I

THE NATURE OF INHERITANCE

The consequences of the blending theory, as drawn by Darwin. Difficulties felt by Darwin. Particulate inheritance. Conservation of the variance. Theories of evolution worked by mutations. Is all inheritance particulate? Nature and frequency of observed mutations.

But at present, after drawing up a rough copy on this subject, my conclusion is that external conditions do extremely *little, except in causing mere variability. This mere variability (causing the child* not *closely to resemble its parent) I look at as* very *different from the formation of a marked variety or new species.* DARWIN, 1856. (*Life and Letters*, ii, 87.)

As Samuel Butler so truly said : '*To me it seems that the "Origin of Variation", whatever it is, is the only true " Origin of Species ".*' W. BATESON, 1909.

The consequences of the blending theory

THAT Charles Darwin accepted the fusion or blending theory of inheritance, just as all men accept many of the undisputed beliefs of their time, is universally admitted. That his acceptance of this theory had an important influence on his views respecting variation, and consequently on the views developed by himself and others on the possible causes of organic evolution, was not, I think, apparent to himself, nor is it sufficiently appreciated in our own times. In the course of the present chapter I hope to make clear the logical consequences of the blending theory, and to show their influence, not only on the development of Darwin's views, but on the change of attitude towards these, and other suppositions, necessitated by the acceptance of the opposite theory of particulate inheritance.

It is of interest that the need for an alternative to blending inheritance was certainly felt by Darwin, though probably he never worked out a distinct idea of a particulate theory. In a letter to Huxley probably dated in 1857 occur the sentences (*More Letters*, vol. i, Letter 57).

Approaching the subject from the side which attracts me most, viz., inheritance, I have lately been inclined to speculate, very crudely and indistinctly, that propagation by true fertilization will turn out to be a sort of mixture, and not true fusion, of two distinct individuals, or rather of innumerable individuals, as each parent has its parents and

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ancestors. I can understand on no other view the way in which crossed forms go back to so large an extent to ancestral forms. But all this, of course, is infinitely crude.

The idea apparently was never developed, perhaps owing to the rush of work which preceded and followed the publication of the *Origin*. Certainly he did not perceive that the arguments on variation in his rough essays of 1842 and 1844, which a year later (1858) he would be rewriting in the form of the first chapter of the *Origin*, would on a particulate theory have required him entirely to recast them. The same views indeed are but little changed when 'The causes of variability' came to be discussed in Chapter XXII of *Variation of Animals and Plants* published in 1868.

The argument which can be reconstructed from these four sources may be summarized as follows:

(*a*) with blending inheritance bisexual reproduction will tend rapidly to produce uniformity;

(*b*) if variability persists, causes of new variation must be continually at work;

(*c*) the causes of the great variability of domesticated species, of all kinds and in all countries, must be sought for in the conditions of domestication;

(*d*) the only characteristics of domestication sufficiently general to cover all cases are changed conditions and increase of food;

(*e*) some changes of conditions seem to produce definite and regular effects, e. g. increased food causes (hereditary) increase in size, but the important effect is an indefinite variability in all directions, ascribable to a disturbance, by change of conditions, of the regularity of action of the reproductive system;

(*f*) wild species also will occasionally, by geological changes, suffer changed conditions, and occasionally also a temporary increase in the supply of food; they will therefore, though perhaps rarely, be caused to vary. If on these occasions no selection is exerted the variations will neutralize one another by bisexual reproduction and die away, but if selection is acting, the variations in the right direction will be accumulated and a permanent evolutionary change effected.

To modern readers this will seem a very strange argument with which to introduce the case for Natural Selection; all that is gained

by it is the inference that wild as well as domesticated species will at least occasionally present heritable variability. Yet it is used to introduce the subject in the two essays and in the *Origin*. It should be remembered that, at the time of the essays, Darwin had little direct evidence on this point; even in the *Origin* the second chapter on 'Variation under Nature' deals chiefly with natural varieties sufficiently distinct to be listed by botanists, and these were certainly regarded by Darwin not as the materials but as the products of evolution. During the twenty-six years between 1842 and 1868 evidence must have flowed in sufficiently at least to convince him that heritable variability was as widespread, though not nearly as extensive, in wild as in domesticated species. The line of reasoning in question seems to have lost its importance sufficiently for him to introduce the subject in 1868 (*Variation*, Chapter XXII) with the words 'The subject is an obscure one; but it may be useful to probe our ignorance.'

It is the great charm of the essays that they show the *reasons* which led Darwin to his conclusions, whereas the later works often only give the *evidence* upon which the reader is to judge of their truth. The antithesis is not so heterodox as it sounds, for every active mind will form opinions without direct evidence, else the evidence too often would never be collected. Impartiality and scientific discipline come in in submitting the opinions formed to as much relevant evidence as can be made available. The earlier steps in the argument set out above appear only in the two essays, while the conclusions continue almost unchanged up to the *Variation of Animals and Plants*. Indeed the first step (*a*), logically the most important of all, appears explicitly only in 1842. In 1844 it is clearly implied by its necessary consequences. I believe its significance for the argument of the *Origin*, would scarcely ever be detected from a study only of that book. The passage in the 1842 MS. is (*Foundations*, p. 2):

> Each parent transmits its peculiarities, therefore if varieties allowed freely to cross, except by the *chance* of two characterized by same peculiarity happening to marry, such varieties will be constantly demolished. All bisexual animals must cross, hermaphrodite plants do cross, it seems very possible that hermaphrodite animals do cross— conclusion strengthened:

together with a partly illegible passage of uncertain position,

> If individuals of two widely different varieties be allowed to cross,

a third race will be formed—a most fertile source of the variation in domesticated animals. If freely allowed, the characters of pure parents will be lost, number of races thus [illegible] but differences [?] besides the [illegible]. But if varieties differing in very slight respects be allowed to cross, such small variation will be destroyed, at least to our senses—a variation just to be distinguished by long legs will have offspring not to be so distinguished. Free crossing great agent in producing uniformity in any breed.

The proposition is an important one, marking as it does the great contrast between the blending and the particulate theories of inheritance. The following proof establishes it in biometrical terms.

Let x and y represent the deviations in any measurement of the two parents from the specific mean; if the measurement is affected not only by inheritance, but by non-heritable (environmental) factors also, x and y stand for the heritable part of these deviations. The amount of variability present in any generation of individuals will be measured by the variance, defined as the mean value of the square of x, or of y. In purely blending inheritance the heritable portions of the deviations of the offspring will be, apart from mutations, equal to $\frac{1}{2}(x+y)$; in the absence of such mutations, therefore, the variance of the progeny generation will be the mean value of $\frac{1}{4}(x^2 + 2xy + y^2)$.

The mean values of x and y are both zero, since they are both defined as deviations from the mean of the species; consequently, in the absence of selective mating, the mean value of xy is also zero, and the variance of the progeny generation is found to be exactly half the variance of the parental generation. More generally the ratio is not $\frac{1}{2}$ but $\frac{1}{2}(1+r)$, where r is the correlation between x and y. r cannot exceed unity, else the average value of the positive quantities $(x-y)^2$ would have to be negative, and can only be unity, if they are all zero, that is, if the size of each individual prescribes exactly the size of its possible mates. Darwin's 'except by the chance of two individuals characterized by same peculiarities happening to marry' is his way of rejecting high correlations as improbable.

The effect of correlation between mates is to hasten, if the correlation is negative, or to retard if positive, the tendency of blending inheritance to reduce the variance; such effects are not of importance, for even if the correlation were as high as 0·5, and mates had to be as much alike as parent and child usually are, the rate of decay would