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Obituary: Allan C. Wilson, 1935–1991

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Dr. Allan C. Wilson, Professor of Biochemistry and Molecular Biology at the University of California, Berkeley, died in Seattle on Sunday, July 21, 1991, at the age of 56. He died while undergoing a bone marrow transplant for leukemia at the Fred Hutchinson Memorial Cancer Institute; the illness had been diagnosed in late November 1990.

Allan felt that the brain was much more important than environmental change in driving morphological evolution of species with learning capabilities. He hypothesized that humans had become uncoupled from the demographic and environmental catastrophes that limit the expansion of new species because of the evolution of language. He trained more than 200 graduate students and postdoctoral fellows in molecular evolution in his laboratory. He was a Fellow of the Royal Society, received two Guggenheim awards, numerous science prizes, and a MacArthur Foundation "genius" award, and was a member of the American Academy of Arts and Sciences.

Allan's principal interest in evolution came from his observation that rates of morphological change and rates of mutation seemed to be uncoupled in many lineages. He was widely knowledgeable about the diversity and behavior of birds, fishes, primates, rodents, bacteria, bats, amphibians, ruminants, and insects. How did behavior drive evolution? What was the true phylogenetic picture that related species to each other, and when did these behavioral changes occur? He was interested in real examples. He had a way of encouraging students to work on projects likely to pay off with the application of new technologies and a phenomenal memory for who had stored what samples in what freezer.

Allan thought that evolutionary biologists needed a more objective way of measuring rates of change because they were often misled by convergence resulting from natural selection. He also thought that they needed a clear phylogenetic perspective for the group under study, because hypothesis testing would be impossible if family relationships among taxa were not known. The fossil record might be incomplete, but that should not stop biologists in the modern world from reconstructing evolutionary history. Allan believed that, to really study evolutionary change, it was best to concentrate on genes and proteins of living animals in a

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simple system and to make the fewest number of assumptions about how DNA mutated over time. What mattered to him was data, and the name or fame of the laboratory producing the data was always secondary.

Allan's contributions to evolutionary biology include (1) the primate molecular clock, which shows that humans and African apes shared a common ancestor as short as 5–7 million years ago in contrast to the 25-million-year divergence once favored by paleoanthropologists; (2) the Lucky Mother hypothesis to account for mtDNA divergence in modern people from an African ancestor who lived about 200,000 years ago; (3) the demonstration that convergence resulting from natural selection can occur at the molecular level in proteins, as evidenced in the same structure and function of a stomach enzyme (lysozyme) in cows and leaf-eating monkeys; (4) the discovery that the immense adaptive radiation of Hawaiian flies in the genus *Drosophila* must have taken place before the current Hawaiian islands were formed, leading to the hypothesis that insects island-hopped down the now submerged seamounts and atolls of the Hawaiian chain as new islands were formed; (5) the demonstration that the survival of DNA in ancient species is common and that it can be sequenced and compared to modern relatives; and (6) a universal framework for measuring rates of morphological evolution in animals and the observation that morphology appears to change faster in species that utilize observational learning in their social behavior (birds and primates). This last discovery formed the core of Allan's interest in big brains and language and the contribution these factors made to increasing the rate of morphological evolution in humans.

Allan wanted to have a statistically robust universal yardstick for measuring morphological change because he was struck by how subjective the opinions of anatomists were when describing evolutionary change within and between taxa. Allan was particularly put off by primate anatomists who attempted to dazzle their audiences with detail but neglected to deal with real issues of biology, notably, low sample sizes, no real understanding of sexual dimorphism, and the unknown link between genes and anatomical structures. Allan thought that the primate anatomists hid behind jargon and constantly attempted to put readers off by speaking in code about particular fossils by number instead of clearly identified terms. Allan spent part of a sabbatical in Kenya in the early 1970s, where he was finally able to see some of the fossil evidence for human evolution firsthand as a result of the help of Alan Walker, now at Johns Hopkins University.

This experience helped solidify Allan's perception that behavior must have been changing fast in human evolutionary history, and his interest in the reorganization of the brain as a response to the demands of language grew. He thought that all modern people shared similar language characteristics because they shared a recent, common origin. He also

believed that, until there was a real understanding of modern human genetic diversity and its origins, linguists would not be able to make much headway in the problem of when modern languages arose and where. Until he went to Seattle for further treatment, Allan was looking forward to future discussions with Derek Bickerton and others about the links between the expansion of modern humans about 100,000 years ago and the spread of particular language groups.

Allan thought that words had power beyond their obvious communication potential. He knew that words could hurt, and that they could also heal. His first years as a professor at Berkeley had embroiled him in some bitter debates, and he understood the necessity of funding long shots if they were likely to yield new evidence. When our Lucky Mother hypothesis was subjected to scathing ridicule after its first publication in 1987, Allan reminded me how sure the anthropological establishment had been that he was wrong too in 1967. Although it seemed impossible to get funding for research and I was almost ready to quit, he encouraged me to keep trying. I am now glad that he had faith in me, and this story could be repeated by a large number of his former students. He used his last years as a MacArthur fellow, when he was released from formal teaching duties, to travel extensively so that he could discuss, explore, and attempt to bridge gaps between biologists and social scientists. His overriding concern was the nature of the evidence that could be gathered, the potential bias in gathering it, the scientist(s) involved, and who would use the data for what eventual purpose. One of Allan's last acts was to coauthor a plea for the incorporation of diverse aboriginal human populations in a study of the human genome.

I knew Allan as an intense, gentle, humble, and humorous individual who packed 28 hours of activity into a 24-hour day. As a teacher, he stressed rigor and elegance in presentation of data. His norm for a good slide was one with less than 10 words on it, all less than 3 syllables long. Allan was a math wiz, but he appreciated that concepts were worth talking about too, because you never knew who was likely to have an important insight into a problem. He disliked pretension of any kind, political expediency, and departmental games. Berkeley was not always a comfortable place for him in this regard.

Most students began their stay with him by thinking that he talked too simply about evolution and left his lab understanding how important it is to talk and think clearly about this complicated subject. He promoted the interests of his students with vigilance and was constantly pressing conference organizers to include women and minorities on their speakers' lists. Gender and race were irrelevant to him, and it was no accident that at one time his laboratory had almost all the women students enrolled in the Department of Biochemistry at Berkeley.

As a friend, Allan enjoyed discussions about science with good food and fine wine, Mozart, single malts, sheep jokes, and simple technology. He and Leona, his wife of 32 years, often hosted memorable parties for hungry students and visiting dignitaries. He would promote these by saying, "Come to dinner. You'll learn what it's like to talk to someone who really thinks like a bat [monkey, camel, mouse, etc.]." His family in California—including Leona, his daughter Ruth, and his son David—often tolerated intrusions into their family life by needy visiting biologists. Allan was a proud citizen of New Zealand and grew up on a cattle ranch. His family there include his mother, Eunice, sister Coleen, and brother Gary. We students were often told to visit New Zealand before it became trendy and to see the one cattle farm in a land of 10 million sheep. Those of us who had the pleasure of working with Allan will always remember his warm smile, and his ready questions, "So, what are you doing lately? Can you stay a minute? I've got a new idea I need to talk over with you."

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