

## OBITUARIES

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### Scientists and Salamanders: A Tribute to David B. Wake, Mentor Extraordinaire

David B. Wake (Figs. 1, 2) is best known professionally for his work on the systematics and biology of salamanders of the lungless family Plethodontidae (Fig. 3), especially those of the *Ensatina* ring species, Slender Salamanders (*Batrachoseps*), and Neotropical groups, as well as for his efforts raising awareness of global amphibian declines. He was also a mentor-extraordinaire—Dave mentored no less than 29 post-docs and 45 graduate students, mostly PhDs, over a period of about 50 years (Figs. 4, 5; for complete list of Dave's students and postdocs see <https://wakelab.berkeley.edu/people/>). Since his recent passing (29 April 2021), several excellent obituaries and retrospectives have been published or are in the works, highlighting his prodigious professional accomplishments and genuine kindness (Hanken 2021; Sandmir 2021; Zamudio 2021; Jockusch *in prep.*). Here, we focus instead on Dave's impact on his many graduate students.

Dave was a genuinely kind person, which was greatly appreciated by his students, and helped blunt the sometimes intense psychological challenges of working on a PhD dissertation. Dave was also a thoughtful but demanding mentor, but never asked any more from his students than he expected from himself (Fig. 6). Once when asked how his Thanksgiving break went, he replied: "It didn't go very well; I didn't get any work done!" Dave's enthusiasm for science was infectious yet tempered with caution. Who can forget his caveat to eager mentees that "Ideas are cheap; data are expensive!" (Comparing notes with other graduate students, this was sometimes turned around: "Data are cheap; ideas are expensive!"). Dave was unusual in that he didn't pay attention to one's status in life—you received his full attention whether you were a high school

PHOTO BY ROBERT HANSEN



FIG. 1. Dave Wake's enthusiasm and excitement for all things salamander is a persistent theme. This photo was taken in July 2018 as Dave examined a remarkable new cave-dwelling *Hydromantes*.

student or a fellow professor at an R1 institution. He collaborated with community college professors, private citizens, government biologists, and academic colleagues across the globe.

Dave described his perspective on mentoring graduate students:

"I HAVE BEEN BLESSED WITH WONDERFUL GRADUATE STUDENTS FROM MY EARLIEST DAYS IN CHICAGO. AND I'VE HAD OVER 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 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 WANTED 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."

—DAVID WAKE INTERVIEW, EMERITI LEGACY PROJECT, JANUARY 2020

To document Dave's impacts we solicited comments, or "mini-retrospectives," from his graduate students. In addition to official graduate students, we have included insights from some unofficial students, who came to lab meetings and interacted a lot with Dave. The following contributions reflect Dave's approach and highlight his breadth of influence, the family atmosphere and community he promoted, his decency towards students, his encyclopedic knowledge and memory (as one of his students noted "Before Google, we could just ask Dave!"), his gift of storytelling, his joy of discovery, his persistent curiosity about natural history, and his openness to new ideas. These characteristics form a common thread in the following stories from his graduate students, which constitute a fitting tribute to this remarkable scientist, mentor, and friend. We have organized these contributions chronologically based on the year when each contributor began their studies at the Museum of Vertebrate Zoology (MVZ), representing the "Early Years" (before 1980), the "Middle Years" (1980–2000), and the "Later Years" (after 2000).

#### SHARYN B. MARKS\*

Department of Biological Sciences, Humboldt State University,  
Arcata, California 95521, USA

#### STANLEY K. SESSIONS

Department of Biology, Hartwick College, Oneonta, New York  
13820, USA

#### NANCY L. STAUB

Biology Department, Gonzaga University, Spokane,  
Washington 99258, USA

\* Corresponding author; e-mail: [sharyn.marks@humboldt.edu](mailto:sharyn.marks@humboldt.edu)



FIG. 2. Any tribute to Dave is also a tribute to his long-time partner and fellow scientist Marvalee H. Wake, who together with Dave created the extended family community of the two Wakelabs. Photo of Dave and Marvalee in Dave's office, 2013.

### THE "EARLY YEARS"

I WAS ONE OF DAVE WAKE'S FIRST THREE GRADUATE STUDENTS. ALTHOUGH AT THAT TIME HE HAD NEVER WORKED WITH TADPOLES, HE HAD NO HESITANCY IN TAKING ME ON AS A GRADUATE STUDENT. HE WAS EQUALLY ENCOURAGING TO ME AS HE WAS TO STUDENTS WHO STUDIED SALAMANDERS. VERY EARLY ON IN MY LIFE AS A GRAD STUDENT, DAVE CHALLENGED ME WITH A FEW QUESTIONS ABOUT WHAT I WAS REALLY INTERESTED IN IN TERMS OF EVOLUTION. I REMEMBER A CONVERSATION WE HAD OVER A HALF CENTURY AGO ABOUT ORGANISMIC DIVERSITY AND WHAT I THOUGHT IT MEANT. HE WAS HAPPY TO SAY, "SO YOU'RE REALLY INTERESTED IN ADAPTATION, AREN'T YOU?!" EVEN THOUGH HIS OWN FOCUS WAS PRIMARILY ON SYSTEMATICS, HE WAS NOT BOTHERED AT ALL BY MY GREATER INTEREST IN FUNCTION THAN PHYLOGENY. HIS SIMPLE QUESTION HELPED ME DEFINE MY WHOLE CAREER. ONE OF DAVE'S THEMES WAS THAT "THE MOST IMPORTANT THING YOU DO AS AN ACADEMIC IS PICK YOUR COLLEAGUES AND YOUR STUDENTS." (I HAVE A VAGUE RECOLLECTION THAT THAT PHILOSOPHY OF ACADEMIA WAS SOMETHING HE CREDITED TO HIS OWN MAJOR PROFESSOR JAY SAVAGE.) AS AN ACADEMIC SON OF DAVE, AND AN ACADEMIC GRANDSON OF JAY SAVAGE, THAT PROVED TO BE GREAT WISDOM. I AM PROUD TO HAVE BEEN DAVE WAKE'S GRADUATE STUDENT AND SIMILARLY PROUD OF THE MANY GOOD STUDENTS THAT I'VE HAD TO WORK WITH. DAVE GETS CREDIT FOR THAT SINCE I TOOK HIS PHILOSOPHY SERIOUSLY.

—RICHARD WASSERSUG (U. CHICAGO AND MVZ 1967–1973), UNIVERSITY OF BRITISH COLUMBIA

THOUGH I WAS NOT DAVE'S MOST DIFFICULT STUDENT, NEITHER WAS I HIS EASIEST, AND I ALLOW THAT WE HAD OUR PHILOSOPHICAL DIFFERENCES. I ADMIRING AND RESPECTED HIS FOCUS ON CREATING EVOLUTIONARY NARRATIVES AND HIS ENTHUSIASM IN SUPPORTING A WIDE RANGE OF APPROACHES. I BELIEVE HE WAS THE IDEAL DIRECTOR FOR THE MVZ IN HIS ERA, BEFORE BIODIVERSITY WAS A WORD AND AS IT STRUGGLED TO FIND ITS PLACE AS A CONCEPT. HIS VISION WAS AHEAD OF ITS TIME. HIS STATURE WAS WELL-EARNED, AND HE WAS CERTAINLY THE APPROPRIATE FIGURE TO BRING FORTH *KARSENIA*, SURELY THE MOST STARTLING DISCOVERY IN A CENTURY OF SALAMANDER BIOLOGY. I SUSPECT DAVE'S GREATEST LEGACY, BEYOND THE ADAPTIVE RADIATION OF IMPORTANT RESEARCH BY HIS STUDENTS, WILL LIE IN HIS ELABORATION OF THE NEGLECTED DIVERSITY OF MIDDLE AMERICAN AND CALIFORNIAN PLETHODONTIDS. IN THAT CONTEXT ELIZABETH JOCKUSCH AND I ARE VERY PLEASED TO HAVE

IN PRESS A DESCRIPTION OF A NEW SPECIES OF *BATRACHOSEPS* NAMED FOR DAVE. FOR ME IT STANDS AS A TESTAMENT TO HIS PROFOUND INFLUENCE ON MY CAREER.

—SAM SWEET (MVZ 1970–1977), UNIVERSITY OF CALIFORNIA SANTA BARBARA

MUCH WILL BE REMEMBERED ABOUT DAVE'S DEVOTION TO SALAMANDERS AND THEIR BIOLOGICAL IMPORTANCE, BUT OF COURSE HIS INTERESTS WERE BROAD AND HE DID NOT PLACE TAXONOMIC RESTRICTIONS ON THE PROJECTS OF HIS STUDENTS. I WAS ONE WHO BENEFITTED FROM HIS VIEW THAT THE EMPHASIS SHOULD BE ON THE QUESTION. I ARRIVED IN BERKELEY IN FALL 1971, WITH A MASTER'S THESIS ON THE ECOLOGY AND BEHAVIOR OF PLETHODONTIDS, SUPERVISED BY JAMES L. VIAL, WHO OVERLAPPED WITH DAVE WHEN THEY WERE GRADUATE STUDENTS AT USC WORKING WITH JAY SAVAGE. DAVE EXPECTED, AS DID I, THAT I WOULD CONTINUE WORKING WITH PLETHODONTIDS. HOWEVER, AS MY INTEREST DRIFTED TOWARD RECENTLY FORMULATED MODELS OF LIZARD LIFE HISTORY EVOLUTION, DAVE ENCOURAGED ME TO DEVELOP A PROPOSAL FOR A PROJECT. HE THEN ENTHUSIASTICALLY PROVIDED THE GUIDANCE AND SUPPORT TO TURN IT INTO A DISSERTATION. DAVE'S CONTRIBUTIONS TO SCIENCE AND THE SCIENTIFIC WORLD ARE MONUMENTAL. I WILL REMEMBER HIM ALSO AS A THOUGHTFUL AND SUPPORTIVE MENTOR.

—JIM STEWART (MVZ 1971–1976), EAST TENNESSEE STATE UNIVERSITY

I WAS AN UNDERGRAD AT BERKELEY WHO HAD THE GOOD FORTUNE TO BECOME INVOLVED IN THE WAKE LAB IN MY FRESHMAN YEAR IN 1974–5 AND TO REMAIN ATTACHED TO IT THROUGH A MASTER'S IN ABOUT 1979. I HAD AN OPPORTUNITY TO VISIT GUATEMALA WITH MY MOTHER AFTER FRESHMAN YEAR. HAVING JUST TAKEN DAVE'S HERP COURSE I ASKED HIM WHERE I COULD COLLECT FOR HIM THAT MIGHT BE USEFUL. HE GAVE ME A XEROXED MAP OF THE COUNTRY AND CIRCLED SEVERAL PLACES. THE BIGGEST AND MOST INTERESTING CIRCLE SURROUNDED THE CARIBBEAN ESCARPMENT OF THE CUCHUMATANES, AN AREA OF EXCEPTIONALLY HIGH RAINFALL WHERE ESSENTIALLY NO SALAMANDER SAMPLING HAD BEEN DONE. HITCHHIKING WITH A BACKPACK FULL OF FORMALIN-FILLED BABY BOTTLES, I WAS ABLE TO VISIT FINCAS BEYOND THE END OF THE ROAD AND BRING BACK SPECIMENS THAT WERE THE FIRST *NYCTANOLIS* AND *BRADYTRITON*. UNBETTER KNOWNST TO ME, THESE PROVED TO BE MISSING LINKS IN THE PHYLOGENY AND SET ME UP FOR A WONDERFUL EDUCATION IN THE LAB, AND A HOME IN THE MUSEUM. I OWE A GREAT DEBT TO DAVE FOR EVERY ASPECT OF THIS PERIOD AND THE FOUNDATION IT PROVIDED FOR A HAPPY AND EVENTFUL LIFE IN THE NEARLY FIFTY YEARS SINCE.

—PAUL ELIAS (MVZ 1974–1979), NAUSHON TRUST

I AM GRATEFUL TO HAVE KNOWN DAVE FOR DECADES... FIRST IN 1970 AS AN UNDERGRADUATE IN HIS EVOLUTION COURSE, THEN AS A GRADUATE STUDENT AND A POST-DOC THROUGH THE 1970s, AS AN OCCASIONAL COLLABORATOR IN INTERVENING YEARS, AND AS A FRIEND ALWAYS. HIS ENTHUSIASM INFECTED AND ENCOURAGED MY WORK ON *BATRACHOSEPS* SYSTEMATICS IN THE ERA WHEN STARCH-GEL ELECTROPHORESIS WAS THE VERY "CUTTING EDGE" OF MOLECULAR TECHNIQUES. A SEEMINGLY ENDLESS NUMBER OF GELS EVENTUALLY REVEALED THAT ALL THOSE CONFUSINGLY SIMILAR *BATRACHOSEPS* COMPRISED A MUCH MORE COMPLEX LINEAGE THAN HAD BEEN SUSPECTED, AND HE ALWAYS WANTED TO KNOW OF EACH NEW DEVELOPMENT. THE "WAKE LAB" AND HERP GROUP SPIRIT OF CAMARADERIE AND COOPERATION OFFERED COLLECTING COMPANIONS, EVEN THOUGH THAT USUALLY MEANT CRAWLING THROUGH POISON OAK IN THE COLD AND/OR RAIN (AND THANK YOU AGAIN TO ANY OF YOU WHO MAY BE READING THIS!). OTHER STUDIES DEMONSTRATED SIMILAR UNEXPECTED INSIGHTS INTO MANY OTHER TAXA, ALL OF WHICH PAVED THE WAY FOR MODERN DNA TECHNIQUES AND APPROACHES. THANKS TO DAVE'S VISION, THE

1970s WAS A TRULY COLLABORATIVE ERA IN THE MVZ. AS WE ALL KNOW, HE CONTINUED TO COLLABORATE UNTIL HIS VERY END. HE WAS A KIND MAN AND LEAVES AN INSPIRATIONAL LEGACY.

—KAY YANEV (MVZ 1970–1984), MVZ AFFILIATE VOLUNTEER

DAVE'S WORK IN EVOLUTIONARY BIOLOGY COMBINED WITH A FIELD PROGRAM IN THE TROPICS ATTRACTED ME TO HIS LAB IN FALL 1976. I COULD NOT HAVE LANDED IN A BETTER PLACE. AT THAT TIME I KNEW I WANTED TO FOCUS ON TROPICAL BIOLOGY, BUT I WAS UNDECIDED ABOUT SPECIFIC QUESTIONS OR ORGANISMS. DAVE WAS AWARE THAT MY INTEREST IN SNAKES WAS AS GREAT OR MORE THAN IN HIS BELOVED SALAMANDERS, AND HE ALLOWED ME TO FOLLOW MY INSTINCTS AND DEVELOP MY OWN TRAJECTORY. I AM SURE THAT HE FELT SOME DISAPPOINTMENT WHEN SNAKES WON OUT, BUT AFTER THAT HE WAS A CONSTANT SUPPORT. HE COULD NOT HAVE BEEN A BETTER MAJOR PROFESSOR FOR ME AT THAT TIME. DAVE NURTURED ME INTELLECTUALLY AND UNDERSTOOD MY ABSENCES IN A SOMETIMES-WAYWARD FIELD PROGRAM. EVEN AFTER 40 YEARS, THE BREADTH OF DAVE'S INTERESTS AND HIS ABILITY TO SEE CONNECTIONS AMONG SO MANY FACETS OF BIOLOGY SEEM REMARKABLE. THAT INCOMPARABLE VISION INSPIRED YOUNG GRAD STUDENTS, WHO GREW FROM THE EXPERIENCE AND CARRIED SOME SMALL PART OF THAT VISION WITH THEM. DAVE'S PERSPECTIVE WAS SO BROAD AND DEEP THAT ONE ALWAYS MARVELED AT THE THREADS HE COULD WEAVE TOGETHER. HE HAD A PROFOUND INFLUENCE ON MY THINKING ABOUT PATTERNS OF EVOLUTION, ADAPTIVE RADIATION, SYSTEMATICS, ANATOMY, DEVELOPMENT, SPECIATION, AND EVOLUTIONARY THEORY. AMONG BIOLOGISTS I HAVE KNOWN, DAVE WAS AMONG THE BEST AT INTEGRATION IN THE BEST SENSE OF THAT WORD. I AM GRATEFUL TO HAVE SHARED SOME TIME WITH HIM.

—JOHN E. CADLE (MVZ 1976–1982), STONY BROOK UNIVERSITY

ONE MORNING IN 1979, I WAS READING PAPERS FOR A SEMINAR CLASS IN THE MVZ READING ROOM, WHEN DAVE WAKE RUSHED THROUGH WITH SOME SURPRISING NEWS: FRANCIS CRICK WAS IN ALLAN WILSON'S OFFICE, AND HE WANTED TO TALK ABOUT SALAMANDERS. DAVE INVITED ME TO JOIN HIM, AND WE HEADED TO AN IMPROMPTU MEETING WITH FRANCIS CRICK, ALLAN WILSON, AND WESLEY BROWN. DAVE INTRODUCED HIS RESEARCH PROGRAM, AND FRANCIS CRICK BEGAN A SERIES OF QUESTIONS, TRYING TO LEARN HOW SALAMANDERS WERE DIFFERENT FROM ALL OTHER ANIMALS. HE KEPT HIS QUESTIONS DELIBERATELY VAGUE TO AVOID BIASING DAVE'S ANSWERS. AFTER THIS MYSTERIOUS INTERROGATION, FRANCIS CRICK TOLD US THAT HE SOON WOULD PUBLISH A NEW THEORY CALLED "SELFISH DNA." IT CLAIMED THAT MANY REPETITIVE DNA SEQUENCES IN THE NUCLEAR GENOME HAD EVOLVED AN AUTONOMOUS ABILITY TO REPLICATE THEMSELVES, AND THAT THEIR EVOLUTIONARY ACCUMULATION WOULD INCREASE GENOME SIZE. SELFISH DNA WAS "THE ULTIMATE PARASITE," PROVIDING NO UTILITY TO THE ORGANISM AND EVENTUALLY CHALLENGING THE LIMITS OF ORGANISMAL GROWTH AND DEVELOPMENT. NATURAL SELECTION WOULD THEN ACT AGAINST SELFISH DNA. SALAMANDERS AS A GROUP HAVE VERY LARGE GENOMES, AND FRANCIS CRICK WANTED TO KNOW HOW THEIR BIOLOGY LET THEM ACCUMULATE SO MUCH MORE SELFISH DNA THAN OTHER ANIMALS DID. HIS INITIAL PUBLICATION ON SELFISH DNA ACKNOWLEDGED DAVE FOR PRELIMINARY EVIDENCE THAT SALAMANDER SPECIES WITH THE LONGEST DEVELOPMENTAL TIMES OFTEN HAVE THE LARGEST GENOME SIZES. FROM THIS MEETING FORWARD TO THE PRESENT TIME, THE SELFISH DNA THEORY HAS STIMULATED MUCH FASCINATING RESEARCH BY DAVE AND HIS STUDENTS AND COLLEAGUES.

—ALLAN LARSON (MVZ 1977–1986), WASHINGTON UNIVERSITY

I FIRST HEARD ABOUT DAVE WAKE WHEN I WAS AN UNDERGRADUATE AT THE UNIVERSITY OF OREGON. I TOOK AN EVOLUTION COURSE WITH ED NOVITSKI, AND JIM KEZER GAVE ONE OF HIS FAMOUS GUEST LECTURES ON THE CYTOGENETICS OF PLETHODONTID SALAMANDERS. KEZER DESCRIBED DAVID WAKE AS THE "WORLD'S AUTHORITY ON PLETHODONTID SALAMANDERS"

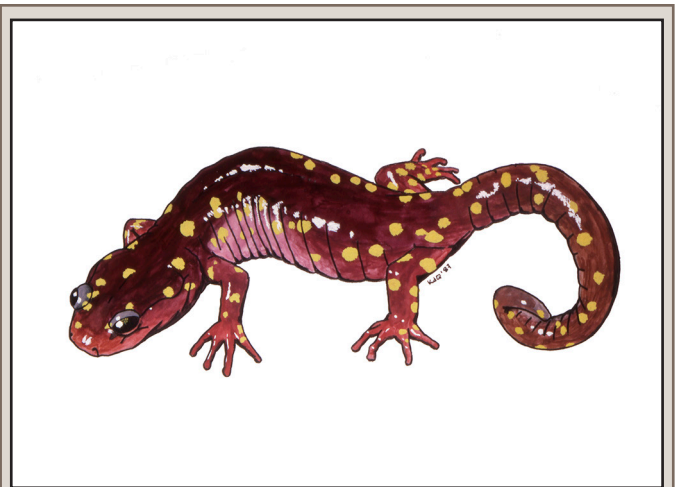


FIG. 3. *Aneides lugubris*, one of Dave's favorite plethodontid salamanders.

ILLUSTRATION BY KEVIN DE QUEIROZ

AND CITED HIS FAMOUS MONOGRAPH (WAKE 1966) ON THE "COMPARATIVE OSTEOLOGY AND EVOLUTION OF THE LUNGLESS SALAMANDERS, FAMILY PLETHODONTIDAE." AS SOON AS THE CLASS WAS OVER, I RUSHED TO THE LIBRARY TO FIND THAT ARTICLE, WHICH I THEN "INHALED." THE COMBINATION OF KEZER'S LECTURE AND DAVE'S MONOGRAPH REINFORCED IN ME AN ALREADY GROWING FASCINATION WITH SALAMANDERS, A FASCINATION THAT MY PARENTS PROMISED WOULD LEAD TO NO GOOD (AND CERTAINLY NO MONEY) BUT AROUND WHICH, I NOW REALIZED, INTERESTING CAREERS COULD BE BUILT. BERKELEY WAS AN UNFORGETTABLE EXPERIENCE THAT PERMANENTLY CHANGED MY LIFE. IT OPENED MY EYES TO NEW WAYS OF LOOKING AT BIOLOGY, AT SCIENCE, AND AT THE WORLD. I THINK PEOPLE WHO HAVE SHARED IN THIS "BERKELEY EXPERIENCE" (AND ESPECIALLY THE "MVZ EXPERIENCE") KNOW EXACTLY WHAT I AM TALKING ABOUT. I AM ESPECIALLY GRATEFUL TO DAVE WAKE FOR ENCOURAGING ME TO DEVELOP THE ABILITY TO THINK INDEPENDENTLY AND CREATIVELY, AND I BELIEVE THAT THIS ABILITY HAS SERVED, AND CONTINUES TO SERVE ME WELL. I FEEL SO LUCKY TO HAVE HAD THIS OPPORTUNITY, AND TO HAVE MET SO MANY REMARKABLE PEOPLE. I AM ESPECIALLY INDEBTED TO DAVE WAKE FOR BEING THE PERFECT PHD ADVISOR, MENTOR, COLLEAGUE, AND FRIEND.

—STANLEY K. SESSIONS (MVZ 1978–1985), HARTWICK COLLEGE

THE YEARS I WORKED AS MANAGER OF MVZ'S HERPETOLOGY COLLECTION AND AS A GRADUATE STUDENT UNDER DAVE WERE AMONG THE BEST YEARS OF MY LIFE. WHEN I BECAME DISILLUSIONED WITH MY ORIGINAL DISSERTATION PROJECT (BIOCHEMICAL DIFFERENTIATION BETWEEN *PLESTIODON* (AKA *EUMECES*) *GILBERTI* AND *P. SKILTONIANUS*), WE DISCUSSED CHANGING MY DISSERTATION PROJECT TO EXAMINING GENETIC DIFFERENTIATION BETWEEN AFRICAN AND EUROPEAN AMPHIBIAN AND REPTILE SPECIES EACH INHABITING BOTH SIDES OF THE STRAIT OF GIBRALTAR. FUNDING FOR MY SKINK PROJECT COULD NOT BE USED TO SUPPORT THE THREE MONTHS OF OVERSEAS WORK NECESSARY; DAVE WAS UNDERSTANDING AND EMPATHETIC, AND LATER ASSISTED ME IN FINDING SOURCES FOR THE FIELD EXPENSES REQUIRED. IT IS BECAUSE OF HIM THAT I ENDED UP AT BERKELEY. IT IS BECAUSE OF HIS SUPPORT AND BELIEF IN MY ABILITY THAT HE APPROVED OF MY CHANGING PH.D. PROJECTS "IN MID-STREAM." DURING MY ENTIRE RESIDENCE AT BERKELEY, DAVE WAS ALWAYS SUPPORTIVE; EVERY CRITICAL REMARK HE MADE WAS DELIVERED AS A MEANS TO IMPROVING MY PERFORMANCE. WHEN HE WROTE "I CAN'T READ THIS SENTENCE" ON A MANUSCRIPT, I FOUND THAT NEITHER COULD I. I AM A BETTER SCIENTIST AND PERSON FOR HAVING HAD DR. DAVID B. WAKE AS A MENTOR.

—STEPHEN D. BUSACK (MVZ 1978–1985), NORTH CAROLINA STATE MUSEUM OF NATURAL SCIENCES





FIG. 4. Dave Wake with some of his academic “children” and “grand-children” at the Sixth Conference on the Biology of Plethodontid Salamanders at the University of Tulsa, Oklahoma, 2014. L to R: Zach Lewis (academic grandchild via Jim Hanken), Chris Evelyn (academic grandchild via Sam Sweet), Sean Reilly (academic grandchild via Sharyn Marks), Tom Devitt (unofficial Ph.D. student), Sean Rovito (postdoc), Peng Zhang (postdoc), Meredith Mahoney (Ph.D. student), Shawn Kuchta (Ph.D. student), Ron Bonnett (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), and Eric Lombard (Ph.D. student and postdoc).

### THE “MIDDLE YEARS”

MY TIME AS A DBW GRAD STUDENT WAS TUMULTUOUS—STIMULATING AND WONDERFUL, YET EXTREMELY CHALLENGING. BY 1985, *CHIROP-TEROTRITION* HAD ME IN ITS INSUFFERABLE GRIP (FACILITATED I’M SURE BY ITS UNUSUAL TARSAL ARRANGEMENT). I WASN’T SURE I COULD FINISH, WASN’T SURE I WANTED TO. I FELT I WAS FAILING, THAT I WAS NOT LIVING UP TO WHAT BEING A DAVE WAKE STUDENT MEANT. THINGS HIT A BREAKING POINT AT THE END OF SPRING SEMESTER. WITH MARVALEE’S SUPPORT AND FORBEARANCE, I FINISHED UP MY T.A. RESPONSIBILITIES FOR COMPARATIVE ANATOMY AS BEST I COULD, LEFT MVZ, AND SPENT THE NEXT SIX MONTHS WORKING AS A CARPENTER’S ASSISTANT WHILE ATTEMPTING TO COME TO TERMS WITH MY FUTURE. THE TIME AWAY PROVED CLARIFYING, AND I DECIDED TO RETURN TO GRAD SCHOOL, AND WITH MUCH NEEDED PERSPECTIVE. I KNEW I WANTED TO FINISH, AND I NOW SAW MY FUTURE NOT AS MOVING INTO A RESEARCH POSITION LIKE MOST OF MY FELLOW GRADUATE STUDENTS, BUT AS BECOMING A TEACHER. BUT WHAT WOULD DAVE THINK? WOULD HE BE DISAPPOINTED? I WAS NERVOUS WHEN I MET WITH DAVE IN HIS OFFICE SOMETIME LATE THAT FALL, BUT OF COURSE I NEED NOT HAVE BEEN. DAVE WAS GRACIOUS, SUPPORTIVE, AND FATHERLY. HE WAS GLAD TO HAVE ME BACK. HE MADE IT CLEAR THAT HE WANTED ME TO FIND MY PATH, FIGURE OUT WHAT MADE ME HAPPY. THIS WAS THE BEGINNING OF A MORE MATURE AND OPEN RELATIONSHIP BETWEEN US, AND I WILL FOREVER BE THANKFUL FOR DAVE’S ENCOURAGEMENT AND FRIENDSHIP THAT DAY AND EVER SINCE.

—DAVE DARDA (MVZ 1980–1987), CENTRAL WASHINGTON UNIVERSITY

WHAT I ADMIRER MOST ABOUT DAVE INTELLECTUALLY WAS HIS BROAD AND INTEGRATIVE PERSPECTIVE. DAVE WAS AN INTEGRATIVE BIOLOGIST IN THE FULL SENSE OF THE TERM. HE NOT ONLY STUDIED PHENOMENA FROM MANY DIFFERENT PERSPECTIVES, INCLUDING DIFFERENT LEVELS OF BIOLOGICAL ORGANIZATION, BUT HE ALSO INTEGRATED THE INFORMATION OBTAINED INTO A “BIG-PICTURE” VIEW. PERHAPS THE CLOSEST I’VE COME TO ACHIEVING SUCH A VIEW IN MY OWN WORK CONCERNS AN AREA WHERE DAVE INFLUENCED MY IDEAS DIRECTLY. WHILE I WAS IN GRADUATE SCHOOL, I HAD THE GOOD FORTUNE OF SERVING SEVERAL TIMES AS A TEACHING ASSISTANT IN DAVE’S LEGENDARY EVOLUTION COURSE. ONE OF THE TOPICS THAT DAVE

COVERED IN GREAT DETAIL IN HIS COURSE WAS SPECIES CONCEPTS, AND AT THAT TIME, MANY SEEMINGLY INCOMPATIBLE IDEAS ABOUT THE NATURE OF SPECIES HAD BEEN PROPOSED. DAVE COVERED THOSE ALTERNATIVE SPECIES CONCEPTS IN A BROAD AND IMPARTIAL WAY, DESCRIBING THE DIFFERENT VIEWS AND DISCUSSING THEIR STRENGTHS AND WEAKNESSES. I HAD ALREADY DEVELOPED AN INTEREST IN CONCEPTUAL ASPECTS OF BIOLOGY, AND THIS WAS MY FAVORITE PART OF THE COURSE. LATER, NEARLY 10 YEARS AFTER I GRADUATED, I HAD THE OPPORTUNITY TO DEVELOP MY OWN VIEWS ON THE SUBJECT, WHICH LED TO A PAPER WHERE I ANALYZED THE SPECIES PROBLEM FROM THE PERSPECTIVES OF DIFFERENT BIOLOGICAL SUBDISCIPLINES AND, DRAWING HEAVILY ON WHAT I HAD LEARNED IN DAVE’S COURSE, ATTEMPTED TO INTEGRATE THOSE PERSPECTIVES INTO A SINGLE, UNIFIED CONCEPT. I CONSIDER THAT PAPER A MILESTONE IN MY INTELLECTUAL DEVELOPMENT—MY BEST APPROXIMATION TO A DAVE-WAKEIAN BIG-PICTURE VIEW AND THUS A CONCRETE MANIFESTATION OF DAVE’S INFLUENCE ON MY THINKING.

—KEVIN DE QUEIROZ (MVZ 1983–1989), NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION

DAVE VALUED CLEAR THOUGHT AND SOLID LOGIC. IT WAS A REAL COMPLIMENT IF HE TOLD YOU YOUR PRACTICE TALK WAS CLEAR. HE ALSO APPRECIATED DIRECT, STRAIGHTFORWARD ANSWERS TO QUESTIONS. I LEARNED THIS WHEN I TOOK EVOLUTION FROM HIM IN THE FALL OF 1982. I REMEMBER WRITING NON-STOP IN BLUE BOOKS FOR THE TESTS. FOR ONE OF MY ANSWERS, IN WHICH I MUST HAVE BEEN GIVING TOO MUCH BACKGROUND INFORMATION, HE WROTE IN THE MARGINS, “CORRECT, BUT MAINLY IRRELEVANT.” I’VE THOUGHT OF THAT COMMENT OFTEN—WHEN WRITING PAPERS AND GRADING TESTS. MY SECOND STORY IS FROM A TRIP TO COSTA RICA WITH DAVE, WHERE WE WERE ON THE LOOKOUT FOR, AND FOUND, THE NEW SPECIES, *BOLITOGLOSSA GRACILIS*. I WAS EATING BREAKFAST WITH DAVE AND A FEW OTHERS ON ONE OF OUR FIRST MORNINGS THERE AND WAS HORRIFIED TO SEE MAGGOTS CRAWLING AROUND IN MY GRANOLA. BEFORE I COULD EVEN ASK “WHAT SHOULD WE DO?” DAVE VERY CALMLY STARTED PICKING THE MAGGOTS OUT OF HIS GRANOLA ONE BY ONE AND THEN PROCEEDED TO EAT (THE GRANOLA, NOT THE MAGGOTS). I WAS STUNNED, BUT AFTER A SECOND OR TWO, FOLLOWED HIS EXAMPLE AND STARTED CALMLY PICKING MAGGOTS OUT OF MY BOWL. AND AFTER THAT FIRST MAGGOT MORNING, WE WOULD START EACH MORNING COMPARING THE MAGGOT-LOAD IN OUR BOWLS. THAT LESSON—OF MAKING THE BEST OUT OF WHAT YOU HAVE—HAS STUCK WITH ME.

—NANCY STAUB (MVZ 1983–1989), GONZAGA UNIVERSITY

DAVE HAD A PROFOUND IMPACT ON MY VIEWS ON EVOLUTION AND SCIENTIFIC INQUIRY. WHILE HE UNDERSTOOD THE IMPORTANCE OF NATURAL SELECTION AS THE MECHANISM FOR EVOLUTION, HE WAS MORE INTERESTED IN WHAT LIMITED THE PHENOTYPIC VARIATION THAT NATURAL SELECTION ACTED UPON. I LOVED THIS PERSPECTIVE ON EVOLUTION AND FOCUSED ON THIS FOR MY GRADUATE WORK. WHILE MAYBE NOT OBVIOUS TO SOME, DAVE WAS THE MOST HYPOTHESIS DRIVEN SCIENTIST I EVER MET. HE ALWAYS TOLD ME HOW MUCH HE PREFERRED PAPERS AND SCIENTISTS WITH CLEAR AND STRONG POINTS OF VIEW BECAUSE AT LEAST THEY PROVIDED A TESTABLE HYPOTHESIS. HE ALMOST HAD A DISDAIN FOR THEORIES THAT SEEMED TO EXPLAIN EVERYTHING, SAYING THEY EXHIBITED “BLOB-LIKE BEHAVIOR.” DAVE LOVED TO MAKE YOU THINK. HE WOULD GET THAT WRY SMILE AND TWINKLE IN HIS EYE WHEN HE POINTED OUT ALTERNATIVE IDEAS THAT I HAD NOT CONSIDERED IN MY INQUIRIES. FINALLY, I WANT TO CONCLUDE WITH WHAT DROVE ME, AND I FEEL, DAVE’S INTEREST IN BIOLOGY. IT WAS OUR EARLY LOVE OF NATURAL HISTORY. THIS IS NICELY REFLECTED BY DAVE’S REVERENCE TOWARDS ALL THE FIELD NOTEBOOKS THE MUSEUM OF VERTEBRATE ZOOLOGY HOUSED. DAVE, I WISH I HAD KEPT UP MY FIELD NOTEBOOKS A TENTH AS WELL AS YOU DID YOURS.

—ANDRES COLLAZO (MVZ 1985–1990), CALIFORNIA INSTITUTE OF TECHNOLOGY



FIG. 5. Dave Wake with Craig Moritz (second from left) and some of Wake's more recent students near the Wake cabin in the Sierra, 22 January 2011; L to R: Ricardo Pereira, Craig Moritz, Rachel Mueller, Tom Devitt, and Dave Wake.

MY FONDEST MEMORIES OF GRADUATE SCHOOL ARE THOSE TIMES SPENT IN THE FIELD WITH DAVE AND MY FELLOW LAB MATES. WHILE THE DESTINATION (TO COLLECT SALAMANDERS, OF COURSE!) WAS IMPORTANT, THE JOURNEY WAS EVEN MORE SO, BECAUSE THESE WERE OPPORTUNITIES FOR DAVE TO SHARE INSIGHTS ABOUT NATURAL HISTORY, GEOLOGICAL HISTORY, EVOLUTIONARY HISTORY AND ECOLOGY, AS WE TRAVERSED CALIFORNIA, THE SOUTHERN APPALACHIANS, AND COSTA RICA. DAVE HAD AN AMAZING MEMORY FOR DETAILS, WAS A CAPTIVATING STORYTELLER, AND HAD A WONDERFUL SENSE OF HUMOR, SO THESE LESSONS WERE DOLED OUT IN SUCH A WAY THAT I JUST SOAKED IT ALL UP WITHOUT EVEN REALIZING WHAT WAS HAPPENING. THESE LESSONS BECAME INTRINSIC TO THE WAY IN WHICH I THINK ABOUT THE NATURAL WORLD AND ORGANISMAL EVOLUTION.

—SHARYN MARKS (MVZ 1987–1995), HUMBOLDT STATE UNIVERSITY

THE FIRST TIME I MET DAVID WAKE WAS WHEN I WAS A PROSPECTIVE GRADUATE STUDENT VISITING BERKELEY. HE SHOWED ME AROUND THE MUSEUM AND INTRODUCED ME TO EVERYONE WE MET. HE SEEMED TO BE TRYING TO IMPRESS ME AND I KEPT THINKING "HE DOES KNOW THAT I AM JUST A PROSPECTIVE STUDENT, DOESN'T HE?" I WAS AMAZED AT HOW GENEROUS HE WAS WITH HIS TIME. WHEN I CAME TO VISIT JUST AFTER *KARSENIA*, THE KOREAN LUNGLESS SALAMANDER, HAD ARRIVED AT BERKELEY, HE HANDED ME A JAR AND ASKED ME WHAT SPECIES I THOUGHT IT WAS. I KNEW IT HAD TO BE SPECIAL BUT I TOLD HIM IT LOOKED LIKE *PLETHODON ELONGATUS*. THAT WAS THE RIGHT ANSWER BECAUSE HE WANTED TO SHOW THAT THIS AMAZING AND DISTINCT (GEOGRAPHICALLY) SALAMANDER WAS LIKE MANY SALAMANDERS—MORPHOLOGICALLY CONSERVED. THE BEST TIMES WITH DAVE WERE IN THE FIELD. THE CONVERSATIONS IN THE CAR WERE ALWAYS GREAT, BOTH FOR TALKING ABOUT SCIENCE AND HAVING THE GREATEST TOUR GUIDE IMAGINABLE WITH A NEVER-ENDING STREAM OF INTERESTING FACTS ABOUT NEARLY EVERYWHERE WE WENT—WHETHER IT WAS THE HISTORY OF SUTTER BUTTES IN THE CENTRAL VALLEY, OR A WINERY THAT USED TO BE A GREAT PLACE TO FIND *ANEIDES FLAVIPUNCTATUS*, OR UNUSUAL GEOLOGICAL FORMATIONS. FOR A KNOW-IT-ALL KID LIKE ME IT WAS WONDERFUL TO HAVE A ROLE MODEL WHO WAS BOTH MODEST AND ENTHUSIASTIC AND WHO REALLY DID KNOW IT ALL. DAVE WILL ALWAYS BE AN IMPORTANT PART OF THE WAY I LOOK AT THE WORLD.

—TODD JACKMAN (MVZ 1988–1994), VILLANOVA UNIVERSITY

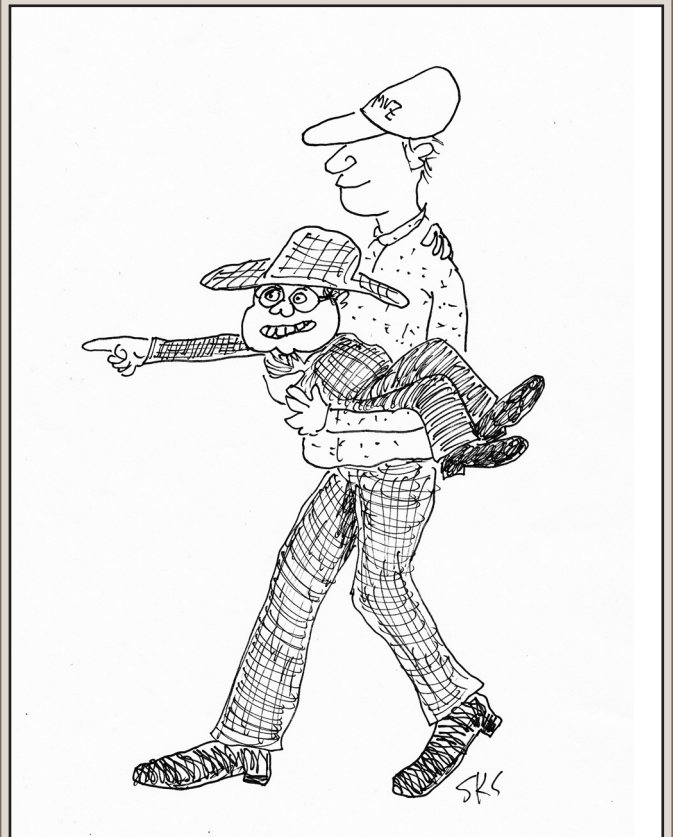


FIG. 6. Dave Wake was physically smaller than most of his students and post-docs, but that never seemed to interfere in his abilities as guide and mentor.

I AM VERY FORTUNATE TO HAVE BEEN ONE OF DAVE'S GRADUATE STUDENTS. IT WAS AT BERKELEY'S WAKELAB WHERE I WAS EXPOSED TO A PLETHORA OF IDEAS, NEW RESEARCH TOOLS, AND ESPECIALLY MY FELLOW LAB-MATES, LED BY OUR ACADEMIC ADVISOR, DAVE. NOW, 33 YEARS LATER, I STILL REMEMBER VIVIDLY OUR WEEKLY WAKE LUNCH, WHERE ALL STUDENTS SHARED THEIR ACADEMIC PROGRESS AND DAVE OFTEN SHARED NEW LITERATURE. DAVE'S LUNCH WAS ALMOST ALWAYS THE SAME: A HOMEMADE SANDWICH, AN APPLE, AND A BOTTLE OF WATER. I ALSO VIVIDLY REMEMBER MVZ LUNCH SEMINARS AND WEEKLY HERP GROUP SEMINARS. DAVE INTRODUCED ME TO THE STUDY OF CALIFORNIA NEWTS, GENUS *TARICHA*. WE SPENT A LOT OF WEEKENDS AND HOLIDAYS COLLECTING SAMPLES FROM THE SISKIYOU MOUNTAINS IN NORTHERN CALIFORNIA TO THE SIERRA NEVADA, WHERE WE SPENT TIME IN DAVE'S FAMILY CABIN. I REMEMBER ONE TRIP TO SONOMA COUNTY, WHEN I WAS THE DRIVER IN A REMOTE AREA. I DROVE THROUGH AN INTERSECTION WITHOUT STOPPING BECAUSE THERE WERE NO OTHER CARS IN SIGHT. DAVE JOKED WITH ME AND TAUGHT ME THAT EVEN WITHOUT TRAFFIC, A STOP AT AN INTERSECTION IS NECESSARY. EVER SINCE, I WILL STOP AT INTERSECTIONS NO MATTER WHETHER THERE IS ANY TRAFFIC OR NOT! DAVE HAS BEEN FAR MORE THAN JUST AN ACADEMIC ADVISOR TO ME, AND TO HIS OTHER STUDENTS. THE MOST IMPORTANT THINGS WE LEARNED FROM DAVE ARE NOT JUST HOW TO DO RESEARCH, BUT ALSO HOW TO LIVE A FRUITFUL LIFE, BE PRODUCTIVE, AND TO HELP OTHERS WHOLEHEARTEDLY.

—ANNING TAN (MVZ 1988–1993), HAWAII DEPARTMENT OF HUMAN SERVICES

I VISITED BERKELEY AS A PROSPECTIVE GRADUATE STUDENT ON A DAY WHEN WAKE LUNCH WAS HAPPENING IN THE MVZ LIBRARY. THERE WERE USGS MAPS OF CALIFORNIA SPREAD OUT ON THE TABLE, AND THEN DAVE STARTED LAYING OUT LITTLE PLASTIC CONTAINERS ON PRECISE LOCATIONS ...





Fig. 7. Dave also knew how to party. Here he is in his polyester leisure suit at the “Bad Music of the 1970s” themed going-away party for one of his students (Andres Collazo) in 1990. L to R: Dave Wake and Todd Jackman.

AND EACH OF THE CONTAINERS HAD A LIVE SALAMANDER IN IT, FROM THAT SITE. AFTER THAT, HOW COULD I POSSIBLY HAVE GONE ANYWHERE ELSE? DAVE TAUGHT ME A LOT ABOUT HOW TO BE AN EVOLUTIONARY BIOLOGIST. HE ALSO TAUGHT ME WHAT GREAT MENTORING LOOKS LIKE: FOR EXAMPLE, HIS TACTIC OF POLITELY INTERRUPTING SOME TERRIBLY IMPORTANT COLLEAGUE CHATting WITH OTHER SENIOR PEOPLE AT A CONFERENCE, INTRODUCING HIS NEW GRAD STUDENT, AND THEN VANISHING—LEAVING THE STUDENT IN THE MIDST OF THE CONVERSATION. HE INSISTED HIS STUDENTS ALL DO PRACTICE TALKS BEFORE HEADING OFF TO MEETINGS, AND HE DID THEM TOO. HE TOOK US SERIOUSLY AS SCHOLARS...AND SHOWED UP IN A POLYESTER LEISURE SUIT AND A BIG GRIN FOR OUR BAD-MUSIC-OF-THE-70s COSTUME PARTY (FIG. 7). MY STANDARDS FOR HOW GRADUATE PROGRAMS SHOULD WORK, HOW ADVISORS SHOULD MENTOR THEIR STUDENTS, AND WHAT A GRADUATE STUDENT COMMUNITY SHOULD LOOK LIKE ALL GO BACK TO WAKELAB. CENTRAL TO DAVE’S PHILOSOPHY AND PRACTICE OF TRAINING GRAD STUDENTS WAS THE PRINCIPLE THAT THE STUDENT’S INTERESTS CAME FIRST: HE WAS DELIGHTED TO TRAIN FUTURE COLLEAGUES WHO’D WORK WITH HIM ON PROJECTS HE’D LAUNCHED, BUT YOU DIDN’T HAVE TO DO HIS STUFF TO BE PART OF WAKELAB. WHEN I SHOWED UP AND SAID “I’M INTERESTED IN EVO-DEVO AND I’M KIND OF A FISH PERSON,” HIS RESPONSE WAS “I THINK THERE ARE SOME FOLKS UP AT DAVIS WHO ARE SPAWNING STURGEONS—WHY DON’T YOU LOOK INTO THAT?” HE SUPPORTED MY WORK ON AN OUTGROUP JUST AS WHOLEHEARTEDLY AS THE PROJECTS THAT WERE INTEGRAL TO HIS OWN RESEARCH.

—JESSICA BOLKER (MVZ 1989–1993), UNIVERSITY OF NEW HAMPSHIRE

AS A GRADUATE STUDENT IN A DEVELOPMENTAL BIOLOGY LAB, MY RESEARCH WAS FOCUSED AT THE LEVEL OF THE CELL AND TISSUE, BUT MY DRIVING INTEREST WAS IN THE EVOLUTION OF THE DEVELOPMENTAL PHENOMENA I STUDIED. BY WELCOMING ME TO PARTICIPATE IN THE INTELLECTUAL LIFE OF HIS LAB, DAVE GAVE ME THE OPPORTUNITY TO ENGAGE WITH THE ORGANISM, POPULATION, SPECIES AND CLADE, AND WITH A COMMUNITY OF EVOLUTIONARY RESEARCHERS AND THEIR WORK, IN A WAY I WOULD NEVER HAVE OTHERWISE BEEN ABLE TO AND WHICH HELPED BRING PURPOSE TO MY WORK. THIS WAS A HIGHLIGHT OF MY TIME AT BERKELEY, AND A GIFT I’LL NEVER FORGET. BUT DAVE ALSO GAVE ME A GIFT ON A MORE PERSONAL LEVEL. WHEN I DECIDED TO EMBARK ON A GENDER CHANGE, DAVE WAS ONE OF THE FIRST PEOPLE AT BERKELEY I SHARED THIS INFORMATION WITH, LONG BEFORE MOST OTHER COLLEAGUES. IT WAS SCARY TO DO, BUT I HAD ALWAYS SENSED DAVE WAS SOMEBODY I COULD CONFIDE IN. WHAT I DIDN’T ANTICIPATE WAS THAT HIS RESPONSE WOULD SET HIM APART FROM EVERYBODY ELSE I EVER SHARED IT WITH, BEFORE OR SINCE. HE SAID SIMPLY, “Wow. THAT MUST BE BOTH SCARY, AND EXCITING.” MOST PEOPLE’S REACTIONS, NO MATTER WHETHER POSITIVE OR NEGATIVE, WERE AT SOME LEVEL ABOUT *THEM*. DAVE WAS THE ONLY PERSON WITH THE EMPATHY TO ZERO IN IMMEDIATELY ON WHAT IT MEANT FOR *ME*—AND NAILED IT, WITH PINPOINT ACCURACY!

—SHARON MINSUK (MVZ 1989–1995), SOFTWARE ENGINEER/INDEPENDENT SCHOLAR

DAVE HAD AN ENORMOUS INFLUENCE ON ME AND OPENED MY EYES TO SO MANY THINGS. HIS SENSE OF WONDER AND CURIOSITY ABOUT THE NATURAL WORLD WAS INSPIRING AND INFECTIOUS. GOING ON FIELD TRIPS WITH HIM WAS AN EDUCATION IN LOOKING AROUND AND SEEING HOW THE WORLD HAS BEEN FORMED AND SHAPED BY NATURAL PROCESSES. AND DAVE WAS SO EXCITED ABOUT EVERYTHING! I REMEMBER HOW MUCH JOY HE TOOK IN THE SKILL THAT ONE OF OUR GROUP MEMBERS HAD IN BEING ABLE TO TELL HOW FAR AWAY A HILL WAS, AND HOW MUCH TIME IT WOULD TAKE TO CLIMB IT. OF COURSE, HE GOT JUST AS EXCITED ABOUT BIG EVOLUTIONARY QUESTIONS. ONE TIME WE HAPPENED TO BE WALKING INTO THE MVZ TOGETHER AND HE STARTED TELLING ME THAT HE HAD JUST REALIZED HOW IMPORTANT THE ROLE OF EXTINCTION IS IN SHAPING EVOLUTIONARY TREES; HE SEEMED THRILLED ABOUT THIS NEW AWARENESS. I EXPERIENCED HIM AS UTTERLY GENUINE. HE WAS PRESENT AND AVAILABLE AND OPEN TO WHAT I BROUGHT TO HIM, AND ALSO, AS I WAS MAKING THE DIFFICULT DECISION TO LEAVE BIOLOGY, TO WHAT I NEEDED. I COUNT MYSELF INCREDIBLY FORTUNATE TO HAVE KNOWN HIM AND TO HAVE BEEN ABLE TO EXPERIENCE AND LEARN ABOUT THE WORLD THROUGH HIS EYES.

—ANNA GRAYBEAL (MVZ 1989–1995), PSYCHOLOGIST

FOUR LESSONS I LEARNED FROM DAVE WAKE: LESSON 1: LISTEN TO YOUR ORGANISMS (BUT BE PREPARED: THE PATH MAY NOT BE STRAIGHT OR CLEAR)! FOLLOWING THE LEAD OF YOUR ORGANISMS CAN YIELD UNEXPECTED QUESTIONS AND INSIGHTS THAT SHAPE BROADER DEBATES. LESSON 2: NEVER TAKE VACATION (BUT GALLIVANTING IS OK). ACTUALLY, NEVER TAKING VACATION IS A LESSON MOST OF US REJECTED, BUT IN MY ERA IN THE LAB, WE REBRANDED OUR “FUN” TIME AS GALLIVANTING. AND I DID EMBRACE THE MESSAGE THAT FIELD WORK CAN SOMETIMES SUBSTITUTE FOR VACATION, SUCH AS ON OUR 1996 FIELD TRIP TO ANNETTE ISLAND, ALASKA, TYPE LOCALITY OF *BATRACHOSEPS CAUDATUS* COPE 1889. LESSON 3: ALWAYS KEEP YOUR DOOR (AND YOUR MIND) OPEN. THIS ACTUALLY ENCAPSULATES TWO LESSONS. THE FIRST IS TO BE AVAILABLE, HENCE THE OPEN DOOR—DAVE SEEMED TO ALWAYS HAVE TIME FOR HIS STUDENTS, REGARDLESS OF WHAT ELSE WAS GOING ON. I DON’T EVER REMEMBER MAKING A FORMAL APPOINTMENT TO MEET WITH HIM—I WOULD JUST STICK MY HEAD IN HIS OFFICE DOOR AND SEE IF HE WAS FREE. THE PAYOFF OF A FEW MINUTES WITH DAVE COULD BE SAGE ADVICE ABOUT MATTERS LARGE OR SMALL OR THE FEELING THAT HE SHARED IN OUR ENTHUSIASM FOR

WHATEVER DISCOVERY WE WERE REPORTING. THE SECOND IS TO BE WILLING TO REVISE YOUR THINKING. FOR EXAMPLE, DAVE'S DISSERTATION WAS REMARKABLY PRESCIENT IN IDENTIFYING SHARED CHARACTERS AND USING DERIVED TRAITS TO IDENTIFY TAXONOMIC GROUPS. ONE OF THE FEW WAYS IN WHICH MOLECULAR DATA CAUSED A MAJOR SHIFT IN OUR UNDERSTANDING OF PLETHODONTID RELATIONSHIPS WAS IN THE PLACEMENT OF *HYDROMANTES*, WHICH FOR DAVE REINFORCED MESSAGES ABOUT MORPHOLOGICAL HOMOPLASY. LESSON 4: SOME QUESTIONS MAY BE IMPOSSIBLE TO ANSWER (BUT THAT DOESN'T MEAN YOU SHOULDN'T TRY). THROUGH DAVE'S EXAMPLE, I LEARNED TO BE COMFORTABLE WITH THE UNCERTAINTY AND SHADES OF GRAY THAT ACCOMPANY ANSWERS TO MANY 'BIG' QUESTIONS IN EVOLUTION AND SYSTEMATICS.

—ELIZABETH JOCKUSCH (MVZ 1990–1996), UNIVERSITY OF CONNECTICUT

I'VE COME TO VALUE DAVE'S APPROACH TO MENTORING MORE AND MORE OVER THE YEARS, PARTICULARLY THE WAY HE GENTLY GUIDED STUDENTS TO PROJECTS BY DRAWING ATTENTION TO UNRESOLVED QUESTIONS, AS WELL AS HIS EMBRACE OF DIVERSITY AND HIS KIND AND WELCOMING NATURE.

—STEPHEN M. DEBAN (MVZ 1991–1997), UNIVERSITY OF SOUTH FLORIDA

AFTER I GRADUATED FROM THE UNIVERSITY OF WASHINGTON, I ANNOUNCED TO MY MENTOR, RAY HUEY, THAT I WANTED TO WORK ON SALAMANDERS. WITHOUT MISSING A BEAT, HE POINTED ME TOWARD DAVID WAKE BECAUSE "DAVE KNOWS MORE THAN ANYONE IN THE WORLD ABOUT SALAMANDERS." IT WAS THE PERFECT RECOMMENDATION. MUCH WILL BE WRITTEN ABOUT DAVE AS A SCIENTIST AND A MAN, BUT I'D LIKE TO BRIEFLY TOUCH ON HIS APPROACH. IN A SUBDIVIDED AND REDUCTIONIST ERA, DAVE WAS A ROUNDED ORGANISMAL BIOLOGIST. HE WAS WIDELY KNOWN AS A SALAMANDER NUT, BUT DAVE WAS JUST AS COMFORTABLE DISCUSSING EVOLUTIONARY THEORY. HE WAS A SYSTEMATIST, BUT NEVER MERELY SO, AND AS A SCHOLAR HE LOOKED BACKWARDS AND FORWARDS AT THE SAME TIME. I RECALL OUR WEEKLY LAB MEETINGS, A MUNDANE ENTERPRISE FOR MANY STUDENTS, WITH SPECIAL FONDNESS. IN THESE MEETINGS WE'D DISCUSS LAB NEWS AND PONDER A READING, WHICH RANGED FROM FUNCTIONAL BIOLOGY TO DEVELOPMENT TO PHILOSOPHY TO SYSTEMATICS. SOMEHOW, ANY BORING PAPER IN DAVE'S HANDS WOULD GLISTEN WITH IMPLICATIONS ("Wow! Why didn't I think of that?"). YES, LAB MEETINGS WERE SIMPLY LUNCH, AND FOR SOME REASON I WILL ALWAYS REMEMBER DAVE CUTTING UP AN APPLE WITH A SMALL KNIFE. AND YET HIS ENLIGHTENED, SIMPLY STATED OBSERVATIONS, ALWAYS DELIVERED WITH THE PERFECT WORD, REGULARLY BLEW MY MIND. DAVID WAKE WAS COMMANDER SALAMANDER, NEVER TO BE MATCHED, BUT ALSO SO MUCH MORE.

—SHAWN KUCHTA (MVZ 1996–2002), OHIO UNIVERSITY

DAVE WAS A WONDERFUL MENTOR TO ME, WITH GEMS OF RESONANT ADVICE GIVEN DURING OTHERWISE UNREMARKABLE MOMENTS. THEY STUCK, AND A FEW STICK OUT EVEN NOW. ONE, WHEN I WAS AGONIZING OVER THE FALSE DICHOTOMY BETWEEN MOTHER AND SCIENTIST: "THE RIGHT TIME FOR A WOMAN TO HAVE A BABY IS WHEN A WOMAN WANTS TO HAVE A BABY" (I NOW HAVE FOUR BABIES). TWO, WHEN I WAS TALKING MYSELF OUT OF A MULTITUDE OF UNSTARTED PhD PROJECTS BECAUSE THEY ALL HAD SOME APPARENT FATAL FLAW: "JUST GET IN THERE AND GET YOUR HANDS DIRTY—JUST DO SOMETHING" (I NOW HAVE MY STUDENTS START WALKING WITH FAITH THAT THE PATH BECOMES DEFINED IN ITS OWN TIME). IT'S HARD TO FATHOM THE IMPACT HE HAD ON MY CAREER AND LIFE!

—RACHEL MUELLER (MVZ 1998–2005), COLORADO STATE UNIVERSITY

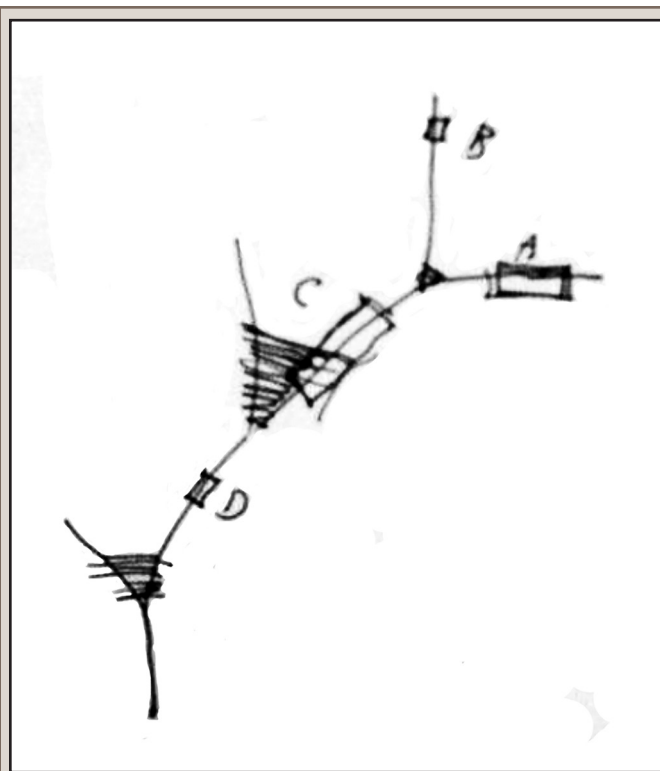


FIG. 8. Dave's sketch of the process of diversification, gene flow, and sampling period (rectangles) in the salamander genus *Ensatina*.

DAVE WAS THE MOST HUMANE ACADEMIC I HAD THE OPPORTUNITY TO WORK WITH. HE TOOK AN ACTIVE INTEREST IN HIS STUDENTS, OFTEN INITIATING CONVERSATIONS WITH US, AND SHARED HIS EXPERIENCE THROUGH VERY HELPFUL AND AT THE SAME TIME AMUSING STORIES. HE CREATED A UNIQUE AND THRIVING ACADEMIC ATMOSPHERE AT THE MVZ. THE MOST AMAZING THING ABOUT DAVE, HOWEVER, WAS HIS CAPACITY TO MAKE OTHER PEOPLE AROUND HIM SUCCESSFUL. I OWE HIM MANY DEFINING EXPERIENCES IN MY LIFE AND I STILL TRY TO IMITATE HIS LEADERSHIP STYLE TO THIS DAY.

—MARTIN JAEKEL (MVZ 2001–2002), ZURICH UNIVERSITY OF APPLIED SCIENCES, SWITZERLAND

### THE "LATER YEARS"

WHEN I THINK OF DAVE WAKE, I WANT TO TELL THE GRAND STORIES OF MY TIME WITH HIM. I WANT TO RELIVE THE LATE NIGHTS OF SALAMANDER HUNTING IN THE RAIN ON ROADS LONG FORGOTTEN. I WANT TO REGALE YOU WITH WHEN WE EXPLORED CAVES AND CAVERNS SEARCHING FOR *HYDROMANTES* AT SHASTA LAKE. I WANT TO SHARE ALL THE EXCITING ADVENTURES I WAS FORTUNATE ENOUGH TO HAVE WITH DAVE. BUT WHAT STRIKES ME MOST WHEN I THINK OF DAVE, ARE THE SEEMINGLY SMALL AND INSIGNIFICANT THINGS THAT HAVE STUCK WITH ME. THE COUNTLESS TIMES I SAT IN HIS OFFICE, SURROUNDED BY ALL HIS BOOKS AND PAPERS. THE BROWN BAG LUNCHES. THE HERP GROUP MEETINGS. THE EVOLUTION LECTURES. HIS GENUINE KINDNESS. HE KNEW ME DURING MY NOSE RING, MOHAWK, AND MUSTACHE PHASES, WHEN I GOT MY FIRST SPEEDING TICKET, AND WHEN I MET MY WIFE. DAVE CARED. WHEN I THINK OF DAVE, I THINK MOST FONDLY ABOUT THE LAST TIME I SAW HIM. WHEN I HAD LUNCH WITH HIM, JUST ME AND HIM, AT A CONFERENCE IN PORTLAND. WE HAD SANDWICHES, AND WE TALKED ABOUT OUR LIVES.

—ROB BINGHAM (MVZ 2001–2007), PORTLAND, OREGON

I'LL NEVER FORGET THE FIRST TIME I MET DAVE. IT WAS AT THE JOINT MEETING OF ICHTHYOLOGISTS AND HERPETOLOGISTS IN KANSAS CITY, MISSOURI IN 2002. AT THE TIME, I WAS A GRADUATE STUDENT AT LOUISIANA STATE UNIVERSITY FINISHING MY MASTER'S DEGREE WITH JIM MCGUIRE. JIM HAD JUST ACCEPTED A JOB AT BERKELEY AND THE MVZ. DAVE KNEW THAT I WAS GOING TO BE FOLLOWING JIM TO BERKELEY TO BEGIN MY PH.D. THERE, BUT WE'D NEVER MET FACE TO FACE. SO THERE I WAS, WALKING DOWN A HALL DURING A BREAK BETWEEN SESSIONS, WHEN I SAW DAVE WALKING TOWARDS ME. I STARTED GETTING NERVOUS AND WASN'T SURE WHAT I WAS GOING TO SAY. HE WALKED UP, REACHED OUT HIS HAND, AND SAID, "Hi, I'm David Wake. Jim has told me a lot about you. I understand you'll be joining us at Berkeley soon. It's very nice to meet you. We're looking forward to having you!" I COULDN'T BELIEVE THAT SOMEONE AS FAMOUS AS DAVE WOULD TAKE THE TIME TO COME UP AND INTRODUCE HIMSELF TO A YOUNG GRADUATE STUDENT HE'D NEVER MET. BUT THAT'S JUST HOW DAVE WAS: ALWAYS HUMBLE, FRIENDLY, AND ENGAGING. WHEN I GOT TO BERKELEY, I THOUGHT I KNEW WHAT I WANTED THE FOCUS OF MY DISSERTATION TO BE, BUT I ENDED UP WORKING ON *ENSATINA* HYBRID ZONES, IN PART BECAUSE I FELT DRAWN TO DAVE AND HIS RESEARCH. WHILE I WAS NEVER OFFICIALLY HIS STUDENT, I ATTENDED HIS LAB MEETINGS AND OFTEN STOPPED BY HIS OFFICE TO CHAT, WHERE HIS DOOR WAS ALWAYS OPEN AND HE WAS ALWAYS WILLING TO TALK. DAVE IS THE KIND OF PERSON THE WORLD NEEDS MORE OF. HE HAD A HUGE IMPACT ON MY LIFE AT A VERY FORMATIVE TIME AND I'LL MISS HIM DEARLY.

—TOM DEVITT (MVZ 2003–2010), UNIVERSITY OF TEXAS AT AUSTIN

"WHAT DO YOU WANT SPECIES TO BE?" THAT'S WHAT DAVE ASKED ME IN ONE OF OUR MANY SPONTANEOUS DISCUSSIONS ABOUT SPECIATION IN *ENSATINA* SALAMANDERS, THE TOPIC OF MY PH.D. AND THAT OF MANY OTHER STUDENTS BEFORE ME. AT FIRST, I FELT A BIT OFFENDED... I THOUGHT THAT IT WAS FAIR TO EXPECT SPECIES TO LOOK MORPHOLOGICALLY DIFFERENT [MOST OF THE TIME?], EXPLORE DIFFERENT HABITATS [EVENTUALLY?], DEFINITELY TO REMAIN GENETICALLY DISTINCT [DEFINITELY?]. BUT, AS DAVE STARTED DRAWING THE EVOLUTIONARY TREE (FIG. 8), REPRESENTING LINEAGES (SOLID BIFURCATING LINES) DIVERGING WITH GENE FLOW (CONNECTING LINES) AND WITH US SAMPLING THESE LINEAGES AT SPECIFIC TIME POINTS (RECTANGLES), I REALIZED THAT HE WAS NOT ACTUALLY EXPECTING AN ANSWER FROM ME. I REALIZED THAT POSING THAT QUESTION ALLOWED ME TO RECOGNIZE MY OWN BIASES, TO STUDY THE PROCESS OF SPECIES FORMATION MORE AGNOSTICALLY, AND MOST OF ALL TO CONSTANTLY REMAIN CURIOUS ABOUT WHAT WE DON'T KNOW. AND THERE'S SO MUCH OF THAT! NOWADAYS, I STILL ASK A SOFTER VERSION OF THAT QUESTION TO MY OWN STUDENTS, "WHAT WOULD WE LIKE SPECIES TO BE?" I GIGGLE TO MYSELF, LISTENING TO MY STUDENTS' THOUGHTS AND NOTE MY OWN CURRENT ASSUMPTIONS.

—RICARDO J. PEREIRA (MVZ 2005–2011), LMU-MUNICH, GERMANY

AS AN UNDERGRADUATE I VIEWED DAVID AS AN ALMOST SUPERHERO-LIKE FIGURE. HIS WORK INSPIRED MY OWN OBSESSION WITH CALIFORNIA SALAMANDERS AND HEAVILY INFLUENCED MY MASTER'S WORK. I DIDN'T THINK I'D EVER MEET HIM, LET ALONE WORK WITH HIM. I WAS INTIMIDATED AND THOUGHT HE'D BRUSH ME OFF WHEN I FIRST REACHED OUT TO HIM, BUT HE WAS SO WELCOMING, ENCOURAGING, AND SUPPORTIVE. WHEN I ARRIVED AT THE MVZ, I'D STOP BY HIS OFFICE REGULARLY AND HE WOULD ALWAYS STOP WHAT HE WAS DOING AND JUST TALK WITH ME, ABOUT HOW I WAS DOING PERSONALLY, MY WORK, AND WHATEVER NEW SALAMANDER

DISCOVERY HE WAS FOCUSED ON. THESE ONE-ON-ONE OFFICE CHATS WERE THERAPEUTIC AND HELPED ME STAY POSITIVE THROUGH STRESSFUL TIMES. HIS PASSION FOR THE ANIMALS AND GETTING OUT IN THE FIELD WAS INCREDIBLE AND INFECTIOUS. MY FAVORITE MEMORIES OF HIM ARE IN THE FIELD, ESPECIALLY WHEN WE'D FIND AN UNUSUALLY COLORED *ANEIDES* OR *ENSATINA* SALAMANDER. HE WAS A UNIQUE MENTOR, BUT I MOSTLY THINK OF HIM AS A FRIEND.

—SEAN B. REILLY (MVZ 2009–2016), UNIVERSITY OF CALIFORNIA, SANTA CRUZ

## CONCLUDING REMARKS

Dave Wake was the quintessential scientist as well as an inspirational mentor. Much of his effectiveness came from an amazing ability to accept new ideas and data, and to convey his confidence in each of his students that they will do fine, regardless of what they decide to do. An example was when one of us (SKS) encountered him at a conference some years ago, soon after new molecular evidence from his own lab completely and profoundly altered our understanding of evolutionary relationships of plethodontid salamanders. Most mortal humans would be understandably devastated, but Dave's reaction to the realization that his own students had provided evidence that overturned most of his main ideas about plethodontid relationships was one of wonder and even elation, underlining the paradoxical truism that it is the lucky scientist who sees their own work overturned in their lifetime! Those who know him and worked with him, and especially those who were mentored by him, would be not at all surprised by this, since Dave was someone who was skilled at encouraging independent thinking, even if it contradicted his own ideas. Dave was a kind and thoughtful mentor, who never imposed expectations on his students, but instead wanted them to follow their own path and to be "happy and productive" in whatever they eventually chose to do. The result was the creation of an astonishingly diverse yet cohesive community of scholars and citizens. We will all miss him.

*Acknowledgments.*—We are grateful to the former Wakelab students who submitted contributions to this retrospective. We also thank Chuck Crumly, Bob Hansen, Elizabeth Jockusch, and Michelle Koo for sharing contact information and photos.

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