biasing effects. Most importantly, he questioned whether a substantial Cenozoic diversity increase is truly supported. He systematically laid out the time-dependent and -independent biases that are 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, that he collectively referred to as the "Pull of the Recent" (bibliog. 33, 45, 49, 53). He also compiled an empirical tabulation of fossil species (bibliog. 44) as an alternative to the

indirect estimates of Valentine and others, which had suggested a ten-fold increase in species richness from the Mesozoic to the Recent. A compromise, of sorts, was struck in the 1981 "Consensus Paper" (bibliog. 63), led by Jack Sepkoski, which argued that several different measures of diversity show similar trajectories over the Phanerozoic, and that these in turn reflect a true biological signal. Ironically, despite signing on to this paper, both Dave and Jim Valentine retained considerable affinity for their initial points of view (Valentine 1989; Miller 2000, 2009; D. Sepkoski personal communication 2015).

Dave was careful to present the idea of non-increasing species richness as a hypothesis consistent with available data, rather than a demonstrated fact. The evenhanded tone of the 1972 paper (bibliog. 33), in which he conveys arguments both for and against increasing diversity, is masterful. His application of rarefaction to biodiversity is similarly balanced with respect to the inferences that can and cannot be drawn from rarefaction curves (bibliog. 42). Ask five paleontologists about the true trajectory of Phanerozoic diversity and the most appropriate methods for getting at it, and you're likely to get at least ten answers. One point on which all would agree, however, is that Dave's insistence on hard data and his willingness to question received wisdom stimulated and set the tone for a vast and important ongoing body of research. What eventually evolved into the Paleobiology Database, in fact, started as an effort to revisit the question of Phanerozoic biodiversity using new approaches for data assembly and analysis (bibliog. 132).

Dave's penchant for questioning conventional views would combine with another of his hallmarks—importing methods and approaches from other fields, in this case equilibrial demographic models—in the seminal papers of the MBL group (so called because the authors began their collaboration at the Marine Biological Laboratory at Woods Hole, Massachusetts) (bibliog. 37–38, 40–41, 43, 48, 54). Dave programmed simulations of the evolutionary branching process to ask how the history of diversity within higher taxa would appear if it behaved as if it were random—meaning that all component lineages had the same inherent propensities to branch, persist, or become extinct in a given time unit—and to ferret out the aspects of biodiversity that fell outside the boundaries of these simulations, such as rapid radiations and extinctions. Dave evidently sought to make stochastic modeling seem less radical than it might appear by pointing out that paleontologists have long sought general evolutionary laws—so the new "nomothetic paleontology" perhaps should not be seen as so new after all—and that other fields close to paleontology, including evolutionary biology, geomorphology, sedimentology, and stratigraphy, had already adopted the modeling approach (bibliog. 43, 47).

One of the principal lessons of the MBL group's work was that "the simulation should be a warning against using patterns of diversity as the *major evidence* for differences in evolutionary potential" (37: p. 534, emphasis in original). One result 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 and one of his books (bibliog. 117) on what he called "the extinction problem." In his Presidential address to the Paleontological Society (bibliog. 51), he likened the extinction of higher taxa to the stochastic disappearance of family surnames, a problem that had been treated mathematically in the 19th century (Watson and Galton 1875). He developed a statistical test (bibliog. 58) for whether extinction rates in different taxa are sufficiently different to justify interpreting them in terms of clade-specific properties—for example, "creodontness" or "blastoidness." In a paper generally cited for its estimate of species-level extinction rates in the late Permian, Dave presented the inescapable conclusion that an event so severe—up to 96% species extinction, by his estimate—simply *must* involve a significant stochastic element to who survived, an "evolutionary founder effect," as he put it (bibliog. 55). And in analyses with Dave Jablonski on Maastrichtian bivalves, he showed that the K/Pg extinction event was not generally selective with respect to life position or trophic mode, nor was there a geographic gradient to extinction intensity (bibliog. 121, 126). Nevertheless, he did not rigidly advocate the lack of biological signal in

extinction. For example, he used mathematical modeling of the time-homogeneous birth-death process, another import from outside paleontology, drawing particularly on the works of Yule (1924), Kendall (1948), and Bailey (1964), to show that trilobites must have had different speciation and/or extinction rates relative to other groups for their diversity to have waned through the Paleozoic (bibliog. 61). He recognized that the simultaneous termination of many independent lineages at major extinction events could not be explained by chance, although it took some evolution in his thinking to reach this viewpoint; and he argued that extinction episodes are biologically selective, even if we do not yet know the specific bases for selectivity (bibliog. 93).

The general theme that apparently strong, non-random patterns could emerge from a stochastic system was repeated in the collaboration with Steve Gould, which added morphology to the MBL simulation model (bibliog. 38). The problem of phylogenetic structuring of biologic traits is now widely recognized in evolutionary biology, thanks to later work by Felsenstein (1985) and many others. 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. This theme also underlies several papers on the random walk as a null model for phenotypic evolution, most notably Dave's collaboration with Rex Crick reanalyzing Brinkmann's classic biometric data on *Kosmoceras* (bibliog. 62), a body of work that helped initiate efforts, still ongoing, to infer evolutionary processes from temporal sequences of morphologic data (e.g., Hunt 2006, 2012). The *Kosmoceras* paper included the sobering message that, even though the data in question should have been ideal for addressing tempo and mode in the context of the punctuation/gradualism debates, it is difficult to reach firm conclusions. Dave's earlier collaboration with David R. Lawrence had a similar message regarding the ability to infer paleoenvironments from taxonomic occurrence data (bibliog. 10–11).

Although simulation studies could be effective for consciousness raising, Dave saw that analytical models may have more power to address evolutionary questions. We already mentioned his application of the birth-death model to the problem of higher taxonomic extinction and of the random-walk model to evolutionary sequences. In a thought experiment with Jim Valentine, Dave made the case that it is at least plausible that life on Earth 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 (bibliog. 73). (One of us once mentioned this paper in Leigh Van Valen's graduate seminar on Evolutionary Processes. Leigh just shook his head and muttered, "I don't know why they ever wrote that paper.") 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, because most pairs of living species share a common ancestor in the Cambrian or Ordovician (bibliog. 74).

Starting in the mid-1970s, Dave considered the question of taxonomic survivorship in the context of Van Valen's "New Evolutionary Law," the proposition that rates of extinction within ecological groups are stochastically constant (Van Valen 1973). (Leigh initially objected to Dave's reference to "Van Valen's Law" as if it were the only one he might propose. Dave countered that the next one would simply be referred to as "Van Valen's *Second* Law.") To provide a rigorous test for constant survivorship, Dave imported a method of statistical analysis from the literature on the failure of manufactured parts (bibliog. 39). He initially suggested that the stratigraphic failure to observe short-lived taxa and the taxonomic tendency to subdivide long-lived groups would lead higher taxa to show spuriously *increasing* rates of extinction with taxon age. He subsequently improved the analysis of taxonomic survivorship by following cohorts through geological time (bibliog. 50). He also realized that, according to the mathematics of the branching model, if speciation and species extinction rates are

constant, the expectation is that supraspecific taxa will show *decreasing* rates of extinction with taxon age. Analyses of genus survivorship by Dave and others have borne this out, although the reasons for age-dependence continue to be investigated (Finnegan et al. 2008). Dave later added models of incomplete sampling to survivorship analysis, showing that sampling and extinction rates could, with certain assumptions, be estimated from a frequency distribution of truncated stratigraphic ranges (bibliog. 129).

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 (bibliog. 78, 82, 93, 98, 100, 128). This question would come to be an integral part of his analyses, many of them with Jack 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, which in turn is based on the stepped pattern of genus-level cohort curves (bibliog. 115). 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 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 populations of events, whether distinguished by cause or by magnitude.

The analysis 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—episodes that have come to be known as the "Big Five" (bibliog. 67, 72, 93). These patterns were initially documented with Jack Sepkoski's family-level compendium, and were later backed up with his genus-level data. Analyzing these genus-level data, Dave, along with George Boyajian (bibliog. 106), also demonstrated that major groups of marine animals show 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" (bibliog. 106: p. 123), namely, widespread, physical perturbations of the biosphere.

The foregoing summary of Dave Raup's work on extinction omits one result on which paleontologists decidedly do not all agree: the finding that extinction events since the late Permian are uniformly spaced with a periodicity, according to the initial estimate, of some 26 million years (bibliog. 76, 91, 92, 94, 100, 107, 114). When Dave produced one of the first figures depicting the even spacing of extinction events, it was so striking that, upon first seeing it, Jack Sepkoski took no more than a moment to exclaim, "Holy shit! Fischer and Arthur were right!"—referring to a provocative paper proposing that major features of biodiversity, oceanography, carbon cycling, and sedimentation vary with a cyclicity of ~32 Myr (Fischer and Arthur 1977).

As has often been stated, the finding of periodicity spawned a broad range of research in fields such as astrophysics that had previously paid little attention to the fossil record. Dave and Jack suggested that the driver was likely extraterrestrial, although to date no culprit has been found. Given that periodicity would be a radical claim, the initial paper on the subject is appropriately, if somewhat amusingly, cautious. After the authors spend some four pages presenting statistical tests that support periodicity, they begin the concluding section of their paper, "*If* periodicity of extinction in the geologic past can be demonstrated, the implications are broad and fundamental" (bibliog. 76: p. 805, emphasis added). 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 his hunch was that extinctions are periodic, he realized the case was not proven, and he viewed periodicity as a live hypothesis that had enough support to merit continued consideration.

The periodicity studies, combined with the evidence for a major bolide impact that may have triggered or at least contributed to the K/Pg extinction event (Alvarez et al. 1980), influenced many essays in which Dave considered the place of Earth and its biosphere in a "cosmic environment"; the history of catastrophism in Earth science; "rules" of extinction; and the role of extinction in evolution (bibliog. 84–85, 89, 104–105, 108, 110–111, 113, 119, 122, 125). In truth, his consideration of life in a cosmic environment led to the periodicity analysis, and not the other way around. In 1981 and 1982, Dave 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*) (bibliog. 83–85). The interactions at these workshops, Dave subsequently wrote in the proceedings, were largely responsible for getting him and Jack Sepkoski to test for periodicity of extinction in the first place. And his work and leadership were instrumental in helping to bring research on complex and higher organisms into the fold of NASA's program in Exobiology. Dave was also a supporter of SETI, while questioning the common assumption that intelligent life elsewhere need be humanoid or even conscious (bibliog. 120, 123).

Astrophysicists had long known that extraterrestrial impacts were quite common throughout the history of life, so Dave realized it made little sense to think that life on Earth is somehow isolated from cosmic events and catastrophes that are rare on human time scales but common in geological time. He therefore felt that Darwin and Lyell had too long held sway in promoting rigidly gradualist thinking, at least in the English-speaking world, with the role of catastrophe downplayed. Biologists tended to ignore extinction, or tacitly assume, without evidence, that it was a simple result of a Darwinian struggle for existence. As Dave often wrote, the vast majority of species that ever lived are extinct, so 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 (bibliog. 118): "field of bullets," or completely random extinction; "fair game," in which species survive because of differential fitness that evolved 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 paleontology and evolutionary biology still have much to learn about which models apply in which events and to which clades.

The probable importance of extraterrestrial influences on terrestrial life led Dave to consider the possibility of impacts as a general cause of extinction (bibliog. 113). 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 (bibliog. 119). He also argued that other candidates for general causes of extinction, such as change in climate or sea level, do not satisfy the requirements set by the distribution of waiting times. Dave was careful to distinguish the question of periodicity from the general role of large-body impacts in extinction events (bibliog. 100). For example, he and physicist Jim Trefil analyzed the cratering record and concluded that the best fit to the data consisted of a model with about one-third periodic events and two-thirds "rogue" events that occurred at random times over the past 250 Myr (bibliog. 101).

Finally, Dave's interest in impacts and extinction predated the Alvarez et al. (1980) paper by at least a few years, motivated in part by Schindewolf's (1963) and McLaren's (1970) suggestions, Urey's (1973) analysis of the timing of impacts and stratigraphic boundaries, and Öpik's (1973) estimates of impact frequencies and the likely geographic extent of their effects. Dave carried out simulations in which he "bombarded the Earth" at random points with perturbations that killed off all life

within randomly chosen "lethal radii." He found that, given the biogeographic distribution of terrestrial and marine animals, it would be necessary to annihilate more than half the globe to produce an event big enough to register as a mass extinction (bibliog. 70). This result implied that the major events we have seen in the history of life must generally have had globally pervasive causes. As mentioned earlier, he tested this idea with Maastrichtian bivalves, finding that extinction rates were effectively uniform across the globe (bibliog. 121). Although the simulation work was presented at a conference in 1981 and published in 1982, it was actually carried out in 1977, well before the Alvarez hypothesis. And curiously enough, whereas the paper was presented at a conference on impacts, it never explicitly mentions impacts as the putative cause of perturbation, although an earlier presentation of these results (bibliog. 61) is clearly in the context of extraterrestrial impacts.

This account of Dave Raup's research contributions touches on his scientific style, which was marked by the broad scope and importance of questions he addressed; importation of ideas and methods from fields outside paleontology; willingness to consider any idea, no matter how unlikely a priori; respect for a diversity of scientific cultures and approaches; skepticism regarding received wisdom as well as his own ideas; tight logic; analytical rigor; and concern for the health of paleontology as a discipline. But he also had a personal style that many of us were fortunate to experience as students and colleagues. 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 surely 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 each reach their potential. He often had a minimalist approach to graduate advising. For example, a manuscript given to Jack Sepkoski might be returned extensively marked up by his editor's blue pencil. The same manuscript would come back from Dave with a concise list of comments or a simple note that said something like, "Nice study. Clear, interesting, and important. Reduce number of tables and figures. And publish." And Dave's reviews would always be returned rapidly; he was notorious for never letting a stratigraphy develop on his desk. 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.

Dave's personality and acumen were also much in evidence during his on-and-off stints as an administrator; he clearly enjoyed the political side of academic life and was a shrewd tactician. During his term as department chairman at Chicago, he was once in the thick of recruiting a new faculty member and was hoping to parlay one faculty line into two. Somehow, he learned that a higher-level administrator who would play a role in deciding whether to grant the extra line was fond of antique scientific instruments. So Dave retrieved two old brass microscopes that were languishing in the basement of the geology building, and presented them to the administrator as a gift. There is really no way to know whether the subsequent permission to hire two faculty was in any way tied to the gift, but it didn't hurt! At the University of Rochester, Dave would talk frequently about the art and frustration of dealing with Deans, noting wryly, "Deans cannot read, but they can count." He also had a bead on the Dean's parking space so he would know when the Dean was on campus even when the Dean's administrative assistant claimed that he was out of town.

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 honest 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. When one of us told him we might not finish the PhD, or might finish and then leave science altogether, he was supportive, but, evidently realizing that other faculty might not feel the

same way, he advised, "That's certainly understandable…but I wouldn't advertise it too broadly if I were you." And he observed that it is possible to be quite successful as a professional paleontologist, even if one is not dedicated to the work 24/7.

Dave was a man of honesty and integrity. He called out evolutionists for misrepresenting the arguments of creationists (bibliog. 71, 75), and 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 *The Nemesis Affair*, which Dave autographed during his visit. Of course, Dave was *not* a creationist, but he was respectful of different viewpoints, and it frustrated him that some of his colleagues did not 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. And he remained available throughout the years for visits and to review manuscripts and provide professional or personal advice whenever it was needed. Clearly, though, he enjoyed the freedom, solitude, and beauty of Washington Island, and he enjoyed traveling the world with Judie.

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

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