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DAVID B. WAKE



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David Wake was an internationally renowned evolutionary biologist and a professor emeritus of integrative biology at the University of California, Berkeley. He was the world's leading expert on salamanders. In addition to fundamental research, David was passionate about biodiversity conservation and was among the first to warn of a sharp global decline in frog, salamander, and other amphibian populations. It is rare to have a person like David as an outstanding scholar, excellent mentor, and visionary leader.

Outstanding Scholarship

David Wake brought an infectious enthusiasm to science, scholarship, and ideas. To be with David was to be pulled into a world of new theories and hypotheses, emerging questions and important scientific histories. Many of us will never forget David's excitement, bordering on wonder, at turning over logs to see clutches of recently laid plethodontid eggs.

David's passion for new ideas sprouted from his open-minded approach to science. He used to describe how the Norwegian Lutheran church of his upbringing in South Dakota had a special person appointed to be a devil's advocate of the preacher, someone who brought a critical approach to the church's teachings. Roots of this personal history are seen in his approach to science. He brought a healthy skepticism to the status quo and was always open to new ways of doing things, which led him to expand his research program with new approaches, collaborators, students, and postdoctoral scholars. For example, unlike many morphologists in the 1980s, David was quick to accept and incorporate molecular data in his analysis of evolutionary trees. This work by David and his colleagues led to the acceptance of relationships among salamander taxa that posed new puzzles for morphologists. Patterns emerged from these evolutionary trees that required new kinds of explanations. The feet of different salamander taxa evolved similar patterns of bones independently; elements of the skull showed similar patterns. The independent evolution of similar traits in different species became a puzzle in need of solving. Bringing molecular approaches to the fore allowed David and others to see productive new questions as they sought to understand evolutionary relationships.

David's approach to solving this puzzle of evolution came from immersing himself in yet another field and learning entirely new approaches. While at his first academic position at the University of Chicago, David was a functional anatomist, par excellence. His studies with Eric Lombard on tongue projection looked at the relations among different bones and muscles of the salamander body to explore how a

tongue could project long distances with extraordinary speed. An understanding of the mechanical linkages that produced this extreme trait led to the development of scenarios for ways in which this adaptation arose. This work exemplified David's approach to morphology at the time—functional morphology and adaptation reigned supreme. In the late 1970s, influenced by *Ontogeny and Phylogeny*, the landmark book by legendary evolutionary biologist Stephen Jay Gould, David helped launch a discussion group at Berkeley that was to change the trajectory of our own work and the field in general. The development of an organism from egg to sexually mature adult became a major theme in the field and linked observations from morphology and paleontology with those of embryology, ecology, and ultimately molecular biology. David, along with his students and colleagues, centered an understanding of development in discussions about rates and patterns of evolutionary change, and thus spawned a new approach to character evolution. To David, this notion revealed that features of evolution that were formerly considered artifacts or noise actually reflected deep processes at work in the formation of variation. Developmental pathways were seen to have influenced variation, leading to some traits evolving more frequently than others. This relationship led to the notion that traits, even very complex ones such as life histories or mechanisms of tongue projection, could evolve multiple times independently. Tellingly, the members of the Berkeley discussion group went on to populate major universities and make transformative discoveries of their own.

David's interest in development and evolution led him to publish several landmark essays on broad topics in evolutionary biology, such as the causes of convergent evolution and the important role of developmental constraints in shaping the evolution of phenotypes. Although in many cases the ideas leading to these papers were born from his studies of salamanders, the ideas themselves were broad and applied widely to all organisms across the tree of life. One of his most impactful essays was a 1979 paper (Alberch et al.) in the journal *Paleobiology*, simply titled "Size and Shape in Ontogeny and Phylogeny," and co-authored with his then-graduate student Pere Alberch (who would go on to assume a professorship at Harvard University and later become the Director of the Museo Nacional de Ciencias Naturales in Madrid), Stephen Jay Gould, and the famous mathematical biologist George Oster. This paper sketched out a formalism for quantifying the several ways in which rates and magnitudes of ontogenetic processes evolved over time and across lineages to generate the diversity of phenotypes we might observe in any given clade. For example, species whose adults exhibit juvenile traits of closely related species might be the result of "paedomorphosis," whereas "peramorphosis" describes the situation in which a lineage

has generated novel phenotypes by adding novel stages or traits to an ancestral developmental program. The scheme for categorizing developmental sequences laid out in this paper was elegant and profound, and quickly swept into general usage across zoological disciplines.

Another concept with which David was deeply concerned was convergent evolution, or homoplasy, which arises when unrelated lineages come to exhibit similar traits. The traditional assumption among evolutionary biologists is that natural selection is the primary driver of such convergence, causing lineages to appear similar when presented with “challenges” from similar environments, such as aridity, or adaptations to moving through air or water. Going against the intellectual grain, as usual, David embraced and promoted the flipside of this idea: instead of repeatedly invoking adaptation driven by external agents such as the environment, he asked whether organisms might display similar phenotypes because the *internal* mechanisms that generate variation might somehow be strongly biased and constrained. Indeed, such internal mechanisms might work against environmental adaptation. For David, the cellular and tissue-level processes of organismal development provided abundant evidence of such constraint. He articulated these concepts, often with examples from plethodontid salamanders, in numerous essays, including a 1987 paper (Wake and Larson), “Multidimensional Analysis of an Evolving Lineage,” and one in 2011 (Wake et al.), “Homoplasy: From Detecting Pattern to Determining Process and Mechanism of Evolution,” both published in *Science*. These papers as well as several others helped cement his worldview that the diversity of organismal form we observe is as much a consequence of the internal, generative processes of development as it is of the action of natural selection. For this reason, David is often regarded as promoting a structuralist approach to evolution (Brown 2023), one in which adaptation to external agents plays a less important role than previously thought.

Excellent Mentorship

By virtually any measure, David Wake had an extraordinarily successful career as a professional mentor of young scientists. It began with his initial faculty appointment at the University of Chicago in 1964 and truly blossomed after he relocated to the University of California at Berkeley in 1969. We count at least 29 postdoctoral fellows, 39 doctoral students, 6 master’s students and 14 undergraduates who were supervised either exclusively or jointly by David.

To be sure, David’s willingness and enthusiasm to oversee student and postdoc training and research was not entirely unselfish. This was especially so once he had made the choice—the commitment, really—to

make the biology of plethodontid salamanders the principal focus of his research. He realized early on that the specialized disciplines involved were so many, the effort required so vast, the taxa involved so numerous and diverse,¹ and the requisite skillsets and talents so demanding that the only satisfactory way to proceed was to recruit students, postdocs, professional colleagues, and even motivated amateurs (what we might today call citizen scientists) to help carry the load. Indeed, David's approach exemplified what the philosopher of science James Griesemer has characterized as the "model-taxon research platform," and it would not have been possible without the dedicated performance of a large number of talented young scientists who cut their teeth on plethodontid biology.² David benefited professionally from the efforts of the large number of students and postdocs who pursued research projects on plethodontids under his supervision.

But it's also important to state that David was an extremely social and intellectually inquisitive individual. Very simply, he enjoyed being around people, and especially enjoyed time with his mentees—discussing the current state of evolutionary biology (but especially salamanders); telling stories of his childhood in South Dakota; learning new things from others. And while most of David's mentees did choose to study plethodontid salamanders (often after substantial encouragement), not all did, and David proved to be an extremely effective and engaged mentor with the latter group as well. Basically, David was engaged by broader topics and debates in evolutionary biology regardless of taxon, and in that capacity he could and did serve as an extremely valuable and successful advisor to all his mentees. David's mentorship also extended beyond simply academic or even exclusively intellectual pursuits. For many students, David became a trusted friend, counselor, and colleague. He cared deeply about his students' welfare, was open-minded and non-judgmental, and respected his students' life choices, both personally and professionally.

David recounted his experience and perspective as a graduate student mentor when he was interviewed for UC Berkeley's Emeriti Legacy Project in November 2019:

I have been blessed with wonderful graduate students from my earliest days in Chicago. And I've had about . . . 40 doctoral students. And it's been a joy. It's really given me the greatest pleasure in my professional career to work with these many talented young people. My goal was

1 Although the Plethodontidae is just one of ten extant salamander families, it accounts for nearly two-thirds of all living species.

2 Griesemer was one of David's undergraduate mentees at UC Berkeley in the 1970s.

to make them into thinking citizens of whatever country. I wanted them to be happy. I wanted them to be productive in their own way. And . . . I didn't have *my* goals for them. I want . . . to see them develop as individuals. Well, a number of them have become professors—even quite distinguished professors at major universities like at Harvard and Cornell and Wash U and University of Washington. The successes are out there in terms of standard academic achievement.

But I'm also very proud of my students who've gone into agencies or who've become successful parents or who've become teachers in small colleges . . . So success comes in many ways. And the top way is for them to be happy and to have felt that they've had a productive life. And I'd like to think that . . . the educational foundation that they had was important in that area.

A number of postdocs entering David's lab from non-herpetological fields or backgrounds ultimately became evangelists for the importance and intellectual excitement of amphibian biology. Being in the field on a herpetological expedition with David was fodder for stories of natural history, local geography, and politics as well as biological discovery. And much of the passion generated by these stories came from the importance of the ideas at stake, including fundamental debates about the nature of evolutionary mechanisms, anatomical evolution, ecological interactions, speciation, and biodiversity loss. David's roster of postdocs spanned the gamut of the field—from quantitative geneticists and developmental biologists to taxonomists and behavioral biologists.

David Wake's intellectual dynamism came to permeate and characterize the academic environment of the Museum of Vertebrate Zoology (MVZ), whose directorship he assumed not long after relocating to Berkeley and which he held for an astonishing twenty-seven years. While one could argue that this academic environment was tremendously influential on everyone at MVZ, it was especially so for those of us at an early career stage who were still learning how science is done and developing our own professional identity. One cannot overstate how important and valuable such an environment can be to the professional and emotional development of a young scientist; for many of us, the lessons learned have lasted for our entire careers. David was well aware of this phenomenon, as he recounted later in his *Emeriti Legacy Project* interview:

My experience as a mentor has been very productive, so that the students have given me a great deal of pleasure and I hope they've gained from the interactions that they've had in Berkeley. Most of the students have a very warm feeling about Berkeley. They feel that they've done well here and they have a warm feeling about the Museum of Vertebrate Zoology, which is small enough so that we have a really

familial sense of belonging to a place. And students . . . carry that sense of belonging with them for many years, that they *never* let us forget that they are still part of us and we love it.

Befitting someone who worked on species in the field (studying hybridization, speciation, and local adaptation), in museum collections (analyzing morphological evolution and variation), and in the laboratory (assessing patterns of development and phylogenetic relationships), David trained an extremely broad group of postdocs. Wake Group, the weekly discussion group he jointly hosted with his wife and fellow biologist, Marvalee Wake, was an intellectual journey through different approaches to natural history, morphology, and evolution. It is not an overstatement to say that, through the students and postdocs whose careers he launched, David had perhaps a greater impact on the human infrastructure of amphibian biology than any contemporary scientist.

David was also generous with his mentorship; he was willing to engage, and indeed support and promote, any deserving student who sought him out. He actively nominated not only his own students but also others he felt worthy of prizes and national recognition. He knew that such largesse was important to promote the many stars rising out of the MVZ, but it also would ultimately benefit the MVZ in terms of global recognition and scholarship.

Visionary Leadership

David Wake provided a wide range of leadership at the university, national, and international levels. At the University of California, Berkeley, he served as the director of the Museum of Vertebrate Zoology from 1972 to 1999. For students and postdocs based there, as well as the many out-of-town visitors who passed through—whether for just a day or two or a yearlong sabbatical—the museum developed a reputation as an extremely interactive, supportive, and intellectually dynamic and vital environment—a global center for the pursuit of evolutionary biology. As MVZ director, David helped set the tone and promoted the intellectual values and academic routine of the museum. But it definitely was a group effort—one that could not have succeeded without the buy-in, enthusiasm, and commitment of several other faculty-curators who served under David's leadership, including James Patton, William Lidicker, Harry Greene, and Robert Stebbins.

At the national and international levels, David assumed numerous important leadership roles. For example, he chaired the committee that made the World Congress of Herpetology a reality. The first congress

was held in 1989 and raised awareness of the decline of amphibians around the world. He also served as president of the Society for the Study of Evolution, the American Society of Naturalists, and the American Society of Zoologists. Furthermore, David was very active in the US National Academy of Sciences and the American Academy of Arts and Sciences as an elected member of both. In a 2019 interview for the University of California, Berkeley Emeriti Association's Legacy Project, David said that of those professional and learned societies "it's the American Philosophical Society that's my favorite. I still play a very active role in it; I try to go to all of their meetings. And I—in my mind that's the highest honor I've received, election to that society. It's the smallest of the learned societies in America and it's the oldest—founded by Benjamin Franklin in 1743." Indeed, one of us (JL) first met David at the 2015 Fall Meeting of APS and had the pleasure and honor of serving with David on the Membership Committee of Class II for several years until his death. David's insights during the committee meetings were truly remarkable. He spent a lot of time carefully reviewing nominees' credentials, usually going beyond the materials provided in the nomination packets. He also nominated several prominent scientists and scholars who have been elected to APS.

Many prestigious honors and awards have recognized David's exceptional accomplishments in scholarship, mentorship, and leadership. These include the Guggenheim Fellowship, the Outstanding Herpetologist Award (Herpetologists' League), the Henry S. Fitch Award (American Society of Ichthyologists and Herpetologists), the Joseph Leidy Medal (Academy of Natural Sciences, Philadelphia), the Quantrell Award for Excellence in Teaching (The University of Chicago), the Berkeley Citation (University of California, Berkeley), and the Joseph Grinnell Medal (Museum of Vertebrate Zoology at the University of California, Berkeley). Besides his membership in the learned societies mentioned above, he was an elected Fellow of the American Association for the Advancement of Sciences and of the California Academy of Sciences. Above all, his incredible legacy will be long-lasting in the scientific community and conservation community worldwide.

Elected to the American Philosophical Society in 1996

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