

APPENDIX B: A REVIEW OF *THE CAUSES OF EVOLUTION* (J.B.S. HALDANE, 1932)

A review, hitherto unpublished, of Haldane, J.B.S. (1932). *The causes of evolution*. Longmans Green, London by R.A. Fisher.

In his preface to this brilliant book Professor Haldane states that it

'is based on a series of lectures delivered in January 1931 at the Prifysgol Cymru, Aberystwyth, and entitled *A Re-examination of Darwinism*. These lectures were endowed by the munificence of the Davies family, with the provision that their substance should be published in book form. This admirable condition ensures that, unlike the average university lectures, which stale with great rapidity, they should only be delivered once, and also that they should be made available before any novelty which they may possess has worn off.'

To the advantages of making books out of lecture series, might be added the brightness and vivacity of Professor Haldane's lecturing style, carrying with it, however, the countervailing disadvantage of an unduly discursive treatment, even to the point of being sometimes merely allusive, of the wide field of topics mentioned; and, what is perhaps more serious, of an unusual prominence of the first person, associated with the bare statement of personal opinions, in many cases where we should have been glad of a presentation of the evidence. Thus in the introduction, p. 33, the sentence 'I can write of natural selection with authority because I am one of the three people who know most about its mathematical theory' has been allowed to stand. On p. 96 it appears that the two other 'authorities' are Professor Sewall Wright, of Chicago, and the reviewer. The last would urge, therefore, that the fact that these three writers have published their analytical efforts more copiously than others need not make them overlook three serious considerations.

(i) The probability that some 300 readers or more have probably assimilated everything of value that they have written, and may well know more about the mathematical theory than any of the three writers named.

(ii) That the points in which these writers are agreed have so far consisted chiefly in clearing the ground of the *debris* of anti-Darwinian criticism, which occupied so much attention in biological literature towards the end of the nineteenth, and the beginning of the twentieth century. As Professor Haldane says (p. 215), statements such as 'Natural selection cannot account for the origin of a highly complex character' will not bear analysis; or, as he emphasizes in his preface (p. vi), a Lamarckian transformation, even if physically operative, would, with particulate inheritance, be demonstrably

ineffectual in producing evolutionary change. While it is, perhaps, of some value to have shown that on such issues the early followers of Darwin were right, and their critics mistaken, the practical test of the mathematical theory of natural selection as a means for the advancement of science, must lie in its power of giving a rational interpretation to biological phenomena, hitherto obscure, and of predicting others not yet observed. Short of this, there is not much to make a song about.

(iii) The third criticism, therefore, of the theory of 'three authorities' is that they show wide disagreement in questions of interpretation, such as the evolutionary modification of dominance, and the existence of selection in species showing a stable polymorphism. Professor Haldane evidently dissents largely, or entirely, from the reviewer's opinions on these points, and it follows unmistakably either that Professor Haldane, or that I, would be a less satisfactory guide than any judicious reader who had formed a just view of the state of the evidence.

How much the book would have gained by expansion considerably beyond the volume of the lectures—the length could easily have been doubled—and especially by supplementing bare, though impressive, opinions, with the reasons on which they are based, may be judged from the four passages in which the theory of the evolutionary modification of dominance is alluded to. (i) (page 134) 'Wright (1931) and I (Haldane 1930a) have criticized this theory, and I doubt if it can stand in its original form. Nevertheless it undoubtedly has some truth in it, and there can be little doubt that mutation pressure has been a cause of evolution, if perhaps a less important one than Fisher believes.' (ii) (page 142) [Fisher's theory of dominance is] '(in my opinion probably false)' (iii) (page 195) 'Fisher's (1930) analysis of the effect of selection on such a population involves his theory of the evolution of dominance, which I do not myself hold. His analysis is very greatly simplified if we restrict ourselves, as I shall do here, to the case where all the genes concerned are fully dominant.' (iv) (page 193) 'Fisher (1931) has based a theory of the evolution of dominance on this basis. He believes that abnormal genes are originally intermediate in dominance, rather than recessive. But modifiers are selected which render the heterozygote normal in its viability. I have criticized this theory (Haldane, 1930a) though I believe it to be true in some cases. Fortunately, however, it is susceptible of experimental proof or disproof (Fisher, 1930, p. 62), and since Fisher is undertaking the necessary experiments there is no need to state the arguments for and against this theory here, since at least one of these arguments will be shown to be fallacious in the near future.'

The reader who is curious to know on what evidence divergent opinions are held is kept guessing. He is not even told whether Haldane still adheres to his former theory that modification of dominance has taken place by the selection of multiple allelomorphs rather than by the selection of modi-

fying factors as proposed by the reviewer. He is left wholly in the dark even as to what truth Haldane holds the theory 'undoubtedly' to contain, or in what class of cases he believes it to be true; and, without an answer to these questions he can scarcely judge of the relevance of much of Haldane's mathematical treatment, for it is of little use that the analysis should be very greatly simplified, if this is at the expense of making an unjustified assumption. But little expansion would have been needed to replace *ex cathedra* pronouncements (including one very curious prophecy) by a reasoned contribution to the subject.

The fact of the evolutionary modification of dominance has been demonstrated by Harland's work for a particular example in cotton, though Harland hesitates to accept the selective theory from which this fact was previously inferred. His experiments demonstrate, moreover, that the differentiation in this case is due to modifying factors, and not to Haldane's proposed mechanism of multiple allelomorphs. It is difficult to imagine why Haldane should not make it clear (i) whether he accepts Harland's observational findings, (ii) whether he questions Harland's genetical analysis of the situation, and (iii) whether, accepting these, he believes in some alternative evolutionary process by which the situation could have been brought about.

The reviewer must protest that Haldane's allusion to the experimental work he has undertaken, with two species of land-snails and with jungle fowl, is highly misleading. These experiments concern possible, though at present uncertain, extensions of the theory to two cases showing rather exceptional dominance phenomena. It should be obvious that the reviewer is not likely in his spare time to attempt to verify the great body of observational data, already well established by others, on which his views on the evolution of dominance have been founded.

The necessity of clearing up a personal point has necessitated giving more space to it than would be otherwise warranted. The examples quoted, however, are not unrepresentative of the style and manner of the rest of the book. One receives the impression more of able conversation on a series of interesting topics, than of a considered treatise on genetical theory; and Haldane's philosophical attitude towards the evolutionary process, developed in Chapter VI, will be found thought-provoking by many who are little concerned with the merely mechanical and scientific aspect of this process.