V

HEREDITY AND VARIATION IN MODERN LIGHTS

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Darwin's work has the property of greatness in that it may be admired from more aspects than one. For some the perception of the principle of Natural Selection stands out as his most wonderful achievement to which all the rest is subordinate. Others, among whom I would range myself, look up to him rather as the first who plainly distinguished, collected, and comprehensively studied that new class of evidence from which hereafter a true understanding of the process of Evolution may be developed. We each prefer our own standpoint of admiration; but I think that it will be in their wider aspect that his labours will most command the veneration of posterity.

A treatise written to advance knowledge may be read in two moods. The reader may keep his mind passive, willing merely to receive the impress of the writer's thought; or he may read with his attention strained and alert, asking at every instant how the new knowledge can be used in a further advance, watching continually for fresh footholds by which to climb higher still. Of Shelley it has been said that he was a poet for poets: so Darwin was a naturalist for naturalists. It is when his writings are used in the critical and more exacting spirit with which we test the outfit for our own enterprise that we learn their full value and strength. Whether we glance back and compare his performance with the efforts of his predecessors, or look forward along the course which modern research is disclosing, we shall honour most in him not the rounded merit of finite accomplishment, but the creative power by which he inaugurated a line of discovery endless in variety and extension. Let us attempt thus to see his work in true perspective between the past from which it grew, and the present which is its consequence. Darwin attacked the problem of Evolution by reference to facts of three classes: Varia-

tion; Heredity; Natural Selection. His work was not as the laity suppose, a sudden and unheralded revelation, but the first fruit of a long and hitherto barren controversy. The occurrence of variation from type, and the hereditary transmission of such variation had of course been long familiar to practical men, and inferences as to the possible bearing of those phenomena on the nature of specific difference had been from time to time drawn by naturalists. Maupertuis, for example, wrote: "Ce qui nous reste à examiner, c'est comment d'un seul individu, il a pu naître tant d'espèces si différentes." And again: "La Nature contient le fonds de toutes ces variétés: mais le hasard ou l'art les mettent en œuvre. C'est ainsi que ceux dont l'industrie s'applique à satisfaire le goût des curieux, sont, pour ainsi dire, créateurs d'espèces nouvelles[1]."

Such passages, of which many (though few so emphatic) can be found in eighteenth century writers, indicate a true perception of the mode of Evolution. The speculations hinted at by Buffon[2], developed by Erasmus Darwin, and independently proclaimed above all by Lamarck, gave to the doctrine of descent a wide renown. The uniformitarian teaching which Lyell deduced from geological observation had gained acceptance. The facts of geographical distribution[3] had been shown to be obviously inconsistent with the Mosaic legend. Prichard, and Lawrence, following the example of Blumenbach, had successfully demonstrated that the races of Man could be regarded as different forms of one species, contrary to the opinion up till then received. These treatises all begin, it is true, with a profound obeisance to the sons of Noah, but that performed, they continue on strictly modern lines. The question of the mutability of species was thus prominently raised.

Those who rate Lamarck no higher than did Huxley in his contemptuous phrase "*buccinator tantum*," will scarcely deny that the sound of the trumpet had carried far, or that its note was clear. If then there were few who had already turned to evolution with positive conviction, all scientific men must at least have known that

[1] *Vénus Physique, contenant deux Dissertations, l'une sur l'origine des Hommes et des Animaux: Et l'autre sur l'origine des Noirs*, La Haye, 1746, pp. 124 and 129. For an introduction to the writings of Maupertuis I am indebted to an article by Professor Lovejoy in *Popular Sci. Monthly*, 1902.

[2] For the fullest account of the views of these pioneers of Evolution, see the works of Samuel Butler, especially *Evolution, Old and New* (2nd edit.) 1882. Butler's claims on behalf of Buffon have met with some acceptance; but after reading what Butler has said, and a considerable part of Buffon's own works, the word "hinted" seems to me a sufficiently correct description of the part he played. It is interesting to note that in the chapter on the Ass, which contains some of his evolutionary passages, there is a reference to "*plusieurs idées très-élevées sur la génération*" contained in the Letters of Maupertuis.

[3] See especially W. Lawrence, *Lectures on Physiology*, London, 1823, pp. 213 f.

such views had been promulgated; and many must, as Huxley says, have taken up his own position of "critical expectancy[1]."

Why, then, was it, that Darwin succeeded where the rest had failed? The cause of that success was two-fold. First, and obviously, in the principle of Natural Selection he had a suggestion which would work. It might not go the whole way, but it was true as far as it went. Evolution could thus in great measure be fairly represented as a consequence of demonstrable processes. Darwin seldom endangers the mechanism he devised by putting on it strains much greater than it can bear. He at least was under no illusion as to the omnipotence of Selection; and he introduces none of the forced pleading which in recent years has threatened to discredit that principle.

For example, in the latest text of the *Origin*[2] we find him saying:

> "But as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.'"

[1] How the chapter contributed to the *Life and Letters of Charles Darwin*, II. p. 195. I do not clearly understand the sense in which Darwin wrote (Autobiography, *ibid.* I. p. 87): "It has sometimes been said that the success of the *Origin* proved 'that the subject was in the air,' or 'that men's minds were prepared for it.' I do not think that this is strictly true, for I occasionally sounded not a few naturalists, and never happened to come across a single one who seemed to doubt about the permanence of species." This experience may perhaps have been an accident due to Darwin's isolation. The literature of the period abounds with indications of "critical expectancy." A most interesting expression of that feeling is given in the charming account of the "Early Days of Darwinism" by Alfred Newton, *Macmillan's Magazine*, LVII. 1888, p. 241. He tells how in 1858 when spending a dreary summer in Iceland, he and his friend, the ornithologist John Wolley, in default of active occupation, spent their days in discussion. "Both of us taking a keen interest in Natural History, it was but reasonable that a question, which in those days was always coming up wherever two or more naturalists were gathered together, should be continually recurring. That question was, 'What is a species?' and connected therewith was the other question, 'How did a species begin?'...Now we were of course fairly well acquainted with what had been published on these subjects." He then enumerates some of these publications, mentioning among others T. Vernon Wollaston's *Variation of Species*—a work which has in my opinion never been adequately appreciated. He proceeds: "Of course we never arrived at anything like a solution of these problems, general or special, but we felt very strongly that a solution ought to be found, and that quickly, if the study of Botany and Zoology was to make any great advance." He then describes how on his return home he received the famous number of the *Linnean Journal* on a certain evening. "I sat up late that night to read it; and never shall I forget the impression it made upon me. Herein was contained a perfectly simple solution of all the difficulties which had been troubling me for months past....I went to bed satisfied that a solution had been found."

[2] *Origin*, 6th edit. (1882), p. 421.

But apart from the invention of this reasonable hypothesis, which may well, as Huxley estimated, "be the guide of biological and psychological speculation for the next three or four generations," Darwin made a more significant and imperishable contribution. Not for a few generations, but through all ages he should be remembered as the first who showed clearly that the problems of Heredity and Variation are soluble by observation, and laid down the course by which we must proceed to their solution[1]. The moment of inspiration did not come with the reading of Malthus, but with the opening of the "first note-book on Transmutation of Species[2]." Evolution is a process of Variation and Heredity. The older writers, though they had some vague idea that it must be so, did not study Variation and Heredity. Darwin did, and so begat not a theory, but a science.

The extent to which this is true, the scientific world is only beginning to realise. So little was the fact appreciated in Darwin's own time that the success of his writings was followed by an almost total cessation of work in that special field. Of the causes which led to this remarkable consequence I have spoken elsewhere. They proceeded from circumstances peculiar to the time; but whatever the causes there is no doubt that this statement of the result is historically exact, and those who make it their business to collect facts elucidating the physiology of Heredity and Variation are well aware that they will find little to reward their quest in the leading scientific Journals of the Darwinian epoch.

In those thirty years the original stock of evidence current and in circulation even underwent a process of attrition. As in the story of the Eastern sage who first wrote the collected learning of the universe for his sons in a thousand volumes, and by successive compression and burning reduced them to one, and from this by further burning distilled the single ejaculation of the Faith, "There is no god but God and Mohamed is the Prophet of God," which was all his maturer wisdom deemed essential:—so in the books of that period do we find the *corpus* of genetic knowledge dwindle to a few prerogative instances, and these at last to the brief formula of an unquestioned creed.

[1] Whatever be our estimate of the importance of Natural Selection, in this we all agree. Samuel Butler, the most brilliant, and by far the most interesting of Darwin's opponents—whose works are at length emerging from oblivion—in his Preface (1882) to the 2nd edition of *Evolution, Old and New*, repeats his earlier expression of homage to one whom he had come to regard as an enemy: "To the end of time, if the question be asked, 'Who taught people to believe in Evolution?' the answer must be that it was Mr. Darwin. This is true, and it is hard to see what palm of higher praise can be awarded to any philosopher."

[2] *Life and Letters*, I. pp. 276 and 83.

And yet in all else that concerns biological science this period was, in very truth, our Golden Age, when the natural history of the earth was explored as never before; morphology and embryology were exhaustively ransacked; the physiology of plants and animals began to rival chemistry and physics in precision of method and in the rapidity of its advances; and the foundations of pathology were laid.

In contrast with this immense activity elsewhere the neglect which befel the special physiology of Descent, or Genetics as we now call it, is astonishing. This may of course be interpreted as meaning that the favoured studies seemed to promise a quicker return for effort, but it would be more true to say that those who chose these other pursuits did so without making any such comparison; for the idea that the physiology of Heredity and Variation was a coherent science, offering possibilities of extraordinary discovery, was not present to their minds at all. In a word, the existence of such a science was well nigh forgotten. It is true that in ancillary periodicals, as for example those that treat of entomology or horticulture, or in the writings of the already isolated systematists[1], observations with this special bearing were from time to time related, but the class of fact on which Darwin built his conceptions of Heredity and Variation was not seen in the highways of biology. It formed no part of the official curriculum of biological students, and found no place among the subjects which their teachers were investigating.

During this period nevertheless one distinct advance was made, that with which Weismann's name is prominently connected. In Darwin's genetic scheme the hereditary transmission of parental experience and its consequences played a considerable role. Exactly how great that role was supposed to be, he with his habitual caution refrained from specifying, for the sufficient reason that he did not know. Nevertheless much of the process of Evolution, especially that by which organs have become degenerate and rudimentary, was certainly attributed by Darwin to such inheritance, though since belief in the inheritance of acquired characters fell into disrepute, the fact has been a good deal overlooked. The *Origin* without "use

[1] This isolation of the systematists is the one most melancholy sequela of Darwinism. It seems an irony that we should read in the peroration to the *Origin* that when the Darwinian view is accepted "Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be a true species. This, I feel sure, and I speak after experience, will be no slight relief. The endless disputes whether or not some fifty species of British brambles are good species will cease." *Origin*, 6th edit. (1882), p. 425. True they have ceased to attract the attention of those who lead opinion, but anyone who will turn to the literature of systematics will find that they have not ceased in any other sense. Should there not be something disquieting in the fact that among the workers who come most into contact with specific differences, are to be found the only men who have failed to be persuaded of the unreality of those differences?

and disuse" would be a materially different book. A certain vacillation is discernible in Darwin's utterances on this question, and the fact gave to the astute Butler an opportunity for his most telling attack. The discussion which best illustrates the genetic views of the period arose in regard to the production of the rudimentary condition of the wings of many beetles in the Madeira group of islands, and by comparing passages from the *Origin*[1] Butler convicts Darwin of saying first that this condition was in the main the result of Selection, with disuse aiding, and in another place that the main cause of degeneration was disuse, but that Selection had aided. To Darwin however I think the point would have seemed one of dialectics merely. To him the one paramount purpose was to show that somehow an Evolution by means of Variation and Heredity might have brought about the facts observed, and whether they had come to pass in the one way or the other was a matter of subordinate concern.

To us moderns the question at issue has a diminished significance. For over all such debates a change has been brought by Weismann's challenge for evidence that use and disuse have any transmitted effects at all. Hitherto the transmission of many acquired characteristics had seemed to most naturalists so obvious as not to call for demonstration[2]. Weismann's demand for facts in support of the main proposition revealed at once that none having real cogency could be produced. The time-honoured examples were easily shown to be capable of different explanations. A few certainly remain which cannot be so summarily dismissed, but—though it is manifestly impossible here to do justice to such a subject—I think no one will dispute that these residual and doubtful phenomena, whatever be their true nature, are not of a kind to help us much in the interpretation of any of those complex cases of adaptation which on the hypothesis of unguided Natural Selection are especially difficult to understand. Use and disuse were invoked expressly to help us over these hard places; but whatever changes can be induced in offspring by direct treatment of the parents, they are not of a kind to encourage hope of real assistance from that quarter. It is not to be denied that through the collapse of this second line of argument the Selection hypothesis has had to take an increased and perilous burden. Various ways of meeting the difficulty have been proposed,

[1] 6th edit. pp. 109 and 401. See Butler, *Essays on Life, Art, and Science*, p. 265, reprinted 1908, and *Evolution, Old and New*, chap. xxii. (2nd edit.), 1882.

[2] W. Lawrence was one of the few who consistently maintained the contrary opinion. Prichard, who previously had expressed himself in the same sense, does not, I believe, repeat these views in his later writings, and there are signs that he came to believe in the transmission of acquired habits. See Lawrence, *Lect. Physiol.* 1823, pp. 436—437, 447 Prichard, Edin. Inaug. Disp. 1808 [not seen by me], quoted *ibid.* and *Nat. Hist. Man*, 1843, pp. 34 f.

but these mostly resolve themselves into improbable attempts to expand or magnify the powers of Natural Selection.

Weismann's interpellation, though negative in purpose, has had a lasting and beneficial effect, for through his thorough demolition of the old loose and distracting notions of inherited experience, the ground has been cleared for the construction of a true knowledge of heredity based on experimental fact.

In another way he made a contribution of a more positive character, for his elaborate speculations as to the genetic meaning of cytological appearances have led to a minute investigation of the visible phenomena occurring in those cell-divisions by which germ-cells arise. Though the particular views he advocated have very largely proved incompatible with the observed facts of heredity, yet we must acknowledge that it was chiefly through the stimulus of Weismann's ideas that those advances in cytology were made; and though the doctrine of the continuity of germ-plasm cannot be maintained in the form originally propounded, it is in the main true and illuminating[1]. Nevertheless in the present state of knowledge we are still as a rule quite unable to connect cytological appearances with any genetic consequence and save in one respect (obviously of extreme importance—to be spoken of later) the two sets of phenomena might, for all we can see, be entirely distinct.

I cannot avoid attaching importance to this want of connection between the nuclear phenomena and the features of bodily organisation. All attempts to investigate Heredity by cytological means lie under the disadvantage that it is the nuclear changes which can alone be effectively observed. Important as they must surely be, I have never been persuaded that the rest of the cell counts for nothing. What we know of the behaviour and variability of chromosomes seems in my opinion quite incompatible with the belief that they alone govern form, and are the sole agents responsible in heredity[2].

[1] It is interesting to see how nearly Butler was led by natural penetration, and from absolutely opposite conclusions, back to this underlying truth: "So that each ovum when impregnate should be considered not as descended from its ancestors, but as being a continuation of the personality of every ovum in the chain of its ancestry, which every ovum *it actually is* quite as truly as the octogenarian *is* the same identity with the ovum from which he has been developed. This process cannot stop short of the primordial cell, which again will probably turn out to be but a brief resting-place. We therefore prove each one of us to *be actually* the primordial cell which never died nor dies, but has differentiated itself into the life of the world, all living beings whatever, being one with it and members one of another," *Life and Habit*, 1878, p. 86.

[2] This view is no doubt contrary to the received opinion. I am however interested to see it lately maintained by Driesch (*Science and Philosophy of the Organism*, London, 1907, p. 233), and from the recent observations of Godlewski it has received distinct experimental support.

If, then, progress was to be made in Genetics, work of a different kind was required. To learn the laws of Heredity and Variation there is no other way than that which Darwin himself followed, the direct examination of the phenomena. A beginning could be made by collecting fortuitous observations of this class, which have often thrown a suggestive light, but such evidence can be at best but superficial and some more penetrating instrument of research is required. This can only be provided by actual experiments in breeding.

The truth of these general considerations was becoming gradually clear to many of us when in 1900 Mendel's work was rediscovered. Segregation, a phenomenon of the utmost novelty, was thus revealed. From that moment not only in the problem of the origin of species, but in all the great problems of biology a new era began. So unexpected was the discovery that many naturalists were convinced it was untrue, and at once proclaimed Mendel's conclusions as either altogether mistaken, or if true, of very limited application. Many fantastic notions about the workings of Heredity had been asserted as general principles before: this was probably only another fancy of the same class.

Nevertheless those who had a preliminary acquaintance with the facts of Variation were not wholly unprepared for some such revelation. The essential deduction from the discovery of segregation was that the characters of living things are dependent on the presence of definite elements or factors, which are treated as units in the processes of Heredity. These factors can thus be recombined in various ways. They act sometimes separately, and sometimes they interact in conjunction with each other, producing their various effects. All this indicates a definiteness and specific order in heredity, and therefore in variation. This order cannot by the nature of the case be dependent on Natural Selection for its existence, but must be a consequence of the fundamental chemical and physical nature of living things. The study of Variation had from the first shown that an orderliness of this kind was present. The bodies and the properties of living things are cosmic, not chaotic. No matter how low in the scale we go, never do we find the slightest hint of a diminution in that all-pervading orderliness, nor can we conceive an organism existing for a moment in any other state. Moreover not only does this order prevail in normal forms, but again and again it is to be seen in newly-sprung varieties, which by general consent cannot have been subjected to a prolonged Selection. The discovery of Mendelian elements admirably coincided with and at once gave a rationale of these facts. Genetic Variation is then primarily the consequence of additions to, or omissions from, the stock of elements which the

species contains. The further investigation of the species-problem must thus proceed by the analytical method which breeding experiments provide.

In the nine years which have elapsed since Mendel's clue became generally known, progress has been rapid. We now understand the process by which a polymorphic race maintains its polymorphism. When a family consists of dissimilar members, given the numerical proportions in which these members are occurring, we can represent their composition symbolically and state what types can be transmitted by the various members. The difficulty of the "swamping effects of intercrossing" is practically at an end. Even the famous puzzle of sex-limited inheritance is solved, at all events in its more regular manifestations, and we know now how it is brought about that the normal sisters of a colour-blind man can transmit the colour-blindness while his normal brothers cannot transmit it.

We are still only on the fringe of the inquiry. It can be seen extending and ramifying in many directions. To enumerate these here would be impossible. A whole new range of possibilities is being brought into view by study of the interrelations between the simple factors. By following up the evidence as to segregation, indications have been obtained which can only be interpreted as meaning that when many factors are being simultaneously redistributed among the germ-cells, certain of them exert what must be described as a repulsion upon other factors. We cannot surmise whither this discovery may lead.

In the new light all the old problems wear a fresh aspect. Upon the question of the nature of Sex, for example, the bearing of Mendelian evidence is close. Elsewhere I have shown that from several sets of parallel experiments the conclusion is almost forced upon us that, in the types investigated, of the two sexes the female is to be regarded as heterozygous in sex, containing one unpaired dominant element, while the male is similarly homozygous in the absence of that element[1]. It is not a little remarkable that on this point—which is the only one where observations of the nuclear processes of gameto-genesis have yet been brought into relation with the visible characteristics of the organisms themselves—there should be diametrical opposition between the results of breeding experiments and those derived from cytology.

Those who have followed the researches of the American school will be aware that, after it had been found in certain insects that the spermatozoa were of two kinds according as they contained or did not contain the accessory chromosome, E. B. Wilson succeeded in

[1] In other words, the ova are each *either* female, *or* male (i.e. non-female), but the sperms are all non-female.

proving that the sperms possessing this accessory body were destined to form *females* on fertilisation, while sperms without it form males, the eggs being apparently indifferent. Perhaps the most striking of all this series of observations is that lately made by T. H. Morgan[1], since confirmed by von Baehr, that in a Phylloxeran two kinds of spermatids are formed, respectively with and without an accessory (in this case, *double*) chromosome. Of these, only those possessing the accessory body become functional spermatozoa, the others degenerating. We have thus an elucidation of the puzzling fact that in these forms fertilisation results in the formation of *females* only. How the males are formed—for of course males are eventually produced by the parthenogenetic females—we do not know.

If the accessory body is really to be regarded as bearing the factor for femaleness, then in Mendelian terms female is DD and male is DR. The eggs are indifferent and the spermatozoa are each male, *or* female. But according to the evidence derived from a study of the sex-limited descent of certain features in other animals the conclusion seems equally clear that in them female must be regarded as DR and male as RR. The eggs are thus each either male or female and the spermatozoa are indifferent. How this contradictory evidence is to be reconciled we do not yet know. The breeding work concerns fowls, canaries, and the Currant moth (*Abraxas grossulariata*). The accessory chromosome has been now observed in most of the great divisions of insects[2], except, as it happens, Lepidoptera. At first sight it seems difficult to suppose that a feature apparently so fundamental as sex should be differently constituted in different animals, but that seems at present the least improbable inference. I mention these two groups of facts as illustrating the nature and methods of modern genetic work. We must proceed by minute and specific analytical investigation. Wherever we look we find traces of the operation of precise and specific rules.

In the light of present knowledge it is evident that before we can attack the Species-problem with any hope of success there are vast arrears to be made up. He would be a bold man who would now assert that there was no sense in which the term Species might not have a strict and concrete meaning in contradistinction to the term Variety. We have been taught to regard the difference between species and variety as one of degree. I think it unlikely that this

[1] Morgan, *Proc. Soc. Exp. Biol. Med.* v. 1908, and von Baehr, *Zool. Anz.* XXXII. p. 507, 1908.

[2] As Wilson has proved, the unpaired body is not a universal feature even in those orders in which it has been observed. Nearly allied types may differ. In some it is altogether unpaired. In others it is paired with a body of much smaller size, and by selection of various types all gradations can be demonstrated ranging to the condition in which the members of the pair are indistinguishable from each other.

conclusion will bear the test of further research. To Darwin the question, What is a variation? presented no difficulties. Any difference between parent and offspring was a variation. Now we have to be more precise. First we must, as de Vries has shown, distinguish real, genetic, variation from *fluctuational* variations, due to environmental and other accidents, which cannot be transmitted. Having excluded these sources of error the variations observed must be expressed in terms of the factors to which they are due before their significance can be understood. For example, numbers of the variations seen under domestication, and not a few witnessed in nature, are simply the consequence of some ingredient being in an unknown way omitted from the composition of the varying individual. The variation may on the contrary be due to the addition of some new element, but to prove that it is so is by no means an easy matter. Casual observation is useless, for though these latter variations will always be dominants, yet many dominant characteristics may arise from another cause, namely the meeting of complementary factors, and special study of each case in two generations at least is needed before these two phenomena can be distinguished.

When such considerations are fully appreciated it will be realised that medleys of most dissimilar occurrences are all confused together under the term Variation. One of the first objects of genetic analysis is to disentangle this mass of confusion.

To those who have made no study of heredity it sometimes appears that the question of the effect of conditions in causing variation is one which we should immediately investigate, but a little thought will show that before any critical inquiry into such possibilities can be attempted, a knowledge of the working of heredity under conditions as far as possible uniform must be obtained. At the time when Darwin was writing, if a plant brought into cultivation gave off an albino variety, such an event was without hesitation ascribed to the change of life. Now we see that albino *gametes*, germs, that is to say, which are destitute of the pigment-forming factor, may have been originally produced by individuals standing an indefinite number of generations back in the ancestry of the actual albino, and it is indeed almost certain that the variation to which the appearance of the albino is due cannot have taken place in a generation later than that of the grandparents. It is true that when a new *dominant* appears we should feel greater confidence that we were witnessing the original variation, but such events are of extreme rarity, and no such case has come under the notice of an experimenter in modern times, as far as I am aware. That they must have appeared is clear enough. Nothing corresponding to the Brown-breasted Game fowl is known wild, yet that colour is a most definite

dominant, and at some moment since *Gallus bankiva* was domesticated, the element on which that special colour depends must have at least once been formed in the germ-cell of a fowl; but we need harder evidence than any which has yet been produced before we can declare that this novelty came through over-feeding, or change of climate, or any other disturbance consequent on domestication. When we reflect on the intricacies of genetic problems as we must now conceive them there come moments when we feel almost thankful that the Mendelian principles were unknown to Darwin. The time called for a bold pronouncement, and he made it, to our lasting profit and delight. With fuller knowledge we pass once more into a period of cautious expectation and reserve.

In every arduous enterprise it is pleasanter to look back at difficulties overcome than forward to those which still seem insurmountable, but in the next stage there is nothing to be gained by disguising the fact that the attributes of living things are not what we used to suppose. If they are more complex in the sense that the properties they display are throughout so regular[1] that the Selection of minute random variations is an unacceptable account of the origin of their diversity, yet by virtue of that very regularity the problem is limited in scope and thus simplified.

To begin with, we must relegate Selection to its proper place. Selection permits the viable to continue and decides that the non-viable shall perish; just as the temperature of our atmosphere decides that no liquid carbon shall be found on the face of the earth: but we do not suppose that the form of the diamond has been gradually achieved by a process of Selection. So again, as the course of descent branches in the successive generations, Selection determines along which branch Evolution shall proceed, but it does not decide what novelties that branch shall bring forth. "*La Nature contient le fonds de toutes ces variétés, mais le hazard ou l'art les mettent en œuvre,*" as Maupertuis most truly said.

Not till knowledge of the genetic properties of organisms has attained to far greater completeness can evolutionary speculations have more than a suggestive value. By genetic experiment, cytology and physiological chemistry aiding, we may hope to acquire such knowledge. In 1872 Nathusius wrote[2]: "Das Gesetz der Vererbung ist noch nicht erkannt; der Apfel ist noch nicht vom Baum der Erkenntniss gefallen, welcher, der Sage nach, Newton auf den

[1] I have in view, for example, the marvellous and specific phenomena of regeneration, and those discovered by the students of "*Entwicklungsmechanik.*" The circumstances of its occurrence here preclude any suggestion that this regularity has been brought about by the workings of Selection. The attempts thus to represent the phenomena have resulted in mere parodies of scientific reasoning.

[2] *Vorträge über Viehzucht und Rassenerkenntniss*, p. 120, Berlin, 1872.

rechten Weg zur Ergründung der Gravitationsgesetze führte." We cannot pretend that the words are not still true, but in Mendelian analysis the seeds of that apple-tree at last are sown.

If we were asked what discovery would do most to forward our inquiry, what one bit of knowledge would more than any other illuminate the problem, I think we may give the answer without hesitation. The greatest advance that we can foresee will be made when it is found possible to connect the geometrical phenomena of development with the chemical. The geometrical symmetry of living things is the key to a knowledge of their regularity, and the forces which cause it. In the symmetry of the dividing cell the basis of that resemblance we call Heredity is contained. To imitate the morphological phenomena of life we have to devise a system which can divide. It must be able to divide, and to segment as—grossly—a vibrating plate or rod does, or as an icicle can do as it becomes ribbed in a continuous stream of water; but with this distinction, that the distribution of chemical differences and properties must simultaneously be decided and disposed in orderly relation to the pattern of the segmentation. Even if a model which would do this could be constructed it might prove to be a useful beginning.

This may be looking too far ahead. If we had to choose some one piece of more proximate knowledge which we would more especially like to acquire, I suppose we should ask for the secret of interracial sterility. Nothing has yet been discovered to remove the grave difficulty, by which Huxley in particular was so much oppressed, that among the many varieties produced under domestication—which we all regard as analogous to the species seen in nature—no clear case of interracial sterility has been demonstrated. The phenomenon is probably the only one to which the domesticated products seem to afford no parallel. No solution of the difficulty can be offered which has positive value, but it is perhaps worth considering the facts in the light of modern ideas. It should be observed that we are not discussing incompatibility of two species to produce offspring (a totally distinct phenomenon), but the sterility of the offspring which many of them do produce.

When two species, both perfectly fertile severally, produce on crossing a sterile progeny, there is a presumption that the sterility is due to the development in the hybrid of some substance which can only be formed by the meeting of two complementary factors. That some such account is correct in essence may be inferred from the well-known observation that if the hybrid is not totally sterile but only partially so, and thus is able to form some good germ-cells which develop into new individuals, the sterility of these daughter-individuals is sensibly reduced or may be entirely absent. The

fertility once re-established, the sterility does not return in the later progeny, a fact strongly suggestive of segregation. Now if the sterility of the cross-bred be really the consequence of the meeting of two complementary factors, we see that the phenomenon could only be produced among the divergent offspring of one species by the acquisition of at least *two* new factors; for if the acquisition of a single factor caused sterility the line would then end. Moreover each factor must be separately acquired by distinct individuals, for if both were present together, the possessors would by hypothesis be sterile. And in order to imitate the case of species each of these factors must be acquired by distinct breeds. The factors need not, and probably would not, produce any other perceptible effects; they might, like the colour-factors present in white flowers, make no difference in the form or other characters. Not till the cross was actually made between the two complementary individuals would either factor come into play, and the effects even then might be unobserved until an attempt was made to breed from the cross-bred.

Next, if the factors responsible for sterility were acquired, they would in all probability be peculiar to certain individuals and would not readily be distributed to the whole breed. Any member of the breed also into which *both* the factors were introduced would drop out of the pedigree by virtue of its sterility. Hence the evidence that the various domesticated breeds say of dogs or fowls can when mated together produce fertile offspring, is beside the mark. The real question is, Do they ever produce sterile offspring? I think the evidence is clearly that sometimes they do, oftener perhaps than is commonly supposed. These suggestions are quite amenable to experimental tests. The most obvious way to begin is to get a pair of parents which are known to have had any sterile offspring, and to find the proportions in which these steriles were produced. If, as I anticipate, these proportions are found to be definite, the rest is simple.

In passing, certain other considerations may be referred to. First, that there are observations favouring the view that the production of totally sterile cross-breds is seldom a universal property of two species, and that it may be a matter of individuals, which is just what on the view here proposed would be expected. Moreover, as we all know now, though incompatibility may be dependent to some extent on the degree to which the species are dissimilar, no such principle can be demonstrated to determine sterility or fertility in general. For example, though all our Finches can breed together, the hybrids are all sterile. Of Ducks some species can breed together without producing the slightest sterility; others have totally sterile offspring, and so on. The hybrids between several *genera* of Orchids are perfectly

fertile on the female side, and some on the male side also, but the hybrids produced between the Turnip (*Brassica napus*) and the Swede (*Brassica campestris*), which, according to our estimates of affinity, should be nearly allied forms, are totally sterile[1]. Lastly, it may be recalled that in sterility we are almost certainly considering a meristic phenomenon. *Failure to divide* is, we may feel fairly sure, the immediate "cause" of the sterility. Now, though we know very little about the heredity of meristic differences, all that we do know points to the conclusion that the less-divided is dominant to the more-divided, and we are thus justified in supposing that there are factors which can arrest or prevent cell-division. My conjecture therefore is that in the case of sterility of cross-breds we see the effect produced by a complementary pair of such factors. This and many similar problems are now open to our analysis.

The question is sometimes asked, Do the new lights on Variation and Heredity make the process of Evolution easier to understand? On the whole the answer may be given that they do. There is some appearance of loss of simplicity, but the gain is real. As was said above, the time is not ripe for the discussion of the origin of species. With faith in Evolution unshaken—if indeed the word faith can be used in application to that which is certain—we look on the manner and causation of adapted differentiation as still wholly mysterious. 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'"[2], and of that Origin not one of us knows anything. But given Variation—and it is given: assuming further that the variations are not guided into paths of adaptation—and both to the Darwinian and to the modern school this hypothesis appears to be sound if unproven—an evolution of species proceeding by definite steps is more, rather than less, easy to imagine than an evolution proceeding by the accumulation of indefinite and insensible steps. Those who have lost themselves in contemplating the miracles of Adaptation (whether real or spurious) have not unnaturally fixed their hopes rather on the indefinite than on the definite changes. The reasons are obvious. By suggesting that the steps through which an adaptative mechanism arose were indefinite and insensible, all further trouble is spared. While it could be said that species arise by an insensible and imperceptible process of variation, there was clearly no use in tiring ourselves by trying to perceive that process. This labour-saving counsel found great favour. All that had to be done to develop evolution-theory was to discover the good in everything, a task which, in the complete absence of any control or test whereby to check the truth of the

[1] See Sutton, A. W., *Journ. Linn. Soc.* XXXVIII. p. 341, 1908.

[2] *Life and Habit*, London, p. 263, 1878.

discovery, is not very onerous. The doctrine "*que tout est au mieux*" was therefore preached with fresh vigour, and examples of that illuminating principle were discovered with a facility that Pangloss himself might have envied, till at last even the spectators wearied of such dazzling performances.

But in all seriousness, why should indefinite and unlimited variation have been regarded as a more probable account of the origin of Adaptation? Only, I think, because the obstacle was shifted one plane back, and so looked rather less prominent. The abundance of Adaptation, we all grant, is an immense, almost an unsurpassable difficulty in all non-Lamarckian views of Evolution; but if the steps by which that adaptation arose were fortuitous, to imagine them insensible is assuredly no help. In one most important respect indeed, as has often been observed, it is a multiplication of troubles. For the smaller the steps, the less could Natural Selection act upon them. Definite variations—and of the occurrence of definite variations in abundance we have now the most convincing proof—have at least the obvious merit that they can make and often do make a real difference in the chances of life.

There is another aspect of the Adaptation problem to which I can only allude very briefly. May not our present ideas of the universality and precision of Adaptation be greatly exaggerated? The fit of organism to its environment is not after all so very close—a proposition unwelcome perhaps, but one which could be illustrated by very copious evidence. Natural Selection is stern, but she has her tolerant moods.

We have now most certain and irrefragable proof that much definiteness exists in living things apart from Selection, and also much that may very well have been preserved and so in a sense constituted by Selection. Here the matter is likely to rest. There is a passage in the sixth edition of the *Origin* which has I think been overlooked. On page 70 Darwin says "The tuft of hair on the breast of the wild turkey-cock cannot be of any use, and it is doubtful whether it can be ornamental in the eyes of the female bird." This tuft of hair is a most definite and unusual structure, and I am afraid that the remark that it "cannot be of any use" may have been made inadvertently; but it may have been intended, for in the first edition the usual qualification was given and must therefore have been deliberately excised. Anyhow I should like to think that Darwin did throw over that tuft of hair, and that he felt relief when he had done so. Whether however we have his great authority for such a course or not, I feel quite sure that we shall be rightly interpreting the facts of nature if we cease to expect to find purposefulness wherever we meet with definite structures or patterns. Such things are, as often

as not, I suspect rather of the nature of tool-marks, mere incidents of manufacture, benefiting their possessor not more than the wire-marks in a sheet of paper, or the ribbing on the bottom of an oriental plate renders those objects more attractive in our eyes.

If Variation may be in any way definite, the question once more arises, may it not be definite in direction? The belief that it is has had many supporters, from Lamarck onwards, who held that it was guided by need, and others who, like Nägeli, while laying no emphasis on need, yet were convinced that there was guidance of some kind. The latter view under the name of "Orthogenesis," devised I believe by Eimer, at the present day commends itself to some naturalists. The objection to such a suggestion is of course that no fragment of real evidence can be produced in its support. On the other hand, with the experimental proof that variation consists largely in the unpacking and repacking of an original complexity, it is not so certain as we might like to think that the order of these events is not pre-determined. For instance the original "pack" may have been made in such a way that at the nth division of the germ-cells of a Sweet Pea a colour-factor might be dropped, and that at the $n+n'$ division the hooded variety be given off, and so on. I see no ground whatever for holding such a view, but in fairness the possibility should not be forgotten, and in the light of modern research it scarcely looks so absurdly improbable as before.

No one can survey the work of recent years without perceiving that evolutionary orthodoxy developed too fast, and that a great deal has got to come down; but this satisfaction at least remains, that in the experimental methods which Mendel inaugurated, we have means of reaching certainty in regard to the physiology of Heredity and Variation upon which a more lasting structure may be built.