

George Christopher Williams (1926 – 2010): Gene's-eye view of evolution

Professor George C. Williams, one of the most influential evolutionary biologists of modern time, died on September 8, 2010 at the age of 84. Professor Williams finished his doctorate at University of California in Los Angeles and his career path led him to State University of New York at Stony Brook where he remained for the rest of his academic life and taught the courses in marine vertebrate zoology. He was the last of the 1999 Crafoord Prize-winning trio, which included the famous Ernst Mayr (1904-2005) and John Maynard Smith (1920-2004). I have had some retrospective thoughts about E. Mayr and J. Maynard Smith and their works in the pages of this journal. Therefore, it is not only enlightening



Figure 1. In 1999, Ernst Mayr (left, in front), George C. Williams (standing), and John Maynard Smith were awarded with the Crafoord Prize in Biological Sciences from the Royal Swedish Academy of Sciences. They were honored for their “pioneering contributions to broadening, deepening and refining our understanding of biological evolution and related phenomena.” (Photo © Royal Swedish Academy of Sciences)

and enlivening, but also fitting to reminisce about the penetrating thinking of this great evolutionary biologist.

Professor Williams was the most outspoken critic of group selection theory. Along with William D. Hamilton and J. Maynard Smith, he pioneered the development of the gene's eye-view of evolution in 1960s. Professor Williams became known for his 1957 paper *Pleiotropy, Natural Selection, and the Evolution of Senescence*, which introduced several fundamental ideas into evolutionary biology. This work was what put Williams at the center of attention. The central idea of *antagonistic pleiotropy*, which still remains the prevailing evolutionary theory of senescence, really was a more fully developed version of Peter Medawar's 1952 idea. Medawar (1952) suggested that lethal mutations that affect later in life accumulate in populations more rapidly than those expressed earlier in life because selection against them is weak. Williams (1957) proposed antagonistic pleiotropy (or *genetic trade-offs*) which states that, because of the greater reproductive value of earlier age classes, an allele that is advantageous early in life has a selective advantage even if it is deleterious later in life (i.e., having genetic trade-offs or pleiotropy). Therefore, senescence follows as it may be one of the costs of reproduction. The 1957 paper also outlined the basics of so-called “*grandmother hypothesis*” that states natural selection might select for post-reproductive life span in females. One of the outgrowths of Williams' 1957 theory of aging is *Darwinian medicine*, which Williams in collaboration with Randolph Nesse (1994) basically founded while exploring so-called diseases of aging in a book *Why We Get Sick: The New Science of Darwinian Medicine*.

His first and best known book was *Adaptation and Natural Selection*, published in 1966. In this book, he criticized the theory of *group selection*, which in layman's terms can be stated as the idea that traits evolve ‘for the good of the species.’ Williams emphasized that selection can only act on individuals. These differences in thinking about the nature of natural selection coalesce at the time of Charles Darwin and Alfred Wallace.