# APPENDIX A: A REVIEW OF 'EVOLUTION IN MENDELIAN POPULATIONS' (S. WRIGHT, 1931)

A review of Wright, S. (1931). Evolution in Mendelian populations. *Genetics* **16**, 97-159 by R.A. Fisher (1932). Reprinted from *Eugenics Rev.* **23**, 88-90.

More than half of this number, pp. 97-159, is occupied by Professor Sewall Wright's long paper on Evolution in Mendelian populations. The mathematical consequences of Mendelian inheritance are here developed in a number of separate investigations, which together form a valuable collection of old and new material, brought together under a common notation. Professor Wright was among the first in the United States to appreciate the importance for evolutionary theory of researches of this kind, which have developed independently in this country, and later in Germany. The results are in striking contrast to the opinions early formed, and tenaciously adhered to by several early writers on Mendelism, in its bearing on evolution. Professor Wright sums up this aspect in the words: 'The conclusion seems warranted that the enormous recent additions to knowledge of heredity have merely strengthened the general conception of the evolutionary process reached by Darwin in his exhaustive analysis of the data available seventy years ago.'

Aside from the scientific conclusions which the independent contributions of workers in several different countries have now set on a firm foundation, Professor Wright makes some philosophical observations on the nature of the evolutionary process, which are of great interest, although necessarily more personal and subjective:

> 'Evolution as a process of cumulative change depends on a proper balance of the conditions, which, at each level of organization—gene, chromosome, cell, individual, local race—make for genetic homogeneity or genetic heterogeneity of the species. While the basic factor of change—the infrequent, fortuitous, usually more or less injurious gene mutations, in themselves, appear to furnish an inadequate basis for evolution, the mechanism of cell division, with its occasional aberrations, and of nuclear fusion (at fertilization) followed at some time by reduction make it possible for a relatively small number of not too injurious mutations to provide an extensive field of actual variations.

One of the most important factors on which this balanee depends, according to Professor Wright, is size of population. He points out that in very small populations the effect of selection is much reduced, so that the chances of individual survival must lead to the occasional establishment of

deleterious mutations, with consequent degeneration and extinction. The reviewer is convinced of the reality of this effect, though the fact that the human breeder working with not very large populations can make substantial progress by the exercise of stringent selection, shows that it is possible to over-emphasize its importance. On the other hand Professor Wright considers that: 'In too large a freely interbreeding population ... there is great variability, but such a close approach to complete equilibrium of all gene frequencies that there is no evolution under static conditions.' He therefore argues that the subdivision of species into partially isolated local races of small size is an important condition not merely, as is obvious, for fission into distinct species, but for progressive evolution. This conclusion is much more debatable, for even under static conditions, unless it is postulated that the organism is as well adapted as it could possibly be (in which case, obviously, evolutionary improvement is impossible), the equilibrium will be broken by the occurrence of any favourable mutation, of which a steady stream will doubtless occur in one or other of the very numerous individuals produced in each generation. The advantage of the large populations in picking up mutations of excessively low mutation rate seems to be overlooked, possibly because the author has throughout his argument taken as the standard of mutation rate, such values as are found in the best known loci in *Drosophila,* mutations which are well known probably only because their mutation rate is high. Moreover, static conditions in the evolutionary sense certainly do not occur, for, apart from geological and climatological changes, the evolutionary progress of associated organisms ensures that the organic environment shall be continually changing.

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