

PHYLOGENETIC INFERENCE, SELECTION THEORY, AND HISTORY OF SCIENCE

Selected Papers of A.W.F. Edwards with Commentaries

A. W. F. Edwards is one of the most influential mathematical geneticists in the history of the discipline. One of the last students of R. A. Fisher, Edwards pioneered the statistical analysis of phylogeny in collaboration with L. L. Cavalli-Sforza, and helped establish Fisher's concept of likelihood as a standard of statistical and scientific inference. In this book, edited by philosopher of science Rasmus Grønfeldt Winther, Edwards's key papers are assembled alongside commentaries by leading scientists, discussing Edwards's influence on their own research and on thinking in their field overall. In an extensive set of interviews with Winther, Edwards offers his thoughts on his contributions, their legacy, and the context in which they emerged. This book is a resource both for anyone interested in the history and philosophy of genetics, statistics, and science, and for scientists seeking to develop new algorithmic and statistical methods for understanding the genetic relationships between and among species both extant and extinct.

A. W. F. EDWARDS, F.R.S., is a Fellow of Gonville and Caius College, Cambridge. In addition to some 250 scientific papers on a wide range of topics, he has published four books including *Likelihood* and *Foundations of Mathematical Genetics*, both with Cambridge University Press. Edwards has been interested in the history and philosophy of science for as long as he has been a contributor to science.

RASMUS GRØNFELDT WINTER is a philosopher of science, researcher, writer, educator, diver, seeker, and explorer. www.rgwinther.com

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Edited by Rasmus Grønfeldt Winther

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- [25] (1963) The reconstruction of evolution. (Abstract) *Heredity* 18, 553, and *Annals of Human Genetics* 27, 104–105. (With L. L. Cavalli-Sforza)
- [27] (1964) Reconstruction of evolutionary trees. In *Phenetic and Phylogenetic Classification*, eds. V. H. Heywood and J. McNeill, The Systematics Association Publication No. 6, London: The Systematics Association, 67–76. (With L. L. Cavalli-Sforza) Reprinted in *Cladistic Theory and Methodology*, eds. T. Duncan and T. F. Stuessy, New York: Van Nostrand Reinhold (1985).
- [28] (1964) Analysis of human evolution under random genetic drift. *Cold Spring Harbor Symposia on Quantitative Biology* 29, 9–20. (With L. L. Cavalli-Sforza and I. Barrai)
- [29] (1965) Analysis of human evolution. Proceedings of the 11th International Congress of Genetics, The Hague 1963. *Genetics Today* 3, 923–933. (With L. L. Cavalli-Sforza)
- [30] (1965) A method for cluster analysis. *Biometrics* 21, 362–375. (With L. L. Cavalli-Sforza)
- [32] (1966) Studying human evolution by computer. *New Scientist* (19th May) 30, 438–440. Reprinted in *Evolution*, ed. M. Ridley, Oxford: Oxford University Press (1997).
- [35] (1966) Estimation procedures for evolutionary branching processes. *Bulletin of the International Statistical Institute* (Proceedings of the 35th session) 41, 803–808. (With L. L. Cavalli-Sforza)
- [36] (1967) Fundamental Theorem of Natural Selection. *Nature* 215, 537–538.
- [37] (1967) Phylogenetic analysis: models and estimation procedures. *Evolution* 21, 550–570. (With L. L. Cavalli-Sforza) Also in *American Journal of Human Genetics*, Supplement 19, 233–257.

- [42] (1969) Statistical methods in scientific inference. *Nature* 222, 1233–1237.
- [46] (1970) Estimation of the branch points of a branching diffusion process. *Journal of the Royal Statistical Society B* 32, 155–174.
- [49] (1971) Review of *Evolution and the Genetics of Populations*, Volume 2, by S. Wright. *Heredity* 26, 332–338.
- [53] (1972) Affinity as revealed by differences in gene frequencies. In *The Assessment of Population Affinities in Man*, eds. J. S. Weiner and J. Huizinga, Oxford: Clarendon Press, 37–47. (With L. L. Cavalli-Sforza)
- [56] (1972) Likelihood. *Bulletin of the Institute of Mathematics and its Applications* 8, 329–331.
- [60] (1974) The history of likelihood. *International Statistical Review* 42, 9–15. Reprinted in *Likelihood* (expanded edition), Baltimore, MD: Johns Hopkins University Press (1992).
- [96] (1986) Are Mendel's results really too close? *Biological Reviews* 61, 295–312.
- [117] (1989) Probability and likelihood in genetic counselling. *Clinical Genetics* 36, 209–216.
- [140] (1994) The Fundamental Theorem of Natural Selection. *Biological Reviews* 69, 443–474.
- [141] (1995) Assessing molecular phylogenies. *Science* 267, 253.
- [146] (1996) The origin and early development of the method of minimum evolution for the reconstruction of phylogenetic trees. *Systematic Biology* 45, 79–91.
- [173] (2001) Darwin and Mendel united: the contributions of Fisher, Haldane and Wright up to 1932. In *Encyclopedia of Genetics*, ed. E. C. R. Reeve, London: Fitzroy Dearborn, 77–83.
- [192] (2003) Human genetic diversity: Lewontin's fallacy. *BioEssays* 25, 798–801.
- [197] (2004) Parsimony and computers. In *Milestones in Systematics*, eds. D. M. Williams and P. L. Forey, The Systematics Association Special Volume, Series 67, Boca Raton, FL: CRC Press, 181–190.
- [225] (2009) Statistical methods for evolutionary trees. *Genetics* 183, 5–12.
- [227] (2011) Mathematizing Darwin. *Behavioral Ecology and Sociobiology* 65, 421–430.
- [235] (2013) Robert Heath Lock and his textbook of genetics, 1906. *Genetics* 194, 529–537.
- [238] (2014) R. A. Fisher's gene-centred view of evolution and the Fundamental Theorem of Natural Selection. *Biological Reviews* 89, 135–147.
- [248] (2016) Analysing nature's experiment: Fisher's inductive theorem of natural selection. *Theoretical Population Biology* 109, 1–5.

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Dedicated to

Luigi Luca Cavalli-Sforza
Pioneer of phylogenetic inference

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on the history and philosophy of statistics and science.

Rasmus Grønfeldt Winther and A. W. F. Edwards