

HISTORICAL PERSPECTIVES

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David Burton Wake

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DAVID BURTON WAKE lives the life of the mind. Well, the mind and the field. His work is intellectually sharp and has deep roots in the natural history of the salamanders he studies. In spite of living in large cities and working at large universities most of his life, Dave is basically a small town kind of guy. He fostered within his lab group that small town atmosphere—where everyone knows one another and will help each other out as needed. Through his decades-long research focus on a single taxon, he and his “small town” uncovered fundamental principles of how organisms develop and function, and how populations of organisms evolve.

CHILDHOOD

Dave spent his first 17 years in Pierpont, South Dakota (born 8 June 1936 in Webster, SD; Fig. 1), and, although these were truly formative years for his life-long work, he was eager to leave. He remembers, from his earliest days, his mother (Ina Solem Wake; unusual for a woman in town because she had a college degree) telling him that he *would* live somewhere else; he would not stay in Pierpont. She also prepped him for college by talking about how much she had enjoyed her college years. She started teaching high school biology and home economics during the depression. She was enthusiastic and enjoyed the simple pleasures of life. For example, Dave remembers eagerly awaiting the first bloom of the Pasque flower, a big event in their household with special honors to the person who found the first flower. His maternal grandparents came to live with them (Dave’s parents and a younger brother and sister) when Dave was 12; when his grandmother died from a stroke at 83, Dave developed a special bond with his grandfather.

Dave credits much of his intellectual curiosity to his grandfather (Henrik Martinus Solem). His grandfather (b. 1862 in Norway) was the first person to get a B.A. in Dakota territory; he was the sole member of his class in the then-new Augustana College. Henrik attended seminary in St. Paul, Minnesota, and was an intellectual leader in the community, as well as a pastor in the “high church” synod of the Norwegian Lutheran Church, the most liberal of the synods. He was also an excellent botanist, having traveled with John Coulter (founder of the Botany Department at The University of Chicago) while Coulter was preparing the *Manual of Rocky Mountain Botany* (1885). Dave remembers keying out plants with his grandfather from an early age; Gray’s *Manual of Botany* was a typical coffee table book in their home. Before his grandparents moved to South Dakota, Dave remembers visiting his grandparents—both Norwegian immigrants—in

Iowa, walking with his grandfather along the railroad tracks through the woods and hearing stories about pollinators, shapes of flowers, and basic natural history. Dave remembers his grandparents discussing world events at great length, in addition to philosophical matters and books; he also remembers his grandfather cautioning him to “be wary of people who know the truth.” Dave heard the word evolution for the first time from his grandfather. That was a different era, when one would learn about the facts of life and evolution from the preacher. His grandfather died in 1961 at age 99, when Dave was in his second year of graduate work. Overall, Dave was steeped in intellectual curiosity about natural history as a child.

Dave acknowledges that his education in Pierpont, South Dakota was unusual. His mind was hungry and he got a good education. There were three teachers in the entire high school, including the superintendent. The superintendent was a marvelous teacher and taught the best course Dave ever had, General Agriculture. Some of the topics covered were plant and animal breeding, genetics, how to plow a straight furrow, and seed and root “physiology”—although they didn’t call it that then. Dave cherishes this class. Dave never got an A in high school in Pierpont. They had a rule—only one A per class, and his classmate Kathryn Johnson always got it. In his class of 11 in Pierpont, three got Ph.D.s and became college professors. Kathryn Johnson became a nurse. Everyone had a nickname in his class and Dave’s was “professor.” It had the same connotation as “stinky.”

At home, Dave’s education continued with his grandfather discussing books and world affairs. His grandfather, who lived in Washington, D.C., for a few years after retirement, absorbed the Washington Post daily (it arrived by train two days late). Dave would read it afterwards, and he still reads the digital version to this day. This kept the family connected with national and world events, despite living in isolated Pierpont (pop. 326 in 1940 census). Because of these experiences, Dave was already a naturalist at a young age. His father sold hardware and farm implements, and Dave remembers going to the store and talking to farmers, with great assurance, about which fertilizer to use. He was a terrible know-it-all at age 14, when he started to work after school and weekends in the store.

In childhood, Dave picked up the habit of doing a job right away; he rarely procrastinates. If something needs to be done, he does it immediately (although some close to him will disagree, especially if it’s a household chore). He reviews articles the first day he gets them. He credits his habit of not procrastinating to growing up in an immigrant household; it

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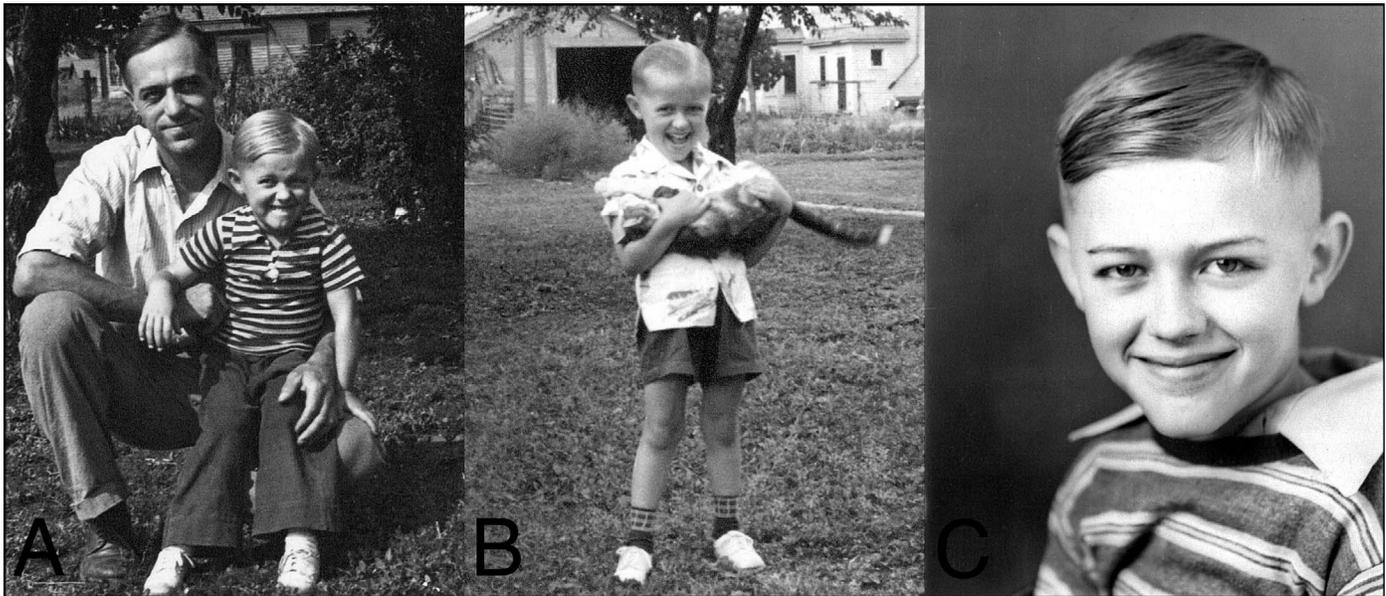


Fig. 1. (A) Dave and his father Tommy. (B) One of the few photos of Dave with a pet. (C) Young Dave.

was very task-oriented as each day had its task—washing on Mondays, etc. Later, in graduate school, Dave’s advisor Jay Savage reinforced this behavior because he would not tolerate procrastination.

His parents saw the writing on the wall about the future of small towns in the rural Midwest. Plus, in order to afford college, the three kids needed to live at home. Dave’s father closed his business and sold the building, and the family moved to Tacoma, Washington in 1953, where Dave finished high school. Dave’s father bought a work-share of a wood-finishing cooperative and his mother started teaching high school again. Dave got his first A in high school there and kept getting As; he couldn’t believe it! He graduated from high school in 1954 and started at Pacific Lutheran College the following year.

COLLEGE

Dave graduated from Pacific Lutheran College in 1958 with a B.A. in Biology, magna cum laude. Entomology, during his senior year, ended up being a pivotal course for him. While building his insect collection, Dave kept finding salamanders under the rocks and logs he’d turn over. He was familiar with *Ambystoma mavortium* (then *Ambystoma tigrinum*) from South Dakota and immediately found *Ambystoma macrodactylum* much more interesting—it was active. He starting seeing species of *Plethodon* and then found *Ensatina*... and that was it. The End. He was captivated, and he tried to learn everything he could about these animals. (Over the subsequent decades, Dave would publish 17 papers—and counting—with *Ensatina* in the title). During this same time, Dave was applying to graduate schools all across the country (UC Berkeley to work on mammals, Cornell to work on plant pathology and botany, University of Kansas, etc.). His entomology teacher, first-year professor Jens Knudsen, said well, why not salamanders if you’re so interested in them? Jens had a degree from USC, where he overlapped with a recently hired herpetologist—a kind of wild guy (but good)—and he suggested Dave apply there. So on a lark, Dave applied to USC to work with Jay Savage. And because Dave didn’t get a teaching assistantship at Berkeley, he went to USC.

GRADUATE SCHOOL

Dave remembers his first day of graduate school well. While waiting to talk to Jay, who was late, Arden Brame (then a 3rd year grad student) introduced himself... and then talked salamanders nonstop for four hours. Among other things, Dave learned from Arden that there were undescribed species of salamanders in California. Dave also heard the name of Berkeley herpetologist Ted Papenfuss for the first time. He didn’t realize at the time that this Ted, who had discovered a new salamander (which Brame later named *Batrachoseps stebbinsi*) was only 16 years old. Dave worked closely with Arden for many years (Wake and Brame, 1966).

Although relatively new, Jay Savage had a group of graduate students already, including Arnold Kluge. At one point, Jay had 14 graduate students (including both ichthyologists, e.g., John Paxton, Bob Lavenberg, and Geoff Moser, and herpetologists, e.g., Kluge and Brame, Roy McDiarmid, Norm Scott, Jim Vial, and, importantly, Marva-lee Hendricks, whom Dave married in 1962; Fig. 2). Dave has many stories about Jay. They called him “Chief.” He liked to be surrounded by minions. The senior graduate student was the principle mentor of the younger ones and needed to “get them in line.” Dave remembers Jay during these years as endlessly interesting and challenging, a very bright guy with a magnetic personality and great leadership skills. Dave got his M.S. in Biology in 1960 (“Comparative Osteology of the Plethodontid Salamander Genus *Aneides*”, published in *Journal of Morphology* in 1963 as his first substantial publication) and then his Ph.D. in 1964 (“Comparative Osteology and Evolution of the Lungless Salamanders, Family Plethodontidae”, published in *Memoirs of the Southern California Academy of Sciences* in 1966 [Wake, 1966a]).

Dave’s graduate studies established the framework for his whole career and provided the foundation for many of his students’ and postdocs’ research programs. When asked recently whether he would have predicted, upon finishing his Ph.D., that he would study salamanders for his entire career, Dave replied that, although he was warned about becoming a “narrow specialist,” there did not seem to be anything wrong with Ernest Williams focusing on anoles! In



Fig. 2. Dave and Marvalee with son Tom and granddaughter Summer, December 2016. Photo by Chrissy Campbell.

fact, in the late 1960s (about the time Dave was moving to Berkeley and Williams had narrowed his focus to anoles), Dave consciously modeled his approach on Williams'. He tirelessly sought to address questions of diversification within lineages from as many levels of biological organization as possible, with talented graduate students and postdocs bringing different perspectives and skillsets as collaborators. When new data yielded results that conflicted with early foundational work, Dave welcomed the discrepancies and sought to learn from them. By his example, he taught his students to never get so attached to their ideas that they forgot the value of data. Ideas, Dave always said, are cheap. Data are gold. Dave's strategy of applying integrative analyses to a single group of organisms is now known as the model taxon approach (Griesemer, 2013).

THE UNIVERSITY OF CHICAGO

Near the end of his time at USC, Dave remembers reading Ernst Mayr's *Animal Species and Evolution* book (published January 1963). He was just finishing his dissertation and was teaching evolution, and he felt completely let down. "My God," he thought, "it's all been done; I'm entering a dead field." But what to work on, specifically, in this dead field? Dave had been advised by Savage to broaden his scope beyond salamanders—to be a herpetologist rather than a narrow specialist. Despite his deep interest in salamanders, one of Dave's first publications was on the Sinaloa narrow-mouthed-toad (1961). He also became interested in coral snake mimicry and, while in graduate school, actually started taking measurements and recording color patterns of

Chionactis (Wake, 1966b). By this point, Dave had several job offers, and he had a different project in mind for each potential faculty position. For example, he decided that, if he accepted the job offer from San Diego State University, he would work on desert snakes. However, he had one chapter of his thesis on vertebral evolution that was unfinished, and he thought if he went to The University of Chicago, he would start by working on that. Dave decided on Chicago, so vertebral evolution won out.

Dave, as a new faculty member at Chicago (1964), met Bob Inger; he remembers walking into Inger's office at the Field Museum one day and being asked, "What do you think of this book?" as Inger threw Sokal and Sneath's *Numerical Taxonomy* (1963) down on his desk. Bob never had time to chit-chat. It was like a qualifying exam all over again. After that conversation, Dave lost his fear of entering a dead field; he knew there was a lot more interesting evolutionary biology to be done. Shortly thereafter, Hennig's *Phylogenetic Systematics* was published in English (1966), and it was key in giving direction on how to organize information in a phylogenetic context.

Dave wrote his first NSF grant application in the fall of 1964 and was funded by spring of 1965. He hired a laboratory technician, had an interested graduate student, and was off and running, never looking back. Although the vertebral evolution project was mopping up his dissertation, it also got the ball rolling in his lab; through this early work at Chicago, Dave saw that there was a lot he could do if he kept his focus on a single taxon. He saw how the intense research focus on *Drosophila* produced a model organism, and he saw value in an in-depth, integrative approach. The anatomy lab

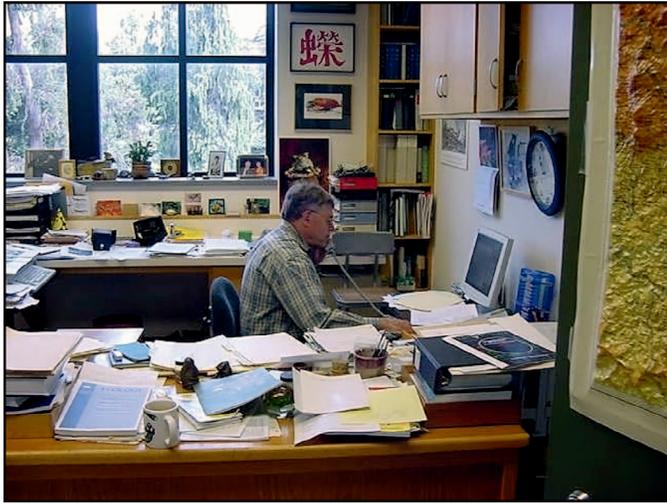


Fig. 3. Typical day at the office at UC Berkeley.

at Chicago, full of equipment and technicians, was an excellent environment in which to tackle problems from different perspectives with different tools. Once he got into this work, there was no question that he was doing what he wanted to do, and he also was benefiting from interactions with good local herpetology friends such as Tom Uzzell (also at Chicago), George Rabb at Brookfield Zoo, and Bob Inger and Hy Marx at the Field Museum. These five years (1964–1969) were continuously rewarding, and Dave often asked himself why he left The University of Chicago, as he was happy there. Nonetheless, the Wakes saw limits in Chicago—for both of them. One day in March, 1968, Dave got a phone call from Oliver Pearson, a mammalogist and director of the Museum of Vertebrate Zoology at UC Berkeley. Pearson asked Dave if he would like to give a seminar at Berkeley. When Dave arrived in Berkeley in April, Pearson met him at the airport and, on the drive to Pearson's home, told Dave that this seminar was actually a job interview. The visit went well, and as Pearson drove Dave back to the airport, he reported that the faculty had already met and decided to offer him an assistant professorship. Dave was just beginning to think about putting together his tenure package. He told Pearson that he thought he had better stay on the tenure track at Chicago, where he had so much invested. Within a week, Pearson called back and upped the ante—an offer of Associate Professor of Zoology with tenure and Associate Curator of Herpetology in the Museum of Vertebrate Zoology, an offer impossible to refuse (Fig. 3).

GRADUATE STUDENTS AND POSTDOCS, FROM CHICAGO TO BERKELEY

Dave had a continuum of graduate students and postdocs that can be grouped into a series of interdigitating cohorts. Although he will admit to having a favorite salamander—"I'd have to say *Ensatina*"—Dave takes great pride in every single one of his students, and working with all of them has been an important and especially rewarding part of his career. During graduate school, his students were treated as his colleagues, and he encouraged them to forge their own career paths both within and outside of academic science. Dave never wanted to create clones of himself, and he was cognizant of his students' differences, both from himself and from one another. He accepted each of his students "as-

is," recognizing that graduate work coincides with a phase of life that can also include substantial bouts of self-discovery, as well as other major lifestyle transitions (e.g., relationships, parenthood). Within his lab, Dave created a small community characterized by both intellectual rigor and tolerance (Fig. 4). Today, Dave describes the rich and rewarding sense of accomplishment he feels from all of the dissertations lined up on his shelf.

Dave's first graduate student group was assembled at The University of Chicago. This group began with his first inherited student, Jim Shafland, and his first selected student, Eric Lombard; it then expanded to include Richard Wassersug and Jim Edwards (both shared with paleontologist E. C. Olson) and, later, Jane Peterson and Nancy Thomas Beck. Also in the group were his first postdocs: Necla Ozeti from Izmir, Turkey, Richard Worthington from Richard Highton's lab, and Ronald Lawson from University of Salford, England, who was a sabbatical visitor, but was in effect a year-long postdoc. Dave also interacted with Olson's graduate students—especially John Bolt and Bill MacLean. Dave had a fascinating group of undergraduates in his group at Chicago: precocious Lewis Larson, who celebrated his 16th birthday after having been in his lab for a year, and Jim Kahn, who later novelized *Return of the Jedi*. This is the group that got Dave started, and he remains grateful to them all.

Dave joined the faculty at Berkeley in 1969. Graduate students Eric Lombard and Richard Wassersug came to Berkeley from Chicago and formed an important bridge. When Olson moved to UCLA, Jim Edwards moved with him, but he then joined Dave in Berkeley. Dave already knew Jim Lynch, who was a graduate student with UC Berkeley ornithologist Ned Johnson; Lynch transferred to Dave's lab, and new graduate students Virginia Maiorana and Sam Sweet rounded out Dave's early 1970s Berkeley group. Dave's first undergrads were Kay Philbrick (later Yanev) and Lynne Houck, both of whom became his graduate students. Jim Hanken later joined the lab as an undergrad, and also became a grad student. Bob Stebbins was still active, and his students included Bruce Bury, Steve Ruth, Kristin Berry, and later Ted Papenfuss, Ron Marlow, and Kristine Tollestrup. Paul Licht's group included grad student Martin Feder, who also worked with Dave. Steve Arnold was Dave's first Berkeley postdoc. Other postdocs during the 1970s were Gerhard Roth (short-term, but very influential), Steve Stearns, Ray Huey, and Bob Kaplan. Al Bennett was a postdoc in the Licht lab, and several undergraduates—Paul Elias, Brad Shaffer, and Jim Griesemer—also made important contributions to the lab. And of course the lab technical crew was very important—it started with Suh Yung Yang. Overall, the herp group was very lively in the 1970s. Field work in the early 1970s was focused in Guatemala, although with Hanken's focus on México, the lab also worked there extensively. Importantly, Harry Greene joined the MVZ in 1979 when Bob Stebbins retired; Dave cherishes their wonderful relationship during Harry's 20 years there.

These first two groups of graduate students and postdocs really launched Dave's career. During the 1980s, the students and postdocs formed a not-so-easily definable group. In some ways, the group was defined by a heavy lab emphasis; Kay Yanev and Monica Frelow were doing electrophoresis non-stop, identifying genetic differentiation among populations that revealed complex evolutionary histories. At the same time, Dave began a ten-year-long venture in comparative neuroanatomy with Gerhard Roth's research group. Dave's graduate student group during the first half of the 1980s



Fig. 4. (A) Typical weekly lab meeting in which Dave would review his interesting mail, students would talk about progress on their projects, literature would be discussed, and birthdays celebrated. Front row L to R: Shawn Kuchta, Erica Rosenblum, (table), Steve Poe, Adam Summers; Back row L to R: Martin Jaekel, Javier Rodriguez, Seth Thomas, Rachel Mueller, Arie van der Meijden, Dave. (B) At the Sixth Conference on the Biology of Plethodontid Salamanders at the University of Tulsa in 2014 there were 12 Ph.D. students (including Sean Reilly, Sean Rovito, and Tom Devitt—with whom Dave worked closely although they were not formally his students), four postdocs, and three academic grandchildren of Dave's. Pictured, left to right, Zach Lewis (academic grandchild via Jim Hanken), Chris Evelyn (academic grandchild via Sam Sweet), Sean Reilly (current collaborator; also academic grandchild via Sharyn Marks), Tom Devitt, Sean Rovito (postdoc), Peng Zhang (postdoc), Meredith Mahoney (Ph.D. student), Shawn Kuchta (Ph.D. student), Ron Bonett (postdoc), Elizabeth Jockusch (Ph.D. student), Dave Wake, Nancy Staub (Ph.D. student), Stan Sessions (Ph.D. student), Sharyn Marks (Ph.D. student), Jim Hanken (Ph.D. student), Lynne Houck (Ph.D. student), Eric Lombard (Ph.D. student and postdoc).

included Jim Stewart, Allan Larson, Pere Alberch, John Cadle, Stan Sessions, Steve Busack, and David Good.

The second half of the 1980s saw the beginnings of a shift in framework, as DNA sequence data began to be used in evolutionary analysis. Dave Darda still used allozyme electrophoresis in his mainly morphological thesis. Allan Larson continued the allozyme electrophoretic work he had

done as a Master's student with Richard Highton, but after completing his Ph.D. with Dave, he joined Allan Wilson's lab in the Department of Biochemistry as a postdoc and ushered in the era of DNA work in Dave's lab. Dave's lab also included Nancy Staub and Kevin DeQueiroz, as well as interactions with Willy Bemis, Kurt Schwenk, and Aaron Bauer in Marvalee's lab. David Good had become a postdoc by this



Fig. 5. Digging pitfall traps for *Ensatina* in the Sierra Nevada. From left: Nancy Staub, Dave, Andres Collazo, Chuck Brown. Photo by George Roderick.

point, joined by Kiisa Nishikawa and David Cannatella. They learned during these years that *Amphiuma* was most likely the sister group to plethodontids, and they could see the revolution coming in figuring out evolutionary relationships based on DNA sequences. Dave sensed that DNA sequencing technology would likely experience some growing pains, and as he waited for the technology to mature, he used the time to develop his broader ideas about genome evolution and tongue evolution. Dave had already done substantial work on tongue anatomy with Eric Lombard. In addition, he had started work on comparative neurology in 1982, while on sabbatical in Germany in former postdoc Gerhard Roth's lab; Roth was also working on tongues in the second half of the 1980s. Dave prepped for this new research focus by giving a series of seminars on tongues in Europe—he called them “The Tongue Seminars.” Dave recounts how he reoriented his research program in his mind towards understanding how the tongue worked—in the context of the entire functioning organism. These projects ran until the early 1990s when DNA tools were developed enough to launch his lab in a more molecular direction. Toward the end of the 1980s, Marvalee and Dave co-sponsored their first and only student, Andres Collazo. Dave recounts how the whole period of the 1980s was a time of transition (although work on *Ensatina* formed a consistent thread throughout his career; Fig. 5). In addition to changes in his research foci, changes in his physical space were afoot; a major renovation was being planned for the Life Sciences Building, and Dave was part of the discussion from the beginning... which meant hours and hours spent in frustrating but ultimately fruitful meetings. Field work had shifted orientation as well. Dave and his group left Guatemala after 1979 because of civil instability, so with Stan Sessions and Dave Darda, the lab focused more on México, Costa Rica, and Panama in the late 1980s.

Dave's memories of the late 1980s and early 1990s are clouded by the agony of redesigning the biology building at Berkeley. He served as Chair of the Program Planning Committee for the Life Sciences Building—a \$96 million

project. The remodeled building, which houses the Museum of Vertebrate Zoology (as well as other natural history museums), turned out beautifully, but its creation took inordinate amounts of time and politicking. Dave blames his heart trouble on this era! Dave had a great group of students and postdocs during this time that helped to keep him sane: Chris Schneider, Todd Jackman, An-Ming Tan, Jessica Bolker, Alex Haas (from University of Tuebingen, Germany), Anna Graybeal, Sharyn Marks, Elizabeth Jockusch, Steve Deban, Meredith Mahoney, Gabriela Parra Olea, and undergraduate Andrew Crawford. Craig Moritz was in the lab as a sabbatical visitor; he later succeeded Dave as Director of the MVZ. The lab started doing DNA sequencing, and with these new data, continued to tackle questions in salamander diversification, species delimitation, and phylogeography, as well as development and morphology. Neil Shubin and Mario Garcia-Paris were important postdocs with whom Dave established long-term working relationships. Kelly Zamudio was a postdoc at the end of the decade, overlapping with Adam Summers, who was cosponsored by Marvalee. Graduate student Gabriela Parra Olea ushered in a new era of tropical salamander work. Field work continued to focus on Costa Rica as well as México, and field work resumed in Guatemala following a long hiatus; Jim Hanken, Gabriela, and Dave continued expeditions to México through 2007.

The 2000s saw the beginning of downsizing in Dave's group, as he approached retirement. However, the group was very lively and active, and included Shawn Kuchta, Vance Vredenburg, Rachel Mueller, Erica Rosenblum, and Ricardo Pereira, as well as Rob Bingham and Yu Zeng (his last two students) and undergraduates Sara Weinstein and Sima Bouzid. João Alexandrino, Javier Rodriguez-Robles, Leslie Rissler, and Steve Poe were all postdocs. Marvalee and Dave took their last sabbatical at Harvard (she as a Radcliffe Fellow, he as an Alexander Agassiz Visiting Professor) in 2002 and then formally retired in 2003. However, Dave applied for and received two very large grants—HerpNet and Amphibia-Tree—and so suddenly found himself very “un-retired,” a status he retains to this day. In recognition of his continued activity, he received the prestigious 2016 Berkeley Emeritus Faculty of the Year award. The Wakes were both recalled as Professors of the Graduate School (positions they still hold), awarded the Berkeley Citation by the university, and were able to hire new postdocs: David Vieites, Ron Bonett, David Buckley, Peng Zhang, and finally Sean Rovito on ATree, as well as Inigo Martinez-Solano and undergraduate Raul Diaz. This was an era of “mopping up”—*Batrachoseps*, *Ensatina*, and tropical salamanders—but also a period of discovery—e.g., *Karsenia*, *Urspelerpes*. AmphibiaWeb, with its emphasis on curating and sharing information about amphibian diversity and conservation, was also a strong focus. The last student with whom Dave worked directly was Sean Reilly, officially Jim McGuire's student, but who essentially did a second Ph.D. with Dave.

Dave's lab members during these later years benefitted from the knowledge accumulated over decades and decades of research. Integrative thinking and synthesis had always been the norm for Dave's group, and by this point, Dave had experience studying salamander evolution through the lenses of many disciplines. Being Dave's student or postdoc meant thinking deeply about all of the core concepts in evolutionary biology, recognizing their incredible (and beautiful) complexity. As an example, the keywords in Dave's 2009 article “What salamanders have taught us about



Fig. 6. Dave and Jim Patton have been colleagues and have shared a lab since 1969. Jim is a mammalogist and served as Associate Director of MVZ during Dave's tenure as Director, and succeeded him as Acting Director for a couple of years before Craig Moritz took over. Photo by Dick Sage, February 2017. Pictured, left to right, Dave, Marvalee, Jim Patton, long-time collaborator Ted Papenfuss, Dick Sage (manager of MVZ's Evolutionary Genetics lab in the 1980s).

evolution" are: adaptive radiation, biodiversity, homoplasy, morphology, multidimensional analysis, ontogeny, phylogeny, species, and species formation. This is just a subset of the concepts that Dave's work has shaped in substantial ways—but even this short list would work for studying for a Ph.D. qualifying exam! Because they were part of his lab group, Dave's students approached their projects with the depth and complexity of these core concepts in mind, and this environment produced deep thinkers. Dave's impact on graduate student training continues, as many of his former students seek to emulate aspects of his mentorship in their own labs. In addition, Dave continues to campaign to get his former graduate students to publish their unpublished work (i.e., that dreaded fourth chapter from the dissertation). With so many students trained over the years (see Appendix 1), it is a big job... but once a major professor, always a major professor (see Fig. 4B for an assortment of Dave's former graduate students and associates at the Sixth Conference on Plethodontid Biology).

UNDERGRADUATE TEACHING

Dave also had substantial impact on education at the undergraduate level that extended well beyond the students that did research in his lab. Dave's teaching philosophy connects back to his experience in Pierpont—it's centered on relationships with students and conveying understanding rather than information, as the superintendent did when teaching General Agriculture. Dave tells his students, "You are surrounded by books and resources. I can't teach you all that information. What I do is to teach you how to think about all that information." He notes that students would frequently ask him, "Do I have to learn the names of all these scientists?" Dave would always say yes. People are ideas.

Their names are tags for ideas, just as country names are tags for landmarks.

Dave taught the Evolution course at UC Berkeley for decades. This course changed the lives of many students. The reading list was memorable; the reader itself (the bound version of the collection of ~50 papers read during the semester) still lurks on the shelves of many former students who are now professors (and who have otherwise gone paperless). "Really, all these papers?" The students did read them though, and in so doing (and through discussions with their TAs), they learned to focus on ideas, the history of ideas, and how evidence is presented in support of ideas. The exams gave them a forum to show what they had learned; they typically consisted of a few questions on a piece of paper and a blue book.

THE MUSEUM OF VERTEBRATE ZOOLOGY

Dave became Director of the Museum of Vertebrate Zoology in 1971, a post he retained until 1998. Dave sums up his legacy as Director by describing two things he is proud of having accomplished. The first is his establishment of a common molecular genetics lab with mammalogy curator Jim Patton (Fig. 6). He and Jim were the new kids on the block when they proposed this idea of a shared lab, and it was met with great skepticism. It was a big, bold decision in MVZ's history, but the lab really proved its worth over the decades, supporting multiple generations of students advised by different MVZ curators. Sharing of physical space was functional and efficient, but the biggest payoff came from the ease with which students and postdocs could share ideas across lab groups. This fostered a real community spirit and sense of collaboration that would have been nearly impossible to achieve across closed doors. Dave is quick to say that

he couldn't have done any of this without Jim, who he describes as "the absolutely best colleague imaginable." The second lasting legacy is his securing of a prominent, functional—and beautiful—space for MVZ during the renovation of the Life Sciences Building (re-named the Valley Life Sciences Building). Access to the research collections in the renovated MVZ was easy and efficient. Over and above this serviceability, however, was an intangible effect of interspersing student and faculty offices with the collections themselves. Physical immersion in the specimens provided a constant reminder of the spectacular diversity of nature, and it proved to be a real inspiration to MVZ researchers.

AMERICAN SOCIETY OF ICHTHYOLOGISTS AND HERPETOLOGISTS

Dave joined ASIH in 1958. He is one of the treasured yearly members, paying dues annually rather than being a life member. He attended his first meeting in San Diego in 1959, and he quickly sensed an excitement and rejuvenation in progress. He met such leaders as Carl Hubbs and was introduced to his academic "grandfather" George Myers. Ed Taylor, who had just retired, made a dramatic announcement at the Board of Governor's meeting: a promising young herpetologist from the University of Michigan, Bill Duellman, had been hired to replace him.

The first meetings, though, were a disappointment in other ways; people drank way too much and behaved poorly, and women were treated badly. For example, at one meeting in Austin, all the women in sight (whether in ASIH or not) were thrown in the swimming pool. At the 1960 meeting, Dave, George Rabb, and Jay Savage plotted to modernize the society; they wanted to shake things up—to go in new directions by raising the professionalism of the group and bringing more intellectual content to the meetings and the journal. Later, while on the Board of Governors, Dave advocated a controversial change to the way *Copeia* was edited. Instead of dividing the publication into sections based on study organism—ichs, herps—he suggested having general herpetology and ichthyology sections, but adding sections based on research fields—Ecology and Ethology; Genetics, Development, and Morphology; and Physiology and Physiological Ecology. This organizational change promoted integration across herpetology and ichthyology and modernized the journal.

A HANDFUL OF HIGHLY MEMORABLE FIELD TRIPS

Dave's first salamander field trip was in 1958, and he continued to do extensive field work for about 50 years. Some of Dave's first trips were with fellow Jay Savage's graduate student Arden Brame. In 1958, Brame introduced Dave to species diversity in *Batrachoseps*—he saw his first *B. simatus*, *B. relictus*, and *B. minor*, all then unnamed. Dave also remembers his first extended field trip to the southern Appalachians during this time period as being amazing. He started at White Top Mountain in Virginia and went down the Blue Ridge Mountains to Highlands, North Carolina, and Rabun County, Georgia, with a detour to the Great Smokies. He saw new species (for him) nearly everywhere he stopped. Especially memorable was a wonderful excursion to Old Yonahlossee Road with Bob Gordon and Jim MacMahon—amazing species diversity, and it led directly to one of Dave's first publications (Gordon et al., 1962).

In 1961, Dave spent the summer with Richard Etheridge in Amazonian Peru (see Wake, 2013, for a more detailed description of the trip). He saw no salamanders there, but he still remembers the amazing frog diversity: "The frogs were fascinating, and the highlight to me was a spectacular large female *Hemiphractus* with 13 large eggs glued to its back, each egg containing a developing embryo with two eyes looking at me!" His last week was spent in a hospital in Lima recovering from cholera, which he got in the field; his evacuation and trip to Lima are memorable to this day! Dave summarizes the impact of his Peru experience:

"While the Peru adventure did not directly impact my future research, it was nevertheless a wonderful experience that contributed significantly to my maturation as a person and as a scientist. It served as a break in my headlong determination to be a successful scientist. I never published a word about that summer, and yet it had a lasting influence on me. Strangely enough, it gave me confidence, it resolved some indecision and it encouraged me to focus on both short and long term goals. The experience also was very important in enabling me to develop a research and teaching program in integrative biology, in which I merged laboratory and field components of my work and developed an organismal-focused program that extended from molecules to communities and from functional and biogeography. As our heroes of the past from Humboldt to Darwin to Wallace, Bates, and many others, so clearly showed, travel and exposure to new places, peoples, and biological communities has lasting impacts on young minds. I hope young scientists of the future will be able to experience some of the stimulation I received from my youthful adventures."

On the way home from Peru, on the spur of the moment, Dave decided to join Jay Savage and several of his graduate students in Costa Rica. He spent several weeks there and saw his first tropical salamanders: five species, present at amazing densities. The lectures in a summer institute run by Jay Savage were just starting, and Dave was able to sit in on several, including one by the legendary tropical ecologist Leslie Holdridge. Dave writes about this time:

"At last I found tropical salamanders! Jim Vial was conducting his dissertation research on *Bolitoglossa* on Cerro de la Muerte, and salamanders were abundant. I also saw specimens of the only other genera in Costa Rica, *Oedipina* (which superficially resembles *Batrachoseps*, the slender salamanders of California) and the diminutive moss salamanders, *Nototriton*. I met many people in Costa Rica, ventured into the field to get the flavor of the country, and was determined to return.

In the end, my adventures that summer had great influence on my future career. Importantly, while I was determined to study tropical salamanders in the future, as I indeed did, it became clear to me that it was time for me to get busy in lab work, develop lab skills and establish a foundation on which I could build that might include tropical studies in the future."

In the spring of 1969, Dave made his first visit to Guatemala and saw the amazing diversity and density of salamanders on what would become his San Marcos transect, extending from near sea level near Tapachula, México, and

continuing to nearly 4000 m on Volcan Tajumulco in extreme western Guatemala. The inspiration for the transect was K. P. Schmidt's work in Guatemala in the early 1930s. The transect was surveyed repeatedly from its establishment by Dave and Jim Lynch in 1971 until 1979, and then again several times between 2005 and 2008. In the beginning, salamanders were very common, with most bromeliads containing salamanders, but habitat destruction and deforestation were proceeding rapidly and salamanders were in decline by late in the decade.

In July 1977, Ted Papenfuss, Dave's son Tom (then 14), and Dave were searching for a highly desirable and very attractive large salamander called *Pseudoeurycea melanomolga* at Las Lajas, an isolated microwave station on the slopes of Cofre de Perote in Veracruz, México. Tom had figured out how to find the animals and had collected the first specimens. Then, scratching into the roadside bank with a potato rake, Dave uncovered a really magnificent animal he had never seen, and he instantly knew it was an undescribed species. Ted and Dave were about 100 meters apart, and Tom was further along the road. Dave started walking quickly towards Ted to show him the specimen, but Ted was already walking quickly towards Dave. They each had found a specimen simultaneously. It became *Isthmura naucampetpetl*, still known from three collecting events and only six specimens (see Li Vigni, 2013, for this and other stories).

Dave's first feelings of foreboding and disquiet about amphibian decline were during his second trip to Parque Nacional El Chico in Hidalgo, México, in the early 1980s. On their first trip there, in 1971, Dave and Marvalee had found hundreds of individuals of two species of salamanders, and in his field notes, Dave stated that they could have collected thousands. Several years later, Jim Lynch and Lynne Houck counted 375 individuals in just a few hours at the same locality. By the early 1980s, everything had changed, and Dave was lucky to see one or two individuals in the field. Dave later had the same experience in other parts of México—at Puerto del Aire on the Puebla-Veracruz border, and at Cerro San Felipe, just north of Ciudad de Oaxaca.

Dave has over 400 publications (including papers, book chapters, and perspective pieces; see <https://ib.berkeley.edu/labs/wake/Papers.html>), and scanning them in chronological order reveals major themes in evolutionary biology. However, Dave has always remained committed to describing the new species he and his colleagues discovered on these field trips. To date, these total 118 species (and counting): two in the family Rhyacotritonidae, and the rest in the family Plethodontidae, including nine new genera (*Aquiloeurycea*, *Bradytriton*, *Cryptotriton*, *Dendrotriton*, *Ixalotriton*, *Nototriton*, *Nyctanolis*, *Urspelerpes*, *Karsenia*) and three new sub-genera.

AMPHIBIAN DECLINES AND AMPHIBIAWEB

Disquiet over salamander declines culminated for Dave during his attendance at the First World Congress of Herpetology in Canterbury in the fall of 1989. Others had similar experiences, and conversations bubbled about the recent disappearance of the Costa Rican Golden Toad. Stopping in Washington on the way home, Dave and biophysicist friend Harold Morowitz approached the National Academy of Sciences, asking that they sponsor an inquiry meeting about this apparently global phenomenon, which was held in Irvine, California, in February of 1990. The meeting caused quite a stir, with a lot of publicity from diverse media (e.g., CNN, New York Times, USA Today). This

led directly to the founding of the Task Force on Declining Amphibian Populations by George Rabb (then President of the Species Survival Commission, IUCN and Director of the Brookfield Zoo), with Jim Vial as the first Coordinator and Dave as the first Chairman. Dave has been deeply involved with the phenomenon ever since. In the late 1990s, he taught seminars on declining amphibians as a problem in conservation biology. These stimulated undergraduate participants to press for a website, which began to be developed by the seminar participants. The founders were computer scientist Joyce Gross, then graduate student Vance Vredenburg, and Dave. AmphibiaWeb went live in February 2000 and has been a resounding success. It provides information on amphibian declines, natural history, conservation, and taxonomy. Dave continues to direct an active, international and highly professional AmphibiaWeb team and spends hours each week on the site. Dave has published seminal papers on amphibian declines, several in Science (e.g., Wake, 1991, 2012; Cheng et al., 2011; Yap et al., 2015) and several in PNAS (e.g., Wake, 2007; Wake and Vredenburg, 2008; Rovito et al., 2009), among others (e.g., Blaustein and Wake, 1990; Wake, 1998).

A HANDFUL OF HIGHLY MEMORABLE "A-HA" MOMENTS

Dave has great enthusiasm about plethodontids and his joy at understanding something new about them is contagious. His greatest "a-ha" moment certainly was the day he unpacked what became *Karsenia koreana*. It took him about ten seconds to recognize that he had in his very hands the first plethodontid salamander found in Asia. Dave considers this to be THE biogeographic discovery of the 21st century. Another "a-ha" moment came much earlier in his career, while examining a specimen of *Batrachoseps* from southern California. Dave was very confused about the genus until he suddenly realized that there were three, rather than two, species in the San Gabriel Mountains; he had been examining the undescribed *Batrachoseps gabrieli*.

AWARDS

Dave has received numerous awards and honors throughout his career, from a pre-doctoral NSF fellowship at USC (1959–1962) and the Quantrell award for Excellence in Undergraduate Education at The University of Chicago (1967) to the recent UC Berkeley Distinguished Emeritus of the Year Award (2016). Dave's contributions to evolutionary biology have been recognized through his 1998 election to the National Academy of Sciences and 1996 election to the American Philosophical Society (APS, founded in 1843 by Benjamin Franklin); it is unusual for herpetologists to receive these honors. He is also a member of the American Academy of Arts and Sciences, as is Marvalee, and he was a Guggenheim Fellow from 1981 to 1982. The honors about which Dave is happiest are the Fellows Medal of the California Academy of Sciences, the Joseph Leidy Medal of the Academy of Natural Sciences, Philadelphia, and the Grinnell Medal from MVZ, as well as those from his peers in the herpetological community: the Henry S. Fitch award from the ASIH and the Distinguished Herpetologist and Honorary Membership from the Herpetologists' League.

NON-SALAMANDER INTERESTS

Dave remains close to his South Dakota roots as a closet botanist and true natural historian, stemming from those

long walks and talks with his grandfather. Graduate students and postdocs remember road trips with Dave always including a running description of plant zones, with tree species identified and their historical distributions noted in passing. Over a decade ago, Dave was elected to the Council of the Save the Redwoods League, a 98-year-old organization responsible for setting aside enormous amounts of territory that protects virtually all remaining old-growth redwood and sequoia trees. The organization also played a critical role in founding the California State Park system. Dave is very active on their Research Committee, evaluating grant proposals, attending several meetings around the state each year, and participating in various conference calls; he is very devoted to the organization and its admirable goals.

FAMILY

Dave met Marvalee (Hendricks) in 1959, while both were students at USC. She was originally headed for medical school, motivated by her strong desire to help others, but at the last minute, she made the difficult decision to do graduate work instead. Marvalee received her M.S. in 1964, her Ph.D. in 1968, and went on to hold faculty positions at the University of Illinois at Chicago and UC Berkeley (where she is currently a Professor of the Graduate School, having served terms as Chair of the Department of Zoology and then as the founding Chair of the new Department of Integrative Biology). She also held leadership roles in the International Society of Vertebrate Morphology, the Society for Integrative and Comparative Biology, the American Society of Ichthyology and Herpetology, the American Institute of Biological Sciences, and the International Union of Biological Sciences. She studies evolutionary morphology and development, with a focus on gymnophione amphibians and reproductive biology, particularly the evolution of viviparity. When asked about his spouse, Dave says that “Marvalee is nothing if not perceptive.” When asked about how his spouse has influenced his work, Dave says that Marvalee has been a true inspiration. They’ve been close colleagues, bouncing ideas off each other all the time. Their professions are all-consuming, so it’s been beneficial being in it together; it’s been seamless. Despite this constant intellectual engagement, however, Dave and Marvalee purposely did not work together early in their careers. Marvalee was intent on establishing her own career, even though she had taken the Wake family name when they married (it was 1962, after all). Their first collaboration was not until their first sabbatical—in London in 1975—and they did not publish that study until 2000! (Wake, M. H., and D. B. Wake. 2000. Developmental morphology of early vertebrateogenesis in caecilians (Amphibia: Gymnophiona): resegmentation and phylogenesis. *Zoology* 103:68–88... so maybe Dave does procrastinate a little bit, occasionally). Their first joint publications came from their 1982–1983 sabbatical in Bremen, Germany, and the only Wake, Wake, and Wake paper with son Tom (born in 1963, raised on salamanders, now a zooarchaeologist at UCLA) was published in 1983 (Wake, T. A., D. B. Wake, and M. H. Wake). Since those early papers, the Wakes have published together extensively, and in more recent years, they were awarded their first joint NSF grant (AmphibiaTree). Dave really cannot adequately summarize how important Marvalee has been to his professional success. They have had a very happy marriage. Marvalee has supported him in so many ways he cannot recount them all, but having a stable, loving, mutually supportive relationship and a wonderful family life

for, now, 54 plus years, Dave cites as the major factor in his success (Fig. 2). Son Tom is now married to Chrissy Campbell, a primatologist and anthropologist at Cal State Northridge, and Dave and Marvalee are the proud grandparents of Summer (Fig. 2), the light of her grandfather’s eye.

REMAINING PLETHODONTID QUESTIONS

Dave gave an invited talk at the 2016 Special Highlands Conference on Plethodontids. In this talk, he presented some of the big questions in plethodontid biology that await answers, or at least, more investigation (see Wake, in press). 1) Relating to the species problem, how many species of plethodontids are there and how many do we want to recognize? For example, is the *Ensatina eschscholtzii* complex one species, four, or 32 (see Kuchta and Wake, 2016 for a discussion of ring species and *Ensatina*)? 2) How robust is the current phylogeny for plethodontids? The tree has been shaken up a few times already, and Dave suspects there may be a true polytomy within the plethodontine clade. 3) Several biogeographic puzzles remain. For example, how did *Hydromantes* get to Europe and *Karsenia* to Korea? Why aren’t there more Old World plethodontids? Did plethodontids evolve into or out of Appalachia? Where did *Bolitoglossa* first evolve and when did it get to South America? What is the history of plethodontids in the Caribbean? Are they still there (Poinar and Wake, 2015)? Dave mentioned the way to resolve these biogeographic puzzles is to find more fossils, find more Eurasian plethodontids, and find Hispaniolan and/or Cuban plethodontids. It sounded as if Dave would be happy to review maps and potential sites. Who’s in?

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Appendix 1. List of David Wake's graduate students and postdocs.

Graduate students	Postdocs
Pere Alberch	Joao Alexandrino
Nancy Thomas Beck	Stevan J. Arnold
Roberto E. Bello	Ronald Bonett
Robert Bingham	David Buckley
Jessica A. Bolker	David C. Cannatella
Stephen D. Busack	Jing Che
John E. Cadle	Lia Ettinger
Andrés Collazo	Jinzhong Fu
David M. Darda	Mario García-París
Stephen M. Deban	David M. Green
Kevin de Queiroz	Raymond B. Huey
James L. Edwards	Robert H. Kaplan
Paul Elias	Mark Kirkpatrick
Juliana H. Feder	Ronald Lawson
David A. Good	R. Eric Lombard
Anna Graybeal	Iñigo Martínez-Solano
James Hanken	Kiisa C. Nishikawa
Alexander Haas	Neclâ Özeti
Lynne D. Houck	Steven Poe
Todd R. Jackman	Leslie J. Rissler
Martin H. Jäkel	Javier A. Rodríguez-Robles
Elizabeth L. Jockusch	Sean Rovito
Shawn R. Kuchta	Michael J. Ryan
Allan L. Larson	Neil H. Shubin
R. Eric Lombard	Skuli Skulason
James F. Lynch	Stephen C. Stearns
Meredith J. Mahoney	Matthias Stöck
Virginia C. Maiorana	Adam P. Summers
Sharyn B. Marks	David R. Vieites
Rachel Lockridge Mueller	Kelly A. Whitaker
Duncan S. Parks	Richard D. Worthington
Gabriela Parra Olea	Kay P. Yanev
Ricardo Pereira	Kelly R. Zamudio
Jane Peterson	Peng Zhang
Erica Bree Rosenblum	
Christopher J. Schneider	
Stanley K. Sessions	
James Shafland	
Nancy L. Staub	
James R. Stewart	
Samuel S. Sweet	
An-Ming Tan	
Brenda Tremper	
Vance Vredenburg	
Richard J. Wassersug	
Kay P. Yanev	
Yu Zeng	