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George C. Williams (1926–2010)

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## RETROSPECTIVE

## George C. Williams (1926–2010)

Richard Dawkins

It has become a cliché that Charles Darwin would not have succeeded as a scientist today. He would not have won big research grants and did not have the mathematics to be a “theorist” by today’s conventions. But the cliché is wrong—for George Williams succeeded. Williams published books, rather than articles in “high impact journals”; he never won huge grants, did not head a big research group, and seldom used mathematics, yet he became one of the most respected figures in late-20th-century evolutionary biology. On 8 September, George Williams died at the age of 84.

Williams, like Darwin, was a world-class thinker. Like Darwin, he drew upon deep wells of knowledge; like Darwin, he wielded words and concepts with the precision that comes from clear thought; and like Darwin, he was correct far more often than a mathematical theorist might think he had any right to be. Also like Darwin, he was gentle and self-effacing, never aggressive or overassertive. He was a tall, rangy, patrician figure whose quiet, contemplative wisdom, as well as his dignified appearance, reminded many of Abraham Lincoln (Darwin’s exact contemporary to the day).

Williams received his Ph.D. in 1955 at the University of California, Los Angeles, and his academic path led him to Stony Brook University in 1960, where he remained for the rest of his career. He first attracted attention in 1957 with his evolutionary theory of senescence, a matured version of the idea sketched by Peter Medawar in 1952. Lethal genes that are expressed late in life outcompete those expressed early. Mutations that have good effects often have other effects too (pleiotropy), many of which will be bad. Natural selection will modify mutational effects such that the bad ones are postponed, and the good ones accelerated. Senescence follows, with the sort of clear logic that typified Williams’s thinking.

His 1966 book *Adaptation and Natural Selection* had a spring-cleaning effect upon evolutionary theory. Neo-Darwinism had fallen into lazy habits since the glory days of Ronald Fisher and the Modern Synthesis. The loose, intellectually shoddy idea of “group selection” was rife, and Williams

dispatched it. “Adaptations” were scattered throughout the literature with no understanding that adaptation is, in Williams’s memorably exacting phrase, “an onerous concept.” It can be studied with scientific rigor, but this first requires a clear answer to the question, “Precisely what is naturally selected?” Williams’s answer is compelling:

“The natural selection of phenotypes cannot in itself produce cumulative change, because phenotypes are extremely temporary manifestations... Socrates... may have been very successful in the evolutionary sense of leaving numerous offspring. His phenotype, nevertheless, was utterly destroyed by the hemlock and has never since been duplicated... The same argument also holds for genotypes. With Socrates’ death, not only did his phenotype disappear but also his genotype... because meiosis and recombination destroy genotypes as surely as death... It is only the meiotically dissociated fragments of the genotype that are transmitted in sexual reproduction, and these fragments are further fragmented by meiosis in the next generation. If there is an ultimate indivisible fragment it is, by definition, ‘the gene’ that is treated in the abstract discussions of population genetics.”

Quite so.

Williams efficiently disposed of “group selection,” which never recovered (except as a muddled version of kin selection). But in *Natural Selection: Domains, Levels and Changes* (1992), where he gathered many threads of thought, he developed the important and superficially similar idea (foreshadowed in *Adaptation and Natural Selection*) of “clade selection” to explain, not “altruism” but macroevolutionary patterns of diversity and—as I would put it—“the evolution of evolvability.”

One of Williams’s gifts was to show that what might seem obvious was not always so. He wrote *Sex and Evolution* (1975) “from a conviction that the prevalence of sexual reproduction in higher plants and animals is

The clear and wide-ranging vision of a great biologist enlightened our understanding of natural selection and adaptation.

inconsistent with current evolutionary theory...there is a kind of crisis at hand in evolutionary biology...” Assuming, as is common in animals, that the father contributes

less than the mother to the economic costs of rearing a child, a mutant female producing only asexual daughters would seem to be a more efficient reproducing machine than her sexual rival, who pours up to half of her resources into economically unproductive sons. *Sex and Evolution* was the first book to wrestle with this paradoxical “twofold cost of sex”—constructively but not entirely successfully. After working through a number of models, including the “aphid-rotifer model,” the “strawberry-coral model,” and the “elm-oyster model,” Williams ended downbeat:

“I am sure that many readers have already concluded that I really do not understand the role of sex in either organic or biotic evolution. At least I can claim...the consolation of abundant company.”

Abundant and distinguished company, for the Williams “crisis at hand” was to provoke later books by, among others, John Maynard Smith and Graham Bell, and absorbed the great W. D. Hamilton (a somewhat similar character to Williams) for most of the latter part of his career.

Williams himself, in the latter part of his career, teamed up with the physician Randolph Nesse to found *The New Science of Darwinian Medicine* (1995). That is the subtitle of their excellent book, whose main title unforgivably mutated as it crossed the Atlantic (publishers do this lamentably often, and they did it with Williams’s only book for laymen). Darwinian medicine is too important for me to expound it briefly but, as I recommended on the cover, “Buy two copies and give one to your doctor.”

George Williams takes his place among the Darwinian immortals: like Darwin himself, a great scientist and a wholly admirable man.

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