

# David B. Wake (1936–2021)

Pioneering evolutionary biologist and amphibian advocate

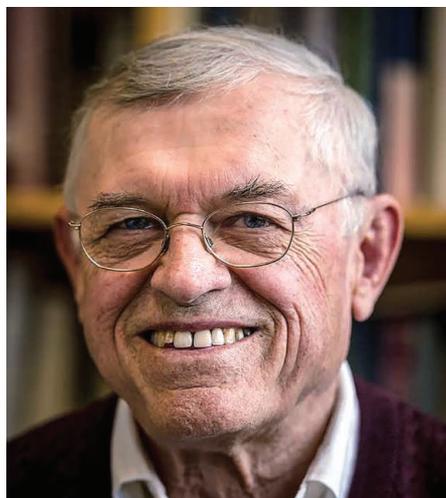
By Kelly R. Zamudio

David B. Wake, a pioneer in the fields of evolutionary morphology, evolutionary developmental biology (evo-devo), and organismal diversification, died on 29 April. He was 84. Wake was a career-long visionary in organismal biology who led evolutionary biologists to examine not only how organisms are different but also how they become different. As a graduate student, he set the framework for his career by detailing the evolutionary relationships and morphological diversity of salamanders. He then delved into functional morphology (how organismal structures work), evolutionary development (how developmental pathways influence diversification of form), and speciation (how species come to be). One of the most influential and integrative biodiversity scientists of his era, Dave was boundlessly curious about all aspects of evolution and unusually open-minded about new techniques and analyses.

Dave was born on 8 June 1936 and raised in South Dakota. He attended Pacific Lutheran College in Tacoma, Washington, where he became fascinated by salamanders after uncovering some while looking for insects for an entomology course. After receiving his BA in biology in 1958, he joined the lab of herpetologist Jay Savage at the University of Southern California (USC). At USC, he met Marvalee Hendricks, a fellow graduate student and scholar of caecilians, another understudied group of amphibians. Dave and Marvalee married in 1962 and became collaborators in life and in science. Dave completed his MS in 1960 and his PhD in 1964, both in biology at USC. He joined the faculty at the University of Chicago for 5 years and then moved to the University of California, Berkeley (UC Berkeley), where he was director of the Museum of Vertebrate Zoology from 1971 to 1998 and professor of integrative biology until his retirement in 2003. Marvalee joined the faculty at UC Berkeley as a tenure-track professor soon after Dave. From the time I first heard of them, they were known as “the Wakes,” and for many of us, they were an early model for successful dual careers in academia.

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An unapologetic organismal biologist, Dave used salamanders as a model taxon (as opposed to a model organism) to ask questions, answer some, and rework others, creating a cycle of ever-deepening inquiry into their evolution. Rather than focusing on a single model organism or particular evolutionary mechanisms, Dave developed extensive knowledge of many salamander species, enough to use the whole taxon as a model platform to inform his many research foci. In doing so, Dave achieved an unprecedented level of integration across approaches to address evolutionary mechanisms and their



consequences for diversification. His exemplary integration inspired a series of papers by James Griesemer in the field of history and philosophy of science. Dave’s salamander research transcended boundaries of methodologies, specialties, lines of inquiry, and disciplines. He developed a distinctive form of scientific problem-solving and iterative questioning that synergistically increased our general understanding of evolution.

Dave developed expertise in phylogenetics, morphology, development, ecology, neurobiology, behavior, and physiology, and his discoveries were groundbreaking in many fields. Coupling knowledge of adult morphology, ontogeny, embryology, function, and selection, he developed predictions about the retention and/or loss of morphological structures during development and became one of the first to frame these findings as part of the nascent field of evo-devo. By combining detailed spatial knowledge of morpho-

logical variation, biogeography, behavior, and genomics, he contributed a classic example of speciation in action with his exploration of the salamander ring species *Ensatina*. These discoveries, none of which could have been made without integrating approaches, span micro- to macroevolution and are now classics in evolutionary biology. His accomplishments led to many accolades, including election to the American Philosophical Society, the American Academy of Arts and Sciences, and the National Academy of Sciences.

In the late 1980s, Dave was an early proponent of action in response to the alarming global decline in amphibians. He chaired the first Declining Amphibian Populations Task Force and raised awareness of the predicament posed to amphibians by anthropogenic changes in climate and landscapes. As with his own research, he promoted diverse approaches in finding the causes of this large-scale biodiversity loss, to the benefit of both the scientific community and amphibians.

I joined the Wake lab in 1996 as a post-doc. It was an exciting time, with many field trips and countless discussions of species concepts, salamander tongues, and amphibian declines. Dave had a work ethic that amazed everyone and often left us challenging our expectations of ourselves. His leadership style emphasized showing, not telling. That work ethic resulted in some humorous “Wakeisms”—when lab members took vacations that he perceived as just a bit long, he began lab meetings by naming those who were absent and stating that “they must be gallivanting around the world.” To this day, former Wake lab members refer to vacationing as doing just that.

Dave set high standards for research and expected us to meet them. He was honest in his delivery of criticism but somehow made it feel like it was for our own good. He was an unwavering supporter of those who worked with him and incredibly loyal to his students and colleagues. No matter how busy, he eagerly welcomed visiting students and early-career scientists, always showing interest in their stories and offering advice about their research and professional development.

Nearly 15 years ago, at a symposium organized around the potential of new genomic approaches in herpetology, Dave regaled the audience with what he saw as the biggest questions still to be answered by integrating this new approach. He genuinely reveled in witnessing the advancement of science, not only through his own work but also through that of his lab members and anyone else who stepped up to the plate. He concluded with a typically positive outlook on science: “I only wish I had another 50 years to live, just to see what you are all going to discover!” ■

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