



## IN MEMORIAM

Timothy Prout  
Professor Emeritus Evolution and Ecology  
UC Davis, UC Riverside  
1923 – 2009

Timothy Prout, professor emeritus, University of California Riverside and Davis, was born in Waterbury, Connecticut to Curtis Prout and Edith MacPhail Prout on June 14, 1923. Tim, as he was known to most, died peacefully at his home in Davis, California on January 5, 2009 after a short illness. He is survived by his wife of 58 years Marjorie, daughter Mary, son David, and two grandchildren Ellen Slatkin and Eric Hu.

Tim grew up in Summit, New Jersey and attended Phillip Exeter Academy an exclusive private boarding school in New Hampshire from which he was expelled after a couple of years. He never completed high school, and instead received a certificate in reading proficiency. Tim freely admitted to this and considered it a badge of honor to have been expelled from a snobby, elitist boarding school, especially given his later academic success. He enrolled at Hobart College in Geneva, New York but before completion volunteered for the army during World War II so that he could serve in the elite ski troops in the 10th Mountain Division a unit with men having previous ski and mountaineering experience or those trained in such. Tim loved skiing, and was already a good skier, having been on the ski team at Hobart before enlisting. He never talked about the war or his combat experiences in Italy very much, but it is well known the unit saw much fierce fighting.

Upon his discharge from the Army, he received a B.A. degree (1948) in Biology from Hobart College under the G I bill. Following this he enrolled as graduate student at Columbia University, New York, where he studied the population genetics of the vinegar fly *Drosophila*. The years at Columbia were an exciting time, as his mentor was the charismatic pioneering evolutionary geneticist Theodosius Dobzhansky, one of the leaders of the modern synthesis of evolutionary biology. He also became friends with the evolutionary biologist Ernst Mayr at the American Museum of Natural History and the behaviorist Herman T. Spieth, a lecturer in the Graduate Division where Spieth taught a course on the Biology of Insects and collaborated with Dobzhansky on the ecology, mating behavior and sexual isolation of *Drosophila*. In 1953, Spieth, who had also taught undergraduates at the City College of New York from 1932 onwards (with a brief time out for service during World War II) was selected to head up the Division of Life Sciences at the newly established undergraduate College of Letters and Sciences at the University of California (UC), Riverside, where he had to assemble its initial faculty. Tim, a newly minted Ph.D., was recruited by Spieth and in 1954, Tim traveled to California to become an Instructor and a founding member of the six- person Division of Life Sciences (later the Department of Life Sciences and later still the Department of Biology).

The focus of UC Riverside during the early years was on undergraduate education — some called it “the Swarthmore of the West”. It was a good fit for Tim as he was an accomplished and well- organized teacher and over the next 20 years, as he rose through the academic ranks to become a professor, he taught courses in Genetics, Population Genetics and Evolution. He even made an occasional foray at lecturing students in Introductory Biology — something he admitted was not his *métier*. In 1959, however, things changed for both

Tim and the College of Letters and Sciences. In that year, the campus was designated a general campus and there was a need to integrate the scientists in the Agricultural Experiment Station with the biologists in the College of Letters and Sciences, the two occupying the same piece of land in Riverside. In 1964, the newly appointed chancellor, Ivan Hinderaker, formed a committee consisting of members drawn from agriculture and Letters and Sciences with Tim as chair. The "Prout Committee" recommended, some say miraculously, pulling the Department of Life Sciences out of Letters and Sciences, and to coordinate this with the nine departments of agriculture to create a unique College of Biological and Agricultural Sciences. Coincident with this, the Department of Life Sciences developed a graduate program. Some in the Department lamented the demise of the focus on undergraduate education, and several faculty were unable or unwilling to direct their energies toward scholarly research and supervision of graduate students. Tim, however, was not one to look back at "the good old days." The graduate program allowed Tim to mentor doctoral and master's degree students, to carry out research on the cytogenetics and ecological genetics of *Drosophila*. He used his considerable mathematical skills to develop models describing the dynamic relationship between density regulation of population size and natural selection. To test these elegant models he used fly- populated population cages. Although Tim sometimes lamented that the population cage results did not always fit his mathematical models this did not deter him from reformulating and re- testing. Tim spent several sabbatical years at Aarhus University in Denmark carrying out population genetic studies. Aarhus University became his second academic home and he received an honorary doctorate degree from it in 1997. Tim meant a great deal to the founding of the Genetics Institute at Aarhus University in 1967 by Professor Ove Frydenberg and Professor Frydenberg invited Tim to become guest professor for one year where he was the de facto supervisor for Freddy B. Christiansen (now Professor of Genetics at Aarhus University) and Jørgen Bundgaard (now Institutleder). It is fair to say that Tim was one of the founding fathers of population genetics and evolution at Aarhus University, Denmark.

In 1972, at the Berkeley Genetics Conference, Tim confided to Mel Green (UC Davis) that he had few colleagues at Riverside with whom he could interact and carry out collaborative research he considered leaving Riverside. Green suggested he come to Davis. The transfer was made, and he remained at Davis for the remainder of his career with a split appointment between Genetics and Entomology. Tim remained active in research and was publishing well past his official retirement (1988). The Prout laboratory in the Department of Genetics and Department of Entomology at Davis was a lively and congenial place where lifelong friendships were made. Jerry Coyne, Fred Cohan, Lawrence Harshman and Ary Hoffmann were post-doctoral students and Gail Simmons and Ian Boussy were graduate students. Tim was exceedingly generous in letting them have the flexibility and freedom to conduct basic research of their own choosing.

Tim was the embodiment of enthusiasm for science contained within the boundaries of critical thinking. His strong sense of skepticism was not limited to science. In relationship to non- scientific issues, he often brought his copy of the "Skeptical Inquirer" to the laboratory where articles were discussed. Tim loved to think about scientific problems and to talk about them. Years of deep thought about theoretical population genetics and evolutionary genetics resulted in a real education on those subjects for members of the laboratory as Tim talked about a broad range of topics in the subfields of genetics and evolution, and always he encouraged the habit of careful, critical thinking.

Tim was fundamentally a kind and gentle person, but not a pushover. To deal with a standoff during the writing of a manuscript, Tim came up with the novel idea of polling people in the hall about which wording sounded best. The final version of the manuscript was democratically arrived at and submitted to the journal *Evolution* for publication. Often, he would go out to the sheepdog trials held during UC Davis' Picnic Day or a trip was made to the Hog Barn during the holiday season. Tim took great pleasure in seeing the variation in these domestic animals (as did Charles Darwin) and such variation is featured prominently in a book he wrote about evolution during retirement.

At both Riverside and Davis Tim was valued by his colleagues as a sound researcher, as well as, for his considerable knowledge. When asked, he was always ready to provide a succinct mathematical formula for a phenomenon, even one outside population biology.

On campus, Tim was known to become so preoccupied with his beloved *Drosophila* that he assumed the demeanor of the classic absent- minded professor, something he was proud of and cultivated. One evening after leaving his office- laboratory he was seen to be wandering in the parking lot looking for his car. When asked by a colleague what the problem was, he said that his missing car had been stolen. The two continued their search for another half hour when it dawned on Tim that the car had not been removed from the parking lot without his knowledge — that day he had walked from home to the campus. On another occasion, he

decided to deal with those people on campus who gave him a hard time about his parking permit, which was applied crookedly to the bumper of his car. This time he said, it was going to be perfectly straight. He went to Parking Services, bought the permit and went to the parking area to apply it immediately; spending much time being sure it was perfectly straight and nicely centered. When he stepped back to admire his work, he realized he had applied the sticker to the car next to his, a campus police car. In his defense, he always pointed out that the campus police used the same white Chevy Impala the Prout family owned at the time. His absent-mindedness did have a benefit: he avoided committee meetings, the bane of his existence as an academic.

Tim was a self-effacing soul without affectations and his consuming attention to research and teaching sometimes led to neglect in personal appearance. He would come to campus dressed neatly (probably as a courtesy of his wife, Marjorie), often with a white shirt and tie, light up his pipe or a cigarette and proceed to do those things most academics do — confer with graduate students, review the results of experiments, lecture, etc. As the day progressed his nails and fingers would become encrusted and blackened as he cleaned out the bowl of his pipe; cigarette and pipe ash covered his once white shirt and trademark black sweater, his tie was askew and the shirttails hung out of his trousers. Oblivious to his changed appearance, he provided to others an example of the universality of the law of entropy!

Tim had a wonderful sense of humor. During his years as a graduate student at Columbia University, New York, he shared an office with Richard Lewontin. One day Tim substituted the contents of Lewontin's sandwich with newspaper and then watched him eat the entire thing while pontificating during the lunch hour discussion. Although Lewontin later claimed that he knew all along about the newspaper, but wasn't about to let on, Tim suggested this face-saving gesture could not be true in view of the sheer enjoyment with which the sandwich was devoured. Tim gained immense joy from nature, whether fly-fishing for trout, skiing or backpacking, and his family and friends (of whom he had many) benefited from that love.

Tim's warmth as a human being will be sorely missed by colleagues, friends, and family. Tim (along with Richard Lewontin, Monroe Strickberger, Bruce Wallace, Lee Ehrman, Abdel Khalek Mourad, Colin Pittendrigh and Francisco Ayala) was a direct intellectual descendent of Dobzhansky. For Tim's entire professional career he carried the banner of his intellectual father by carrying out experimental studies of the components of fitness in Darwinian evolution. Regrettably, future generations of University of California students, attracted to the beauty of population genetics and its contribution to the understanding of evolutionary biology, will have missed an opportunity to be in the presence of this exceptional educator and researcher, Timothy Prout.

Irwin W. Sherman  
Jorgen Bundegaard  
Mel Green  
Lawrence Harshman  
Mary Prout  
David Prout