

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

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

be little more than halved. The important consequence of the blending is that, if not safeguarded by intense marital correlation, the heritable variance is approximately halved in every generation. To maintain a stationary variance fresh mutations must be available in each generation to supply the half of the variance so lost. If variability persists, as Darwin rightly inferred, causes of new variability must continually be at work. Almost every individual of each generation must be a mutant, i. e. must be influenced by such causes, and moreover must be a mutant in many different characters.

An inevitable inference of the blending theory is that the bulk of the heritable variance present at any moment is of extremely recent origin. One half is new in each generation, and of the remainder one half is only one generation older, and so on. Less than one-thousandth of the variance can be ten generations old; even if by reason of selective mating we ought to say twenty generations, the general conclusion is the same; the variability of domesticated species must be ascribed by any adherent of the blending theory to the conditions of domestication as they now exist. If variation is to be used by the human breeder, or by natural selection, it must be snapped up at once, soon after the mutation has appeared, and before it has had time to die away. The following passage from the 1844 essay shows that Darwin was perfectly clear on this point (pp. 84-6).

Let us then suppose that an organism by some chance (which might be hardly repeated in 1,000 years) arrives at a modern volcanic island in process of formation and not fully stocked with the most appropriate organisms; the new organism might readily gain a footing, although the external conditions were considerably different from its native ones. The effect of this we might expect would influence in some small degree the size, colour, nature of covering, &c., and from inexplicable influences even special parts and organs of the body. But we might further (and this is far more important) expect that the reproductive system would be affected, as under domesticity, and the structure of the offspring rendered in some degree plastic. Hence almost every part of the body would tend to vary from the typical form in slight degrees, and in no determinate way, and therefore *without selection* the free crossing of these small variations (together with the tendency to reversion to the original form) would constantly be counteracting this unsettling effect of the extraneous conditions on the reproductive system. Such, I conceive, would be the unimportant result without selection. And here I must observe that the foregoing remarks are equally applicable to

that small and admitted amount of variation which has been observed in some organisms in a state of nature; as well as to the above hypothetical variation consequent on changes of condition.

Let us now suppose a Being with penetration sufficient to perceive differences in the outer and innermost organization quite imperceptible to man, and with forethought extending over future centuries to watch with unerring care and select for any object the offspring of an organism produced under the foregoing circumstances; I can see no conceivable reason why he could not form a new race (or several were he to separate the stock of the original organism and work on several islands) adapted to new ends. As we assume his discrimination, and his forethought, and his steadiness of object, to be incomparably greater than those qualities in man, so we may suppose the beauty and complications of the adaptations of the new races and their differences from the original stock to be greater than in the domestic races produced by man's agency: the ground-work of his labours we may aid by supposing that the external conditions of the volcanic island, from its continued emergence, and the occasional introduction of new immigrants, vary; and thus to act on the reproductive system of the organism, on which he is at work, and so keep its organization somewhat plastic. With time enough, such a Being might rationally (without some unknown law opposed him) aim at almost any result.

Difficulties felt by Darwin

The argument based on blending inheritance and its logical consequences, though it certainly represents the general trend of Darwin's thought upon inheritance and variation, for some years after he commenced pondering on the theory of Natural Selection, did not satisfy him completely. Reversion he recognized as a fact which stood outside his scheme of inheritance, and that he was not altogether satisfied to regard it as an independent principle is shown by his letter to Huxley already quoted. By 1857 he was in fact on the verge of devising a scheme of inheritance which should include reversion as one of its consequences. The variability of domesticated races, too, presented a difficulty which, characteristically, did not escape him. He notes (pp. 77, 78, *Foundations*) in 1844 that the most anciently domesticated animals and plants are not less variable, but, if anything more so, than those more recently domesticated; and argues that since the supply of food could not have been becoming much more abundant progressively at all stages of a long history of

domestication, this factor cannot alone account for the great variability which still persists. The passage runs as follows:

If it be an excess of food, compared with that which the being obtained in its natural state, the effects continue for an improbably long time; during how many ages has wheat been cultivated, and cattle and sheep reclaimed, and we cannot suppose their *amount* of food has gone on increasing, nevertheless these are amongst the most variable of our domestic productions.

This difficulty offers itself also to the second supposed cause of variability, namely changed conditions, though here it may be argued that the conditions of cultivation or nurture of domesticated species have always been changing more or less rapidly. From a passage in the *Variation of Animals and Plants* (p. 301), which runs:

Moreover, it does not appear that a change of climate, whether more or less genial, is one of the most potent causes of variability; for in regard to plants Alph. De Candolle, in his *Geographie Botanique*, repeatedly shows that the native country of a plant, where in most cases it has been longest cultivated, is that where it has yielded the greatest number of varieties.

it appears that Darwin satisfied himself that the countries in which animals or plants were first domesticated, were at least as prolific of new varieties as the countries into which they had been imported, and it is natural to presume that his inquiries under this head were in search of evidence bearing upon the effects of changed conditions. It is not clear that this difficulty was ever completely resolved in Darwin's mind, but it is clear from many passages that he saw the necessity of supplementing the original argument by postulating that the causes of variation which act upon the reproductive system must be capable of acting in a delayed and cumulative manner so that variation might still be continued for many subsequent generations.

Particulate inheritance

It is a remarkable fact that had any thinker in the middle of the nineteenth century undertaken, as a piece of abstract and theoretical analysis, the task of constructing a particulate theory of inheritance, he would have been led, on the basis of a few very simple assumptions, to produce a system identical with the modern scheme of Mendelian or factorial inheritance. The admitted non-inheritance of

scars and mutilations would have prepared him to conceive of the hereditary nature of an organism as something none the less definite because possibly represented inexactly by its visible appearance. Had he assumed that this hereditary nature was completely determined by the aggregate of the hereditary particles (genes), which enter into its composition, and at the same time assumed that organisms of certain possible types of hereditary composition were capable of breeding true, he would certainly have inferred that each organism must receive a definite portion of its genes from each parent, and that consequently it must transmit only a corresponding portion to each of its offspring. The simplification that, apart from sex and possibly other characters related in their inheritance to sex, the contributions of the two parents were equal, would not have been confidently assumed without the evidence of reciprocal crosses; but our imaginary theorist, having won so far, would scarcely have failed to imagine a conceptual framework in which each gene had its proper place or locus, which could be occupied alternatively, had the parentage been different, by a gene of a different kind. Those organisms (homozygotes) which received like genes, in any pair of corresponding loci, from their two parents, would necessarily hand on genes of this kind to all of their offspring alike; whereas those (heterozygotes) which received from their two parents genes of different kinds, and would be, in respect of the locus in question, crossbred, would have, in respect of any particular offspring, an equal chance of transmitting either kind. The heterozygote when mated to either kind of homozygote would produce both heterozygotes and homozygotes in a ratio which, with increasing numbers of offspring, must tend to equality, while if two heterozygotes were mated, each homozygous form would be expected to appear in a quarter of the offspring, the remaining half being heterozygous. It thus appears that, apart from dominance and linkage, including sex linkage, all the main characteristics of the Mendelian system flow from assumptions of particulate inheritance of the simplest character, and could have been deduced *a priori* had any one conceived it possible that the laws of inheritance could really be simple and definite.

The segregation of single pairs of genes, that is of single factors, was demonstrated by Mendel in his paper of 1865. In addition Mendel demonstrated in his material the fact of dominance, namely that the heterozygote was not intermediate in appearance, but was almost or

quite indistinguishable from one of the homozygous forms. The fact of dominance, though of the greatest theoretical interest, is not an essential feature of the factorial system, and in several important cases is lacking altogether. Mendel also demonstrated what a theorist could scarcely have ventured to postulate, that the different factors examined by him in combination, segregated in the simplest possible manner, namely independently. It was not till after the rediscovery of Mendel's laws at the end of the century that cases of linkage were discovered, in which, for factors in the same linkage group, the pair of genes received from the same parent are more often than not handed on together to the same child. The conceptual framework of loci must therefore be conceived as made of several parts, and these are now identified, on evidence which appears to be singularly complete, with the dark-staining bodies or chromosomes which are to be seen in the nuclei of cells at certain stages of cell division.

The mechanism of particulate inheritance is evidently suitable for reproducing the phenomenon of reversion, in which an individual resembles a grandparent or more remote ancestor, in some respect in which it differs from its parents; for the ancestral gene combination may by chance be reproduced. This takes its simplest form when dominance occurs, for every union of two heterozygotes will then produce among the offspring some recessives, differing in appearance from their parents, but probably resembling some grandparent or ancestor.

Conservation of the variance

It has not been so clearly recognized that particulate inheritance differs from the blending theory in an even more important fact. There is no inherent tendency for the variability to diminish. In a population breeding at random in which two alternative genes of any factor, exist in the ratio p to q , the three genotypes will occur in the ratio $p^2 : 2pq : q^2$, and thus ensure that their characteristics will be represented in fixed proportions of the population, however they may be combined with characteristics determined by other factors, provided that the ratio $p : q$ remains unchanged. This ratio will indeed be liable to slight changes; first by the chance survival and reproduction of individuals of the different kinds; and secondly by selective survival, by reason of the fact that the genotypes are probably unequally fitted, at least to a slight extent, to their task of

survival and reproduction. The effect of chance survival is easily susceptible of calculation, and it appears, as will be demonstrated more fully (Chapter IV), that in a population of n individuals breeding at random the variance will be halved by this cause acting alone in $1.4 n$ generations. Since the number of individuals surviving to reproduce in each generation must in most species exceed a million, and in many is at least a million-fold greater, it will be seen that this cause of the diminution of hereditary variance is exceedingly minute, when compared to the rate of halving in one or two generations by blending inheritance.

It will be seen in Chapter IV that selection is a much more important agency in keeping the variability of species within limits. But even relatively intense selection will change the ratio $p : q$ of the gene frequencies relatively slowly, and no reasonable assumptions could be made by which the diminution of variance due to selection, in the total absence of mutations, would be much more than a ten-thousandth of that ascribable to blending inheritance. The immediate consequence of this enormous contrast is that the mutation rate needed to maintain a given amount of variability is, on the particulate theory, many thousand times smaller than that which is required on the blending theory. Theories, therefore, which ascribe to agencies believed to be capable of producing mutations, as was 'use and disuse' by Darwin, a power of governing the direction in which evolution is taking place, appear in very different lights, according as one theory of inheritance, or the other, is accepted. For any evolutionary tendency which is supposed to act by favouring mutations in one direction rather than another, and a number of such mechanisms have from time to time been imagined, will lose its force many thousand-fold, when the particulate theory of inheritance, in any form, is accepted; whereas the directing power of Natural Selection, depending as it does on the amount of heritable variance maintained, is totally uninfluenced by any such change. This consideration, which applies to all such theories alike, is independent of the fact that a great part of the reason, at least to Darwin, for ascribing to the environment any considerable influence in the production of mutations, is swept away when we are no longer forced to consider the great variability of domestic species as due to the comparatively recent influence of their artificial environment.

The striking fact, of which Darwin was well aware, that whole

brothers and sisters, whose parentage, and consequently whose entire ancestry is identical, may differ greatly in their hereditary composition, bears under the two theories two very different interpretations. Under the blending theory it is clear evidence of new and frequent mutations, governed, as the greater resemblance of twins suggests, by temporary conditions acting during conception and gestation. On the particulate theory it is a necessary consequence of the fact that for every factor a considerable fraction, not often much less than one half, of the population will be heterozygotes, any two offspring of which will be equally likely to receive unlike as like genes from their parents. In view of the close analogy between the statistical concept of variance and the physical concept of energy, we may usefully think of the heterozygote as possessing variance in a potential or latent form, so that instead of being lost when the homozygous genotypes are mated it is merely stored in a form from which it will later reappear. A population mated at random immediately establishes the condition of statistical equilibrium between the latent and the apparent form of variance. The particulate theory of inheritance resembles the kinetic theory of gases with its perfectly elastic collisions, whereas the blending theory resembles a theory of gases with inelastic collisions, and in which some outside agency is required to be continually at work to keep the particles astir.

The property of the particulate theory of conserving the variance for an indefinite period explains at once the delayed or cumulative effect of domestication in increasing the variance of domesticated species, to which Darwin calls attention. Many of our domesticated varieties are evidently ill-fitted to survive in the wild condition. The mutations by which they arose may have been occurring for an indefinite period prior to domestication without establishing themselves, or appreciably affecting the variance, of the wild species. In domestication, however, not only is the rigour of Natural Selection relaxed so that mutant types can survive, and each such survival add something to the store of heritable variance, but novelties of form or colour, even if semi-monstrous, do undoubtedly attract human attention and interest, and are valued by man for their peculiarity. The rapidity with which new variance is accumulated will thus be enhanced. Without postulating any change in the mutation rates due to domestication, we should necessarily infer from what is known of the conditions of domestication that the variation of domesticated

species should be greater than that of similar wild species, and that this contrast should be greatest with those species most anciently domesticated. Thus one of the main difficulties felt by Darwin is resolved by the particulate theory.

Theories of evolution worked by mutations

The theories of evolution which rely upon hypothetical agencies capable of modifying the frequency or direction in which mutations are taking place, fall into four classes. In stating these it will be convenient to use the term 'mutation', to which many meanings have at different times been assigned, to denote simply the initiation of any heritable novelty.

(A) It may be supposed, as by Lamarck in the case of animals that the mental state, and especially the desires of the organism possess the power of producing mutations of such a kind, that these desires may be more readily gratified in the descendants. This view postulates (i) that there exists a mechanism by which mutations are caused, and even designed, in accordance with the condition of the nervous system, and (ii) that the desires of animals in general are such that their realization will improve the aptitude of the species for life in its natural surroundings, and also will maintain or improve the aptitude of its parts to co-operate with one another, both in maintaining the vital activity of the adult animal, and in ensuring its normal embryological development. The desires of animals must in fact, be very wisely directed, as well as being effective in provoking suitable mutations.

(B) A power of adaptation may be widely observed, both among plants and animals, by which particular organs, such as muscles or glands, respond by increased activity and increased size, when additional physiological calls are made upon them. It may be suggested, as it was by Darwin, that such responses of increased functional activity induce, or are accompanied by, mutations of a kind tending to increase the size or activity of the organ in question in future generations, even if no additional calls were made upon this organ's activity. This view implies (i) that the power which parts of organisms possess, of responding adaptively to increased demands upon them, is not itself a product of evolution, but must be postulated as a primordial property of living matter: and requires (ii) that a mecha-

nism exists by which the adaptive response shall itself tend to cause, or be accompanied by, an appropriate mutation.

Both these two suggested means of evolution expressly aim at explaining, not merely the progressive change of organic beings, but the aptitude of the organism to its place in nature, and of its parts to their function in the organism.

(C) It may be supposed that the environment in which the organism is placed controls the nature of the mutations which occur in it, and so directs its evolutionary course; much as the course of a projectile is controlled by the field of force in which it flies.

(D) It may be supposed that the mutations which an organism undergoes are due to an 'inner urge' (not necessarily connected with its mental state) implanted in its primordial ancestors, which thereby directs its predestined evolution.

The two last suggestions give no particular assistance towards the understanding of adaptation, but each contains at least this element of truth; that however profound our ignorance of the causes of mutation may be, we cannot but ascribe them, within the order of Nature as we know it, either to the nature of the organism, or to that of its surrounding environment, or, more generally, to the interaction of the two. What is common, however, to all four of these suppositions, is that each one postulates that the direction of evolutionary change is governed by the predominant direction in which mutations are taking place. However reasonable such an assumption might have seemed when, under the blending theory of inheritance, every individual was regarded as a mutant, and probably a multiple mutant, it is impossible to let it pass unquestioned, in face of the much lower mutation rates appropriate to the particulate theory.

A further hypothetical mechanism, guiding the evolution of the species according to the direction in which mutations are occurring, was suggested by Weismann. Weismann appreciated much more thoroughly than many of his contemporaries the efficacy of Natural Selection, in promoting the adaptation of organisms to the needs of their lives in their actual habitats. He felt, however, that this action would be aided in a subordinate degree if the process of mutation could acquire a kind of momentum, so that a series of mutations affecting the increase or decrease of a part should continue to occur, as a consequence of an initial chance tendency towards such increase or decrease. Such an assumed momentum in the process of mutation

he found useful in two respects: (i) it would enable an assumed minimal mutation in an advantageous direction to be increased by further mutations, until it 'attains selection value'; (ii) it explains the continuous decrease of a useless organ, without assuming that each step of this decrease confers any advantage upon the organism manifesting it.

The concept of attaining selection value, which is fairly common in biological literature, seems to cover two distinct cases. In the first case we may imagine that, with increasing size, the utility of an organ shows no increase up to a certain point, but that beyond this point increasing size is associated with increasing utility. In such a case, which, in view of the actual variability of every organism, and of the parts of related organisms, must be regarded as somewhat ideal, we are really only concerned with the question whether the actual variability in different members of the species concerned, does or does not reach as far as the critical point. If it does not do so the species will not be able to take the advantage offered, simply because it is not variable enough, and the postulate of an element of momentum in the occurrence of mutations, was certainly not made in order to allow organisms to be more variable than they would be without it.

The second meaning, which is also common in the literature, depends upon a curious assumption as to the manner in which selective advantage increases with change of size of the organ upon which this advantage is dependent; for it is sometimes assumed that, while at all sizes an increase of size may be advantageous, this advantage increases, not continuously, but in a step-like manner; or at least that increases below a certain limit produce an advantage which may be called 'inappreciable', and therefore neglected. Both the metaphor and the underlying idea appear to be drawn from psychophysical experience. If we compare two physical sensations such as those produced by the weights of two objects, then when the weights are sufficiently nearly equal the subject will often be unable to distinguish between them, and will judge them equal, whereas with a greater disparity, a distinct or appreciable difference of weight is discerned. If, however, the same test is applied to the subject repeatedly with differences between the weights varying from what is easily discernible to very much smaller quantities, it is found that differences in the weights, which would be deemed totally inappreci-

able, yet make a significant and perfectly regular difference to the *frequency* with which one is judged heavier than the other. The discontinuity lies in our interpretation of the sensations, and not in the sensations themselves. Now, survival value is measured by the

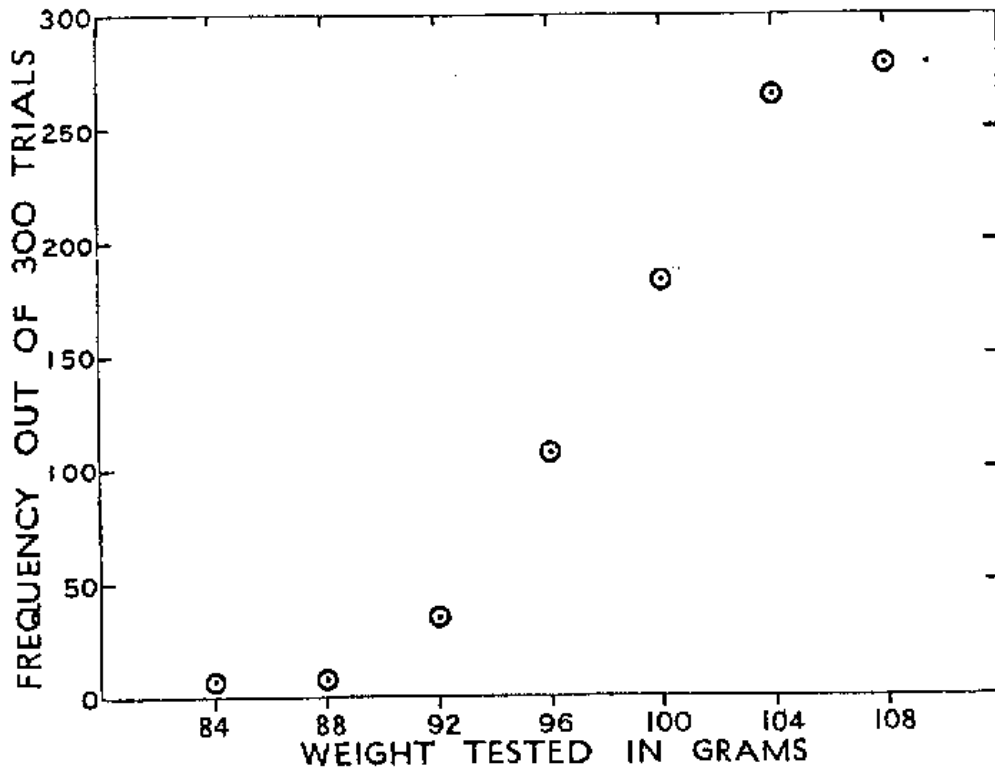


FIG. 1. The frequency with which test objects of different weights are judged heavier than a standard 100 gram weight. (Urban's data, for a single subject.) Illustrating the fact that with a sufficient number of trials, differences in weight, however 'inappreciable', will affect the frequency of the judgement.

frequency with which certain events, such as death or reproduction, occur, to different sorts of organisms exposed to the different chances of the same environment, and, even if we should otherwise be in doubt, the psychophysical experiments make it perfectly clear that the selective advantage will increase or decrease continuously, even for changes much smaller than those appreciable to our own senses, or to those of the predator or other animal, which may enter into the biological situation concerned. If a change of 1 mm. has selection value, a change of 0.1 mm. will usually have a selection value approximately one-tenth as great, and the change cannot be ignored because we deem it inappreciable. The rate at which a mutation increases in numbers at the expense of its allelomorph will indeed depend on the selective advantage it confers, but the rate at which a species responds to selection in favour of any increase or decrease of parts depends on the total heritable variance available, and not

on whether this is supplied by large or small mutations. There is no *limen* of appreciable selection value to be considered.

The remaining advantage which Weismann sought in postulating his mechanism of germinal selection was to supply an explanation of the progressive diminution of useless organs, even when these are of so trifling a character that the selective advantage of their suppression is questionable. The subject is an interesting one, and deserves for its own sake a more extended discussion than would be suitable in the present book. For our present purpose it will be sufficient to notice (i) that to assert in any particular case that the progressive suppression of an organ brings with it no progressive selective advantage appears to be very far beyond the range of our actual knowledge. To take a strong case from Weismann—the *receptaculum seminis* of an ant is assuredly minute; but the ant herself is not very large, nor are we concerned only with the individual ant, but with the whole worker population of the nest. As an economic problem we certainly do not possess the data to decide whether the suppression of this minute organ would or would not count as an appreciable factor in the ant polity. Human parallels might be given in which the elimination of very minute items of individual waste, can lend an appreciable support to social institutions which are certainly not negligible. I do not assert that the suppression of the *receptaculum* has been useful to the ant, but that in this as in other cases, if we pause to give the matter due consideration, it is at once apparent that we have not the knowledge on which to base any decided answer. (ii) In the second place Weismann's view that in the absence of all selection a useless organ might diminish, degenerate, and finally disappear, by the cumulative action of successive mutations, and especially his view that this is the only type of progressive change, which could take place by mutations only, without the guidance of Natural Selection, is fully in accordance with modern knowledge of the nature of mutations. The special mechanism, however, by which he sought to explain the successive occurrence of degenerative mutations must be judged to be superfluous. It is moreover exposed to the logical objection that the driving force of his mechanism of germinal selection is an assumed competition for nutriment between the chromatin elements which represent the degenerating organ, and those which represent the rest of the body. The degenerating organ itself is assumed to be so unimportant that

its demands upon the general nutrition of the body are to be neglected; and it may well be asked if it is legitimate to bring in, in respect of the well-nourished germ cell, the factor of nutritional competition which is to be ignored in the occasionally ill-nourished body.

Is all inheritance particulate?

The logical case for rejecting the assumption that the direction of evolutionary change is governed by the direction in which mutations are taking place, and thereby rejecting the whole group of theories in which this assumption is implicit, would be incomplete had not modern researches supplied the answer to two further questions: (i) May it not be that in addition to the mechanism of particulate inheritance, which has been discovered and is being investigated, there is also, in living organisms, an undiscovered mechanism of blending inheritance? (ii) Do the known facts within the particulate system render a mechanism, which could control the predominant direction of mutation, inoperative as a means of governing the direction of evolutionary change?

On the first point it should be noted briefly that, whereas at the beginning of the century there were several outstanding facts of inheritance which seemed to demand some sort of blending theory, these have all in the course of research been shown, not only to be compatible with particulate inheritance, but to reveal positive indications that such is their nature. The apparent blending in colour in crosses between white races of man and negroes is compatible with the view that these races differ in several Mendelian factors, affecting the pigmentation. Of these some may have intermediate heterozygotes, and of the remainder in some the darker, and in some the lighter tint may be dominant. The Mendelian theory is alone competent to explain the increased variability of the offspring of the mulattoes.

The biometrical facts as to the inheritance of stature and other human measurements, though at first regarded as incompatible with the Mendelian system, have since been shown to be in complete accord with it, and to reveal features not easily explicable on any other view. The approximately normal distribution of the measurements themselves may be deduced from the simple supposition that the factors affecting human stature are approximately additive in their effects. The correlations found between relatives of different

degrees of kinship are, within their sampling errors, of the magnitudes which would be deduced from the assumption that the measurement is principally determined by inheritance, and that the factors controlling it show, like most Mendelian factors, complete or almost complete dominance. The presence of dominance is a Mendelian feature, which is shown in the biometrical data by the well-established fact that children of the same parents are, on the average, somewhat more alike than are parent and offspring.

So far we have merely established the negative fact that there are no outstanding observations which require a blending system of inheritance. There is, however, one group of modern researches which, at least in the organisms investigated, seems to exclude it, even as a possibility. In certain organisms which are habitually self-fertilized, as Johanssen was the first to show with a species of bean, it is possible to establish so-called pure lines, within which heritable variability is, apart from exceptional mutations, completely absent. Within these lines the selection of the largest or the smallest beans, even where this selection was continued for ten or twenty generations, constantly produced offspring of the same average size. This size differed from one line to another, showing that heritable variability existed abundantly in the species, and among the thousands of beans examined two distinct mutants were reported. If, however, any appreciable fraction of the variance in bean size were ascribable to elements which blend, the mutations necessary to maintain such heritable variability would, in ten generations, have had time to supply it almost to its maximum extent, and must inevitably have been revealed by selection. Experiments of this type seem capable of excluding the possibility that blending inheritance can account for any appreciable fraction of the variance observed.

Nature and frequency of observed mutations

The assumption that the direction of evolutionary change is actually governed by the direction in which mutations are occurring is not easily compatible with the nature of the numerous mutations which have now been observed to occur. For the majority of these produce strikingly disadvantageous deformities, and indeed much the largest class are actually lethal. If we had to admit, as has been so often assumed in theory, that these mutations point the direction of evolution, the evolutionary prospects of the little fruit-fly *Drosophila*

would be deplorable indeed. Nor is the position apparently different with man and his domesticated animals and plants; as may be judged from the frequency with which striking recessive defects, such as albinism, deaf-mutism, and feebleness of mind in man, must have occurred in the comparatively recent past, as mutations. Mutant defects seem to attack the human eye as much as that of *Drosophila*, and in general the mutants which occur in domesticated races are often monstrous and predominantly defective, whereas we know in many cases that the evolutionary changes which these creatures have undergone under human selection have been in the direction of a manifest improvement.

In addition to the defective mutations, which by their conspicuousness attract attention, we may reasonably suppose that other less obvious mutations are occurring which, at least in certain surroundings, or in certain genetic combinations, might prove themselves to be beneficial. It would be unreasonable, however, to assume that such mutations appear individually with a frequency much greater than that which is observed in the manifest defects. The frequency of individual mutations in *Drosophila* is certainly seldom greater than one in 100,000 individuals, and we may take this figure to illustrate the inefficacy of any agency, which merely controls the predominant direction of mutation, to determine the predominant direction of evolutionary change. For even if selective survival were totally absent, a lapse of time of the order of 100,000 generations would be required to produce an important change with respect to the factor concerned, in the heritable nature of the species. Moreover, if the mutant gene were opposed, even by a very minute selective disadvantage, the change would be brought to a standstill at a very early stage. The ideas necessary for a precise examination of the nature of selective advantage will be developed in Chapter II; but it will be readily understood that if we speak of a selective advantage of one per cent., with the meaning that animals bearing one gene have an expectation of offspring only one per cent. greater than those bearing its allelomorph, the selective advantage in question will be a very minute one; at least in the sense that it would require an enormous number of experimental animals, and extremely precise methods of experimentation, to demonstrate so small an effect experimentally. Such a selective advantage would, however, greatly modify the genetic constitution of the species, not in 100,000 but in

100 generations. If, moreover, we imagine these two agencies opposed in their tendencies, so that a mutation which persistently occurs in one in 100,000 individuals, is persistently opposed by a selective advantage of only one per cent., it will easily be seen that an equilibrium will be arrived at when only about one individual in 1,000 of the population will be affected by the mutation. This equilibrium, moreover, will be stable; for if we imagine that by some chance the number of mutants is raised to a higher proportion than this, the proportion will immediately commence to diminish under the action of selection, and evolution will proceed in the direction contrary to the mutation which is occurring, until the proportion of mutant individuals again reaches its equilibrium value. For mutations to dominate the trend of evolution it is thus necessary to postulate mutation rates immensely greater than those which are known to occur, and of an order of magnitude which, in general, would be incompatible with particulate inheritance.

Summary

The tacit assumption of the blending theory of inheritance led Darwin, by a perfectly cogent argument, into a series of speculations, respecting the causes of variations, and the possible evolutionary effects of these causes. In particular the blending theory, by the enormous mutation rates which it requires, led Darwin and others to attach evolutionary importance to hypothetical agencies which control the production of mutations. A mechanism (Mendelism) of particulate inheritance has since been discovered, requiring mutations to an extent less by many thousandfold. The 'pure line' experiments seem to exclude blending inheritance even as a subordinate possibility. The nature of the mutations observed is not compatible with the view that evolution is directed by their means, while their observed frequency of occurrence shows that an agency controlling mutations would be totally ineffectual in governing the direction of evolutionary change.

The whole group of theories which ascribe to hypothetical physiological mechanisms, controlling the occurrence of mutations, a power of directing the course of evolution, must be set aside, once the blending theory of inheritance is abandoned. The sole surviving theory is that of Natural Selection, and it would appear impossible to avoid the conclusion that if any evolutionary phenomenon

appears to be inexplicable on this theory, it must be accepted at present merely as one of the facts which in the present state of knowledge seems inexplicable. The investigator who faces this fact, as an unavoidable inference from what is now known of the nature of inheritance, will direct his inquiries confidently towards a study of the selective agencies at work throughout the life history of the group in their native habitats, rather than to speculations on the possible causes which influence their mutations. The experimental study of agencies capable of influencing mutation rates is of the highest interest for the light which it may throw on the nature of these changes. We should altogether misinterpret the value of such researches were we to regard them as revealing the causes of evolutionary modification.