

BIO

David B. Wake

Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720, USA
Correspondence (email: wakelab@berkeley.edu)



As a teenager in a South Dakota hamlet (Pierpont, population 326 in the 1940 census) I had no idea that I would become a scientist. The only formal science course my tiny high school (40 students in four grades, taught by three teachers) offered was physics, taught by the sports coach (a history major) and featuring the “dissection” of a 1928 Overland (teacher: “I have been told that the modern automobile illustrates all principles of mechanics.”). I was strongly influenced by my maternal grandfather, H. M. Solem, a Lutheran pastor and amateur naturalist who spent a summer as a youth in the late 19th century traveling with John M. Coulter, studying the botany of the Rocky Mountains. He took me on many botanizing walks through northeastern Iowa, where he lived, and when my grandparents moved to our South Dakota home when he was 88 our botanizing continued. I eagerly absorbed the Latin names he used when identifying plants. My grandfather was well-educated and, in retrospect, enlightened, and

it was from him that I learned about evolution and first heard Darwin’s name. He often said that there could be no conflict between his religion and facts of science; if there were, we must have made some biblical misinterpretations. My main goal as a teenager was escaping Pierpont, and when my parents announced that we all were moving to the state of Washington so that I could finish in a proper high school and my two younger sibs and I could attend a Lutheran college and live at home, I was elated.

I thought I might become a lawyer. Four of my uncles were lawyers and I was impressed with them and their success. So I declared a history major at Pacific Lutheran College and took a botany course to fulfill my science requirement. It took me only a few weeks (taking General Botany, with my then 93-year-old grandfather accompanying me on botanizing trips) to realize that I was destined to become a biologist. I was encouraged in this decision by my mother, Ina, a high school biology teacher (involved in testing and development of the Yellow Version of the ground-breaking Biological Sciences Curriculum Study high school books project). I enjoyed my college days, especially the science courses, including Vertebrate Embryology. I began research projects, and in my senior year a new professor (Jens Knudsen) joined the faculty, fresh from graduate school at USC. I was admitted to several graduate schools (including Berkeley and Cornell) but went to USC on the strength of Knudsen’s strong endorsement of Jay Savage as a potential major professor.

I prospered under Savage’s guidance. I wanted to understand, at a deep level, how lineages diversify and I selected salamanders, in part because at that time there were about as many species as there were people in my home town and I knew I could easily remember that many names and a great deal about each one. I quickly came to understand how important neoteny, and paedomorphosis more generally, had been in salamander phylogenetic history, and that rapid and profound morphological evolution could be a result. I gained some insight into phenomena like homoplasy and stasis that became themes in my later career. I was especially interested in the developmental basis for the morphological traits (characters) that differentiated taxa. For me the greatest opportunities seemed to lie in the adaptive radiation of New World tropical salamanders. I was influenced by the writings of Julian Huxley,

de Beer and Schmalhausen, and absorbed Nelson's book on vertebrate comparative embryology.

Based mainly on my publication record as a graduate student, I was hired by the University of Chicago without a postdoc in 1964 and joined the Biology program in the College, as well as the Department of Anatomy, where my lab was located. My 5 years in Chicago were wonderful intellectually. My interests in evolution, development, and morphology became focused. Although my perspective was always organismal and phylogenetic, I was surrounded by histologists, neuroanatomists, paleontologists, geneticists, and cell and developmental biologists, and I learned much from them.

In 1968 I was offered a tenured faculty position at Berkeley, as well as a curator position in the Museum of Vertebrate Zoology. Although happy in Chicago, this was my dream job and I eagerly accepted. I have been at Berkeley since 1969. In 1971, I was appointed Director of the Museum and served for 27 years. I became emeritus in 2003, but soon was offered a special post (Professor of the Graduate School) that permits me to maintain a laboratory operation and share in the direction of graduate students, so I have remained active in research through the present.

The early 1970s were exciting years with stimulating colleagues and wonderful graduate students, several of whom were actively involved in what we now know as evo-devo. In particular, my graduate students Pere Alberch and Jim Hanken were studying development in relation to evolution and phylogenesis. When Steve Gould's masterful book on *Ontogeny and Phylogeny* appeared in 1977 we were more than ready to absorb it, and my colleague, theoretician George Oster and I offered graduate seminars on evo-devo. Our first task was to take a central chapter in the Gould book, dealing with Steve's "clock-face" model, and formalize it. Pere Alberch took the lead in this project, and when we had a working draft we sent it to Steve and invited him to join us if he approved, which he did. We published "Size and shape in ontogeny and phylogeny" in *Paleobiology* in 1979 and it became one of my most-cited articles.

I met my future wife, Marvalee, when as a senior undergraduate she took a course I taught while still a graduate student at USC, where she also became a graduate student. We married in 1962. When we moved to Chicago in 1964, Marvalee taught at the old Navy Pier and then at the downtown campus of the University of Illinois and did the research for her doctoral dissertation in my lab at Chicago (Jay Savage at USC was also her major professor). When she finished her PhD she was offered an Assistant Professorship at the new Chicago Circle campus. Marvalee and I have shared many professional and research interests, and while we have always had separate labs and graduate student groups, we began a formal collaboration during our first sabbatical in London in 1975. I had been studying vertebral development in salamanders for some years and we jointly examined caecilian vertebral development. We share a strong interest in factors promoting morphological stasis

during phylogenesis and other aspects of what we now call evo-devo, especially homoplasy, which remains a focus of our research. At the time of our retirement we obtained our first joint NSF grant, for studies of the Amphibian Tree of Life. The one doctoral student we cosponsored, Andres Collazo, did his thesis work on amphibian evo-devo. Several jointly sponsored post-doctoral fellows have worked on evo-devo projects, including David Buckley and Steve Poe.

Field work has always been a component of my research activity. I frequently visited the salamander-rich areas of the southern Appalachian highlands, where I centered my lab and field activities at the Highlands (NC) Biological Station. But most field work was in California and Middle America. In the mid to late 1980s, I became aware that salamanders and especially frogs were becoming hard to find in many areas, even in protected areas where there had been little evident habitat modification. I obtained support from the National Academy of Sciences for a workshop, held in Irvine, CA, in February, 1990, and partly as a result the plight of amphibians became widely known. I was a founder of the Task Force on Declining Amphibian Populations and served as its first chairperson. Recently, my group resurveyed sites in Middle America, which we first studied in the late 1960s, and documented losses of species and populations of salamanders. These activities led to recent articles from my group in *PNAS* on the "Sixth Extinction" (2008) and "dramatic declines in neotropical salamander populations" (2009).

Although my research program has been broad and taxon-focused, evo-devo has been a persistent theme. I regularly offered graduate seminars on evo-devo topics, occasionally with Marvalee, or my valued colleague David Lindberg, and have sponsored a number of graduate students with interests in evo-devo, notably Pere Alberch, Jessica Bolker, Steve Deban, Andres Collazo, Kevin de Queiroz, James Hanken, Elizabeth Jockusch, Allan Larson, Sharyn Marks, Stan Sessions, and Richard Wassersug. Additional evo-devo postdocs include Neil Shubin and Kiisa Nishikawa.

I follow progress in the field of evo-devo (and eco-evo-devo) avidly. Although in awe of the many exciting discoveries tying molecular and developmental genetics to evolution, I focus my personal attention more at the organismal level, where I see promise for integration of organismal and molecular biology in evo-devo. The problems that initiated my interest in the field still intrigue me: conservative morphological evolution in the face of extensive molecular change, limits on morphological change that lead to extensive, sometime overwhelming amounts of homoplasy in evolving lineages (e.g., amphibians), and apparent restrictions or biases on the direction of evolution. I have returned to some of the questions that initiated my interests in evo-devo. I continue to explore salamander ontogenies (e.g., loss and re-evolution of larvae), which are a rich source for understanding the origins and extent of morphological homoplasy—more extensive than I ever would have predicted.