PNAS RETROSPECTIVE

James W. Valentine (1926–2023): Trailblazing paleobiologist with an enduring legacy

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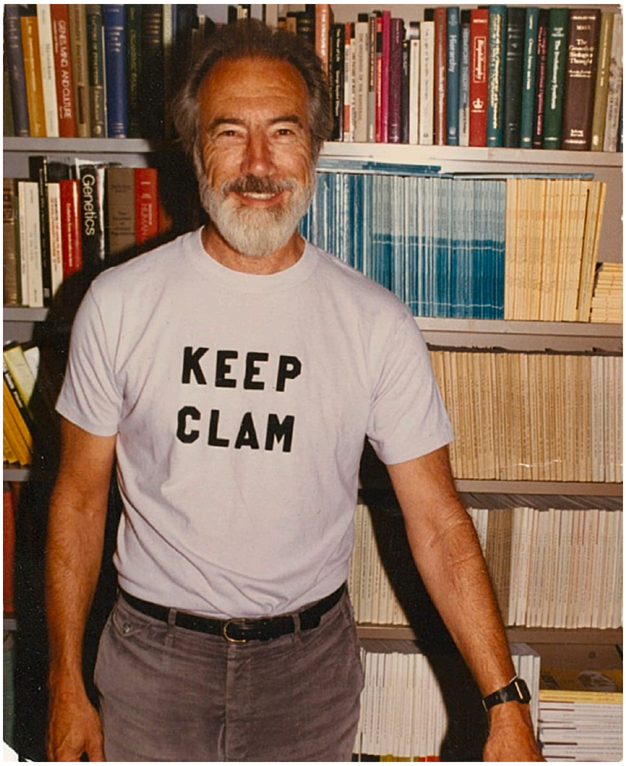
On April 7, 2023, the geological and biological communities lost one of the most creative and influential scientists working at that interface: the paleobiologist James W. Valentine. It is difficult to imagine the current vibrant and interdisciplinary state of paleobiology without his remarkable contributions to our understanding of the origin, maintenance, and spatial dynamics of biological diversity through geologic time to the present. His wide-ranging contributions have shaped the field, influencing multiple generations of scientists within paleontology and far beyond its conventional limits.

Jim Valentine was born in Los Angeles on November 10, 1926. Following an obstreperous adolescence, he served on US Navy landing craft in World War II during some of the fiercest battles in the Pacific. Remarkably, he served under Harry Hess, one of the architects of plate tectonics (a view of the Earth that would later figure into some of Valentine's important paleobiological contributions), and even—without knowing their importance—took some of the soundings that Hess would eventually use to demonstrate the link between deep-sea topography and the operation of plate tectonics. Supported by the GI Bill, Valentine then attended Philipps College in Enid, Oklahoma, before pursuing a PhD at the University of California, Los Angeles (UCLA). From there, he took a faculty position in the Department of Geology, the University of Missouri at Columbia, after which he returned to the University of California system, starting at UC Davis, then at UC Santa Barbara, and finally at UC Berkeley in the Department of Integrative Biology and the UC Museum of Paleontology, transitioning to Emeritus Professor there in 1993.

Valentine is most widely known as a theoretician and thinker on the grandest scales, but his PhD research at UCLA was on the Pleistocene molluscan faunas of California and Mexico. Although not always obvious, much of his subsequent work flowed naturally from a deep understanding of these fossil assemblages, which he continued to study even as he wrote field-defining and agenda-setting papers and books spanning the entire history of multicellular life. This early work initiated a series of influential papers on the role of climate gradients, geographic barriers, and biological adaptations in generating marine diversity and provinciality. It was also the springboard to even larger-scale questions. For example, Valentine used these faunas to demonstrate the negligible effects of the substantial Pleistocene sea-level oscillations on species extinction and origination and the role of physical barriers and regional seasonality differences in setting the boundaries and properties of natural biogeographic units. They also led to recognizing the individualistic movement of species (instead of cohesive communities) during climate changes, forming "thermally anomalous assemblages"—a dynamic later discovered independently by others using the Pleistocene–Holocene terrestrial pollen record.



James W. Valentine in his office. Photo credit: Cathryn Campbell, with thanks to Kaustuv Roy.

Valentine's interest in the spatial organization of biological diversity led him to explore the relationships between two hierarchies: taxonomic (from species through families to phyla) and ecologic (from populations through provinces to biomes). He drew on this hierarchical framework along many fruitful avenues. Thus, he viewed the origin and demise of discrete biogeographic provinces as an integral part of global diversity dynamics, and with Eldredge Moores was the first to explore the role of the newly validated model of plate tectonics in regulating global diversity via provinciality (1, 2).

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Some details have not held up, as our fuller understanding of the end-Paleozoic mass extinction makes it unlikely to have been driven by the amalgamation of the Pangaea supercontinent. But he also proposed in these early analyses that the post-Paleozoic diversity rise was promoted in part by the early Mesozoic fragmentation of the Pangaea supercontinent, along with later cooling at the poles that steepened temperature gradients, allowing discrete provinces to form along north–south coastlines. It was a compelling vision of how global biodiversity operates, and the basic outlines have been confirmed and extended in many ways (3).

This hierarchical approach also pervaded his enormously influential early book, *Evolutionary Paleoecology of the Marine Biosphere* (4), which synthesized marine ecology, biogeography, and paleobiology in terms of the processes structuring biodiversity across scales and levels. He laid the foundation for a view of spatial patterns of biodiversity shaped by solar energy and seasonality and concluded with an ecological history of the marine biosphere that still reads as provocative and forward-looking. Here, too, his ideas spurred many lines of research and have been widely corroborated. It was striking, in just one example, to see in ref. (5) that the biogeographic provinces that Valentine recognized in 1973 are a better fit to ocean compartments defined by satellite data (unavailable in 1973) than later biogeographic schemes. His view of life's history and the processes that shape it was further integrated into the larger evolutionary picture in a well-received textbook, with a stellar cast of coauthors (6).

Valentine's hierarchical view also powered his pioneering 1969 analyses of his taxonomic database spanning the Cambrian–Recent (i.e., Phanerozoic) fossil record, which revealed different dynamics at different hierarchical levels: Most taxonomic Phyla and Classes appeared early in the history of multicellular animals, but the number of species, genera, and families continued to accumulate within the major metazoan clades, with interruptions and rebounds, over the ensuing 500 million years. He interpreted the early appearance of higher taxa in terms of the establishment of major body plans, signifying what he later treated in terms of developmental changes and what has come to be called an "early burst" of morphological and ecological disparity. In contrast, he viewed the rise of species- (and genus- and family-) richness as largely reflecting ecological and biogeographic processes, i.e., lineage diversification via niche subdivision and specialization, along with increasing provincialization. The low diversity/high disparity evolutionary pattern of the Cambrian Explosion was confirmed for many clades as more powerful computers allowed direct analysis of body form rather than the indirect proxies available to Valentine. Spurred by a niche-based view of diversifications, with priority effects playing a key role, he developed a two- dimensional, checkerboard-like conceptual model that has proved strikingly effective in accounting for large-scale patterns in the fossil record (7). When tuned using empirical extinction and origination rates, in collaboration with his student Timothy Walker, it even yielded a plausible estimate of the number of empty ecological niches present in a macroevolutionary system (8).

Valentine made many contributions toward understanding this unique episode of what he called "morphological profligacy," synthesizing invertebrate anatomy, paleontology, phylogeny, functional morphology, and development in a string of ambitious papers and two books, *The Origin of Phyla* (9) and, with his former PhD student Douglas Erwin, *The Cambrian Explosion* (10). The two major hypotheses for the Cambrian Explosion of animal disparity, and its subsequent slowdown, were both framed by Valentine: that the geologically sudden production of body plans was promoted by the ecological opportunities of the Early Cambrian and their waning by the filling of ecospace, or by the origin or expansion of a powerful developmental toolkit that evolved toward a more heavily buffered and less flexible state over time. At first, the initial assembly of regulatory systems seemed a potential trigger for the Explosion. However, as the floodgates opened on the modern era of molecular developmental biology, he (and others) realized that many of the genes and much of the genetic machinery must have been in place prior to the emergence of such disparate forms as Early Cambrian arthropods, mollusks, echinoderms, and chordates. A more subtle increase in developmental complexity was required to promote and then slow the Cambrian radiation. He realized that the hypotheses need not be mutually exclusive; indeed, that ecological and developmental mechanisms seemed likely to be working in tandem. That debate continues, although impoverished by the loss of one of its great luminaries.

Valentine received considerable recognition for his contributions, including Fulbright, Guggenheim, and Rockefeller Foundation Fellowships; election to the American Academy of Arts and Sciences, the US National Academy of Sciences, and the American Philosophical Society; the Medal of the Paleontological Society and the Lapworth Medal of the Palaeontological Association (UK), both societies' highest honors; and a Festschrift (11) with contributions by 22 of his admiring colleagues. He was elected President of the Paleontological Society (1974 to 1975) and in that capacity played another major role in the development of the field, as one of the prime movers in establishing the journal *Paleobiology*, which immediately became the chief forum for the discipline.

In my own experience, Valentine's impact came from an exceptional combination of skills: an ability to draw on insights gained from constantly shifting among disciplines, to extend disparate quantitative findings into large-scale synthetic inferences, and to apply intuitions sparked by his mental model of how the natural world works. Even his most abstract theoretical work was underlain by a strong empirical foundation, an approach that paid big dividends. It was not that he knew more facts than other scientists, but rather the way he pulled them together in new and surprising ways that made his work so lasting and influential. It was simultaneously delightful and humbling to watch him assimilate a new, hard-won time series, scatterplot, or diversity map into his worldview, producing a fresh view of the new data and its larger significance. And then, this laconic and soft-spoken revolutionary would gently push his collaborators to really come to grips with what we had found. As he often impressed upon me and many younger colleagues, Jim saw it as both the privilege and the obligation of scientists breaking new ground to be bold in exploring the implications of their discoveries. This he unfailingly did throughout his long career, opening new ways of seeing how evolution drives, and is driven by, the ecologies, biogeographies, and embryologies of the present-day and ancient biosphere. He leaves a scientific legacy that will continue to challenge and inspire us.

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