



Richard G. Harrison

November 19, 1945 – April 12, 2016

Dr. Richard G. Harrison, or Rick as colleagues and friends knew him, was born in Baltimore, Maryland on November 19, 1945. His parents, Helen and Harold Harrison, were scientists at Johns Hopkins School of Medicine, and his father, a physician, served as Chief of Pediatrics at Baltimore City Hospital for over 35 years. Rick had one sibling, older brother Steve, who also pursued an academic research career and is a gifted mentor and professor at Harvard Medical School and the Howard Hughes Medical Institute.

Rick was an undergraduate at Harvard, where he met Ellen Zucker through his classmate, Andy Zucker, her brother. After graduation, Rick spent a year as a Churchill Fellow in Cambridge England before returning to Harvard as a graduate student, but changed to work at the Children's Cancer Research Institute, which qualified him for an occupational deferment from the military draft. Rick and Ellen married in 1971 shortly before moving to Ithaca, NY for graduate school at Cornell; he earned his Ph.D. in 1977 working with Peter Brussard in Ecology and Evolutionary Biology, with a thesis titled "Patterns of variation and genetic differentiation in closely related species: the field crickets of eastern North America"). During their time in Ithaca, Ellen earned her Masters Degree in geological science. Twin daughters, Rebekah and Melissa, were born in 1976 and a year later the family moved to New Haven, CT, where Rick had

accepted a position as Assistant Professor at Yale. After a very successful decade at Yale, he was lured back to Cornell in 1986, where he remained on the faculty until his untimely death. Ellen engaged in her environmental interests both at Cornell and in the community.

Rick was a true scholar. He aspired to understand how one species became two separate species, and explored in particular the transitional stage during which diverging organisms continued to hybridize and share at least some genes, thus providing “windows on the evolutionary process” (Harrison 1990 *Oxford Surveys of Evolutionary Biology* 7:69129). Rick was respected by his peers worldwide for his eloquent and thoughtful talks and writing, and for the fact that he never engaged in hype—if he published something, you could believe the results completely, and trust that his interpretation was balanced and objective. This level of intellectual honesty is all too rare, will be sorely missed, and was one reason Rick was chosen as senior editor of the journal *Evolution*.

He used the closely related, reproductively isolated but hybridizing species of field crickets *Gryllus pennsylvanicus* and *G. firmus* as his primary research system throughout his career. He continuously brought emerging molecular methodologies to bear on his efforts to document and gain mechanistic understanding of the evolutionary, behavioral and ecological forces that shaped genetic variation within and between species and to identify genetic regions associated with reproductive isolation. Rick had his scientific focus and encouraged his students and postdocs to develop their own, though he certainly encouraged studying common questions in diverse organisms ranging from corn borers to stone crabs, *Heliconius* butterflies to wood rats, sea squirts to iris. This diversity of organisms and evolutionary questions contributed significantly to the intellectual culture that thrived in his lab and attracted many graduate and postdoctoral students to work with him. This was fed further by Rick’s terrific mentorship style, clear and critical mind, and willingness to confront the complex realities of biological organisms without trying to force results to fit preconceived concepts or models. Rick was also very successful attracting undergraduates into his laboratory, where they received training in cutting-edge research, often leading to Honors theses, and future enrollment in prestigious post-graduate programs in biology and medicine. Steve Bogdanowicz, who ran Rick’s lab for nearly 30 years, contributed greatly to teaching and mentoring students.

Rick's careful studies of field crickets revealed unexpected geographic and genomic complexity in zones of hybridization, and laid the groundwork for much of the work on hybrid zones in other species, as well as paved the path to his insights into the evolutionary forces shaping patterns of diversification across genomes. Genomic islands of differentiation had been viewed by some to signify the location of genes key to reproductive isolation. True to Rick's intellectual honesty and critical nature, his last publication was very thoughtful in providing reasoned and insightful caution to such simple interpretations. Yet within those signals are likely the functional variants that contribute to the reproductive isolation of these species in the face of hybridization, results sadly he will not see himself.

As an advisor, Rick had an open door policy. And since his door was always open, students as well as colleagues would stop by to talk and to seek his insights or advice. He said that there were a lot of things that we "could" do as scientists, but the hard part was determining what we "should" do. Through his keen mind and especially his generosity, he helped his many academic progeny to sift through ideas and questions to get to the ones that they should and "must" address in their research.

Rick Harrison was recognized for his long and distinguished service as an inspirational teacher with the Harry T. Stinson Award for Outstanding Service to Undergraduates at Cornell in 2013 and the CALS Edgerton Career Award in 2015. Rick began his academic career teaching evolution at Yale for a decade before moving to Cornell in 1986 where he assumed teaching a course in Evolution that was required of Biology majors concentrating in Ecology and Evolution and had an enrollment of approximately 60-70 students, with three lectures per week, plus weekly discussion sections and was taught once a year. A few years later, the Division of Biology voted to make the course a requirement of all Biology majors, regardless of concentration. This led to a jump in course enrollment to 150-200 to now 300 per semester. While many faculty members shy away from teaching large introductory courses, because of the administrative burdens and the difficulty in getting to know students well, Rick has always stepped forward to participate. He was committed to these courses (and the students!) because he firmly believed that an understanding of evolutionary biology is essential to every biologist's training. He was responsible for bringing in an intensive writing component to the majors course. There is always a temptation in large courses to make lectures

into performance pieces, and often, in the process, make instruction less rigorous. Rick was always more measured in this delivery, but was nevertheless thoroughly engaging because of his obvious intellect, humor, and respect for the audience. Students respected Rick tremendously and learned a great deal from his engaging, thoughtful, and well-organized lectures. He taught this course through several curriculum changes until 2011.

In 2011, Rick moved from the biology majors' course in Evolutionary Biology to the non-majors' course on Evolution because of his desire to show a broad range of students the importance of evolutionary principles in all aspects of science and daily affairs. This is an extremely important course for the science distribution requirement of non-majors, and the fact that Rick took this on demonstrates his dedication to the importance of a liberal arts education. Rick also initiated a new upper-level course on "Speciation: Genetics, Ecology and Behavior" which he co-taught with Dr. Kerry Shaw for several years. Rick added this course to the curriculum because upper-level course offerings in evolutionary biology were slim and because Speciation is a fundamental component of evolution. The course was very popular with upperlevel undergraduates and beginning graduate students from multiple departments.

In a course on grant writing for graduate students, Rick was both insightful in his criticism and always encouraging in his constructive suggestions. Through his dedicated and thoughtful advising, Rick trained and launched the careers of many successful students, from undergraduates to postdocs, who are now spread throughout academia in the US and abroad.

From 1996-2001 and 2006-2009, Rick served as Department Chair in Ecology and Evolutionary Biology. Rick distinguished himself by always holding the interests of the whole department to heart. He recognized that the department's strength lay in the breadth of research areas encompassed by its faculty, and he sought to strengthen them all. During his tenure he was instrumental in recruiting five new faculty members to the department, in areas ranging from mathematical ecology to molecular developmental biology. Rick was also a good ambassador and link to the many other evolutionary biologists across campus.

Rick was recognized for his contributions to scholarship in evolutionary biology by being elected as a Fellow of the American Association for the Advancement of Science in 1998. He contributed invaluable service as Editor on many scholarly publications, including as Editor in Chief for *Evolution*, and as member of the Editorial Boards of *Genetics*, *Molecular Biology and Evolution*, *Proceedings of the Royal Society B*, *Annual Review of Ecology and Systematics* and *American Scientist*.

Rick's family played a very important part in his life, a mindset he sought to instill in his students and colleagues, as well as his daughters. He loved the outdoors, stargazing, good cooking, wine and good friends (often together), and, together with his wife, was a passionate and accomplished gardener. Rick was also an avid runner for 40 years, and valued his friends and fellow pavement pounders in the High Noon runners club at Cornell and which shaped his calendar on many days as his noon runs were a priority for him. It was this active life and exercise routine that made his untimely death even more unbelievable to his friends and colleagues.

As important as his scientific contributions were, so were his contributions to students and many colleagues through his mentorship. Rick was a passionate teacher, even of his twin daughters growing up. He always appreciated and valued the individual, and had a knack for bringing out the best in his advisees and mentees. To say he is beloved by his current and former students is an understatement. And it is fair to say that we, his colleagues and friends, felt the same way about him. Sadly, Rick died suddenly and unexpectedly on April 12, 2016 at age 70 while snorkeling with Ellen on the Great Barrier Reef in Australia. In many ways, he passed away at the peak of his scientific career, and at a time when he seemed genuinely happy and enthusiastic to pursue writing a major new book on Speciation. We have so many wonderful memories of Rick. What is terribly sad is that we will no longer benefit from new scientific, professional and personal insights from Rick, but we will always cherish our wonderful memories of our past scientific and academic discussions, debates and simply casual conversations with Rick. We are all better scientists, teachers, people, and advisors for having known Rick.

He is survived by his wife Ellen, their twin daughters, Rebekah who is an emergency physician with Kaiser Permanente (residing in Lincoln, CA with husband Jeff and daughter Serafina) and Melissa who is an assistant professor in

the Department of Biomolecular Chemistry at the University of WI (residing in Madison, WI with husband Andrew Mehle and son Ryder), and by his older brother Steve of Boston, MA.

Charles "Chip" Aquadro, chair; Harry Greene and Monica Geber