

## OBITUARY



## Obituary in memoriam of Professor William G. (Bill) Hill

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On December 17th, Professor William G. (Bill) Hill passed away in Edinburgh at the age of 81. As Bruce Walsh said at the inaugural lecture of the fourth Quantitative Genetics Conference held in Edinburgh in 2012, Bill Hill was indisputably the best quantitative geneticist in the world at that time, a belief shared by the majority of people working in the field, as had previously happened with his PhD thesis supervisor Alan Robertson.

Bill stood out in numerous fields, beginning with quantitative genetics applied to animal breeding, which was further extended to population and evolutionary genetics. His theoretical studies on artificial selection in finite populations and the effect of linkage on the evolution of genetic variation under selection, developed with Alan Robertson (the famous Hill–Robertson effect) were a milestone of great relevance, for example in the interpretation and application of current genomic analyses. Another of his main theoretical contributions was the extension of the theory of limits to artificial selection, developed initially by Alan Robertson in 1960 by focusing on the fate of the genetic variants present in the base population, to incorporate the contribution of new mutations that emerged during the selection process. The experimental verification of the theory was the subject of the doctoral thesis of one of us, supervised by another whose PhD thesis was, in turn, supervised by Bill. His numerous contributions to the study of the causes of the maintenance of genetic variability added an extraordinary dimension to the understanding of the evolution of biological diversity. Bill made many more contributions to quantitative and population genetics such as those related to the prediction of the effective population size, the maintenance of genetic variance generated by mutation, the variation of the genetic resemblance between individuals, the heterogeneity of the environmental variance, the estimation of heritabilities and genetic correlations, and the developments of a number of quantitative genetics applications to the analysis of genomic data.

Bill was widely recognized for his excellent work in population genetics, quantitative genetics and applications to evolutionary biology and animal breeding. He was elected a Fellow of the Royal Society of Edinburgh in 1979, a Fellow of the Royal Society in 1985 and appointed Order of the British Empire (OBE) in 2004. He was awarded, among others, The Royal Society's Darwin Medal for his contribution to our understanding of the genetics of quantitative traits and response to selection in 2018, and The Genetics Society's Mendel Medal for his contribution to quantitative genetics in 2019. Bill was able to bring together other distinguished figures from the field of evolutionary genetics, such as Nick Barton and Brian and Deborah Charlesworth, to the Institute of Evolutionary Biology at the University of Edinburgh.

Edinburgh became, from the times of Alan Robertson and Douglas Falconer but greatly strengthened by Bill Hill, the world epicenter of quantitative genetics, enhanced by the frequent visits of international colleagues and the consequent scientific discussions. We, fortunate enough to work under Bill's direction for several years at different times, were able to benefit from and enjoy the continuous contact with the prominent visitors to the center. Just in the 1990's, numerous renowned scientists such as Mark Kirkpatrick, Michael Turelli, Russ Lande, Joe Felsenstein, Leo Dempfle, Bruce Weir, Daniel Gianola, Ruth and Frank Shaw, and Tom Meagher, among many others, as well as former students of Alan or Bill, such as Asko Maki-Tanila, Daniel Sorensen, Zhao-Bang Zeng and Trudy Mackay visited the institute.

As usual, Bill and his wife Rosemary warmly welcomed visitors with a dinner or lunch at their home in Gordon Street. Bill was a very kind and friendly person, always treating his students, collaborators and visitors very nicely, and it was a real pleasure to work with him. His scientific capacity was unrivalled and endless, as a scientist conducting cutting-edge research, as a supervisor to numerous predoctoral and postdoctoral students (on the order of a hundred during his career), as a collaborator with colleagues from the Roslin Institute, the Scottish Agricultural College as well as other centers, as Head of Department first and Dean of the Faculty of Science and Engineering later, as chief editor of prominent journals such as the *Proceedings of the Royal Society B* and *Genetics Research*, and as his scientific consultancies for animal breeding companies. Whenever you handed him some manuscripts or results, he would return them to you the next morning, with detailed corrections and enlightening comments because, as he said, he should never delay the work of his collaborators. Bill's ability was unlimited, being able to make a mathematical deduction in a few seconds on a piece of paper in the middle of a corridor or even after a dinner, as happened at the house of one of us where he derived the formulation of the theory that he was developing at the time.

Bill promoted an exquisite and sustained intellectual environment in his lab in Edinburgh. The famous mid-morning coffees, where a good part of the development of quantitative genetics was cooked, initially held in Alan Robertson's office at the Institute of Animal Genetics, with the presence of Douglas Falconer, Crad Roberts and Eric Reeve, among others, were later continued in the new place in King's Buildings with the additional participation of other important scientists, creating an education and research environment unparalleled in the field of population genetics. Bill was for us and for many of his students and collaborators, the model of the scientist to imitate.

Rest in peace, Bill.

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### COMPETING INTERESTS

The authors declare no competing interests.

### ADDITIONAL INFORMATION

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