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Title: Darwin, and After Darwin, Volume II (of 3)

Post-Darwinian Questions: Heredity and Utility

Author: George John Romanes

Release Date: October 15, 2011 [eBook #37759]

Language: English

Character set encoding: ISO-8859-1

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DARWIN, AND AFTER DARWIN

II

POST-DARWINIAN QUESTIONS

HEREDITY AND UTILITY

BY THE SAME AUTHOR.

DARWIN AND AFTER DARWIN. An Exposition of the Darwinian Theory and a Discussion of Post-Darwinian Questions.

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THE OPEN COURT PUBLISHING COMPANY,
324 DEARBORN STREET, CHICAGO.



DARWIN, AND AFTER DARWIN
AN EXPOSITION OF THE DARWINIAN THEORY
AND A DISCUSSION OF
POST-DARWINIAN QUESTIONS

BY THE LATE
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Honorary Fellow of Gonville and Caius College, Cambridge

II
POST-DARWINIAN QUESTIONS
HEREDITY AND UTILITY

FOURTH EDITION

Chicago London
THE OPEN COURT PUBLISHING COMPANY
1916

CHAPTER 1 COPYRIGHTED BY
THE OPEN COURT PUBLISHING CO.
CHICAGO, ILL., 1895

PRINTED IN THE
UNITED STATES OF AMERICA

PREFACE

[Pg v]

As its sub-title announces, the present volume is mainly devoted to a consideration of those Post-Darwinian Theories which involve fundamental questions of Heredity and Utility.

As regards Heredity, I have restricted the discussion almost exclusively to Professor Weismann's views, partly because he is at present by far the most important writer upon this subject, and partly because his views with regard to it raise with most distinctness the issue which lies at the base of all Post-Darwinian speculation touching this subject—the issue as to the inheritance or non-inheritance of acquired characters.

My examination of the Utility question may well seem to the general reader needlessly elaborate; for to such a reader it can scarcely fail to appear that the doctrine which I am assailing has been broken to fragments long before the criticism has drawn to a close. But from my previous experience of the hardness with which this fallacious doctrine dies, I do not deem it safe to allow even one fragment of it to remain, lest, hydra-like, it should re-develop into its former proportions. And I can scarcely think that naturalists who know the growing prevalence of the doctrine, and who may have followed the issues of previous discussions with regard to it, will accuse me of being more over-zealous in my attempt to make a full end thereof. [Pg vi]

One more remark. It is a misfortune attending the aim and scope of Part II that they bring me into frequent discord with one or other of the most eminent of Post-Darwinian writers—especially with Mr. Wallace. But such is the case only because the subject-matter of this volume is avowedly restricted to debateable topics, and because I choose those naturalists who are deservedly held in most esteem to act spokesmen on behalf of such Post-Darwinian views as appear to me doubtful or erroneous. Obviously, however, differences of opinion on particular points ought not to be taken as implying any failure on my part to recognize the general scientific authority of these men, or any inability to appreciate their labours in the varied fields of Biology.

G.
J. R.

CHRIST CHURCH, OXFORD.

NOTE

[Pg vii]

Some time before his death Mr. Romanes decided to publish those sections of his work which deal with Heredity and Utility, as a separate volume, leaving Isolation and Physiological Selection for the third and concluding part of *Darwin, and after Darwin*.

Most of the matter contained in this part was already in type, but was not finally corrected for the press. The alterations made therein are for the most part verbal.

Chapter IV was type-written; in it, too, no alterations of any moment have been made.

For Chapters V and VI there were notes and isolated paragraphs not yet arranged. I had promised during his life to write for Mr. Romanes Chapter V on the basis of these notes, extending it in such ways as seemed to be desirable. In that case it would have been revised and amended by the author and received his final sanction. Death annulled this friendly compact; and since, had I written the chapter myself, it could not receive that imprimatur which would have given its chief value, I have decided to arrange the material that passed into my hands without adding anything of importance thereto. The substance of Chapters V and VI is therefore entirely the author's: even the phraseology is his; the arrangement only is by another hand. [Pg viii]

Such parts of the Preface as more particularly refer to Isolation and Physiological Selection are reserved for publication in Part III. A year or more must elapse before that part will be ready for publication.

Mr. F. Howard Collins has, as a kindly tribute to the memory of the author, read through the proofs. Messrs. F. Darwin, F. Galton, H. Seebohm, and others, have rendered incidental assistance. After much search I am unable to give the references to one or two passages.

I have allowed a too flattering reference to myself to stand, in accordance with a particular injunction of Mr. Romanes given shortly before that sad day on which he died, leaving many to mourn the loss of a personal friend most bright, lovable, and generous-hearted, and thousands to regret that the hand which had written so much for them would write for them no more.

C. LL.
M.

UNIVERSITY COLLEGE, BRISTOL,

APRIL, 1894.

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CHAPTER I.

[Pg 1]

INTRODUCTORY: THE DARWINISM OF DARWIN, AND OF THE POST-DARWINIAN SCHOOLS.

It is desirable to open this volume of the treatise on *Darwin and after Darwin* by taking a brief survey of the general theory of descent, first, as this was held by Darwin himself, and next, as it is now held by the several divergent schools of thought which have arisen since Darwin's death.

The most important of the questions in debate is one which I have already had occasion to mention, while dealing, in historical order, with the objections that were brought against the theory of natural selection during the life-time of Darwin^[1]. Here, however, we must

consider it somewhat more in detail, and justify by quotation what was previously said regarding the very definite nature of his utterances upon the matter. This question is whether natural selection has been the sole, or but the main, cause of organic evolution.

Must we regard survival of the fittest as the one and only principle which has been concerned in the progressive modification of living forms, or are we to suppose that this great and leading principle has been assisted by other and subordinate principles, without the co-operation of which the results, as presented in the animal and vegetable kingdoms, could not have been effected? Now Darwin's answer to this question was distinct and unequivocal. He stoutly resisted the doctrine that natural selection was to be regarded as the only cause of organic evolution. On the other hand, this opinion was—and still continues to be—persistently maintained by Mr. Wallace; and it constitutes the source of all the differences between his views and those of Darwin. Moreover, up to the time of Darwin's death, Mr. Wallace was absolutely alone in maintaining this opinion: the whole body of scientific thought throughout the world being against him; for it was deemed improbable that, in the enormously complex and endlessly varied processes of organic evolution, only a single principle should be everywhere and exclusively concerned^[2]. But since Darwin's death there has been a great revolution of biological thought in favour of Mr. Wallace's opinion. And the reason for this revolution has been, that his doctrine of natural selection as the sole cause of organic evolution has received the corroborative support of Professor Weismann's theory of heredity—which has been more or less cordially embraced by a certain section of evolutionists, and which appears to carry the doctrine in question as a logical corollary, so far, at all events, as adaptive structures are concerned. [Pg 2]

Now in this opening chapter we shall have to do merely with a setting forth of Darwin's opinion: we are not considering how far that opinion ought to be regarded as having been in any measure displaced by the results of more recent progress. Such, then, being the only matter which here concerns us, I will supply a few brief quotations, to show how unequivocally Darwin has stated his views. First, we may take what he says upon the "Lamarckian factors^[3];" and next we may consider what he says with regard to other factors, or, in general, upon natural selection not being the sole cause of organic evolution. [Pg 3]

"Changed habits produce an inherited effect, as in the period of the flowering of plants when transported from one climate to another. With animals the increased use or disuse of parts has had a more marked influence^[4]."

"There can be no doubt, from the facts given in this chapter, that extremely slight changes in the conditions of life sometimes, probably often, act in a definite manner on our domesticated productions; and, as the action of changed conditions in causing indefinite variability is accumulative, so it may be with their definite action. Hence considerable and definite modifications of structure probably follow from altered conditions acting during long series of generations^[5]."

"How, again, can we explain the inherited effects of the use and disuse of particular organs? The domesticated duck flies less and walks more than the wild duck, and its limb bones have become diminished and increased in a corresponding manner in comparison with those of the wild duck. A horse is trained to certain paces, and the colt inherits similar consensual movements. The domesticated rabbit becomes tame from close confinement; the dog, intelligent from associating with man; the retriever is taught to fetch and carry; and these mental endowments and bodily powers are all inherited. Nothing in the whole circuit of physiology is more wonderful. How can the use or disuse of a particular limb or of the brain affect a small aggregate of reproductive [Pg 4]

cells, seated in a distant part of the body, in such a manner that the being developed from these cells inherits the characters of either one or both parents?... In the chapters devoted to inheritance, it was shown that a multitude of newly acquired characters, whether injurious or beneficial, whether of the lowest or highest vital importance, are often faithfully transmitted^[6]."

"When discussing special cases, Mr. Mivart passes over the effects of the increased use and disuse of parts, which I have always maintained to be highly important, and have treated in my 'Variation under Domestication' at greater length than, as I believe, any other writer^[7]."

So much for the matured opinion of Darwin touching the validity of the theory of use-inheritance. Turning now to his opinion on the question whether or not there are yet any further factors concerned in the process of organic evolution, I think it will be sufficient to quote a single passage from the *Origin of Species*. The first paragraph of the "Conclusion" is devoted to a *résumé* of his views upon this matter, and consists of the following most emphatic words.

"I have now recapitulated the facts and considerations which have thoroughly convinced me that species have been modified, during a long course of descent. This has been effected chiefly through the natural selection of numerous successive, slight, favourable variations; aided in an important manner by the inherited effects of the use and disuse of parts; and in an unimportant manner, that is in relation to adaptive structures, whether past or present, by the direct action of external conditions, and by variations which seem to us in our ignorance to arise spontaneously. It appears that I formerly underrated the frequency and value of these latter forms of variation, as leading to permanent modifications of structure independently of natural selection. 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.' This has been of no avail. Great is the power of steady misrepresentation; but the history of science shows that fortunately this power does not long endure."

[Pg 5]

In the whole range of Darwin's writings there cannot be found a passage so strongly worded as this: it presents the only note of bitterness in all the thousands of pages which he has published. Therefore I do not think it is necessary to supply any further quotations for the purpose of proving the state of his opinion upon the point in question. But, be it carefully noted, from this great or radical difference of opinion between the joint originators of the theory of natural selection, all their other differences of opinion arise; and seeing that since the death of Darwin a large number of naturalists have gone over to the side of Wallace, it seems desirable here to state categorically what these other or sequent points of difference are. Without at present discussing them, therefore, I will merely set them out in a tabular form, in order that a clear perception may be gained of their logical connexion with this primary point of difference.

[Pg 6]

<i>The Theory of Natural Selection according to Darwin.</i>	<i>The theory of Natural Selection according to Wallace.</i>
Natural Selection has been the main means of modification, not excepting the case of Man.	Natural Selection has been the sole means of modification, excepting in the case of Man.

(a) Therefore it is a question of evidence whether the Lamarckian factors have co-operated.	(a) Therefore it is antecedently impossible that the Lamarckian factors can have co-operated.
(b) Neither all species, nor, <i>a fortiori</i> , all specific characters, have been due to natural selection.	(b) Not only all species, but all specific characters, must necessarily have been due to natural selection.
(c) Thus the principle of Utility is not of universal application, even where species are concerned.	(c) Thus the principle of Utility must necessarily be of universal application, where species are concerned.
(d) Thus, also, the suggestion as to Sexual Selection, or any other supplementary cause of modification, may be entertained; and, as in the case of the Lamarckian factors, it is a question of evidence whether, or how far, they have co-operated.	(d) Thus, also, the suggestion as to Sexual Selection, or of any other supplementary cause of modification, must be ruled out; and, as in the case of the Lamarckian factors, their co-operation deemed impossible.
(e) No detriment arises to the theory of natural selection as a theory of the origin of species by entertaining the possibility, or the probability, of supplementary factors.	(e) The possibility—and, <i>a fortiori</i> the probability—of any supplementary factors cannot be entertained without serious detriment to the theory of natural selection, as a theory of the origin of species.
(f) Cross-sterility in species cannot possibly be due to natural selection.	(f) Cross-sterility in species is probably due to natural selection ^[8] .

As it will be my endeavour in the ensuing chapters to consider the rights and the wrongs of these antithetical propositions, I may reserve further quotations from Darwin's works, which will show that the above is a correct epitome of his views as contrasted with those of Wallace and the Neo-Darwinian school of Weismann. But here, where the object is merely a statement of Darwin's theory touching the points in which it differs from those of Wallace and Weismann, it will be sufficient to set forth these points of difference in another and somewhat fuller form. So far then as we are at present concerned, the following are the matters of doctrine which have been clearly, emphatically, repeatedly, and uniformly expressed throughout the whole range of Darwin's writings. [Pg 7]

1. That natural selection has been the main means of modification.
2. That, nevertheless, it has not been the only means; but has been supplemented or assisted by the co-operation of other causes.
3. That the most "important" of these other causes has been the inheritance of functionally-produced modifications (use-inheritance); but this only because the transmission of such modifications to progeny must always have had immediate reference to *adaptive* ends, as distinguished from merely useless change.
4. That there are sundry other causes which lead to merely useless change—in particular, "the direct action of external conditions, and variations which seem to us in our ignorance to arise spontaneously." [Pg 8]

5. Hence, that the "principle of utility," far from being of universal occurrence in the sphere of animate nature, is only of what may be termed highly general occurrence; and, therefore, that certain other advocates of the theory of natural selection were mistaken in representing the universality of this principle as following by way of necessary consequence from that theory.

6. Cross-sterility in species cannot possibly be due to natural selection; but everywhere arises as a result of some physiological change having exclusive reference to the sexual system—a change which is probably everywhere due to the same cause, although what this cause could be Darwin was confessedly unable to suggest.

Such, then, was the theory of evolution as held by Darwin, so far as the points at present before us are concerned. And, it may now be added, that the longer he lived, and the more he pondered these points, the less exclusive was the *rôle* which he assigned to natural selection, and the more importance did he attribute to the supplementary factors above named. This admits of being easily demonstrated by comparing successive editions of his works; a method adopted by Mr. Herbert Spencer in his essay on the *Factors of Organic Evolution*.

My object in thus clearly defining Darwin's attitude regarding these sundry points is twofold.

In the first place, with regard to merely historical accuracy, it appears to me undesirable that naturalists should endeavour to hide certain parts of Darwin's teaching, and give undue prominence to others. In the second place, it appears to me still more undesirable that this should be done—as it usually is done—for the purpose of making it appear that Darwin's teaching did not really differ very much from that of Wallace and Weismann on the important points in question. I myself believe that Darwin's judgement with regard to all these points will eventually prove more sound and accurate than that of any of the recent would-be improvers upon his system; but even apart from this opinion of my own it is undesirable that Darwin's views should be misrepresented, whether the misrepresentation be due to any unfavourable bias against one side of his teaching, or to sheer carelessness in the reading of his books. Yet the new school of evolutionists, to which allusion has now so frequently been made, speak of their own modifications of Darwin's teaching as "pure Darwinism," in contradistinction to what they call "Lamarckism." In other words, they represent the principles of "Darwinism" as standing in some kind of opposition to those of "Lamarckism": the Darwinian principle of natural selection, they think, is in itself enough to account for all the facts of adaptation in organic nature. Therefore they are eager to dispense with the Lamarckian principle of the inherited effects of use and disuse, together with the direct influence of external conditions of life, and all or any other causes of modification which either have been, or in the future may possibly be, suggested. Now, of course, there is no reason why any one should not hold these or any other opinions to which his own independent study of natural science may lead him; but it appears to me that there is the very strongest reason why any one who deviates from the carefully formed opinions of such a man as Darwin, should above all things be careful to be absolutely fair in his representations of them; he should be scrupulously jealous, so to speak, of not letting it appear that he is unjustifiably throwing over his own opinions the authority of Darwin's name.

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But in the present case, as we have seen, not only do the Neo-Darwinians strain the teachings of Darwin; they positively reverse those teachings—representing as anti-Darwinian the whole of one side of Darwin's system, and calling those who continue to accept that system in its entirety by the name "Lamarckians." I know it is sometimes said by members of this school, that in his utilization of Lamarckian principles as accessory to his own, Darwin was actuated by motives of "generosity." But a more preposterous suggestion could not well be made. We may fearlessly challenge any one who speaks or writes in such

a way, to show any other instance where Darwin's great generosity of disposition had the effect of influencing by one hair's breadth his still greater loyalty to truth. Moreover, and with special regard to this particular case, I would point out that in no one of his many allusions to, and often lengthy discussions of, these so-called Lamarckian principles, does he ever once introduce the name of Lamarck; while, on the other hand, in the only places where he does so—whether in his books or in his now published letters—he does so in order to express an almost contemptuous dissatisfaction, and a total absence of obligation. Hence, having regard to the "generosity" with which he always acknowledged obligations, there can be no reasonable doubt that Darwin was not in the smallest degree influenced by the speculative writings of Lamarck; or that, even if Lamarck had never lived, the *Origin of Species* would have differed in any single particular from the form in which it now stands. Finally, it must not be forgotten that Darwin's acceptance of the theory of use-inheritance was vitally essential to his theory of Pangenesis—that "beloved child" over which he had "thought so much as to have lost all power of judging it^[9]."

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What has just been said touching the relations between Darwin's theory and that of Lamarck, applies with equal force to the relations between Darwin's theory and any other theory appertaining to evolution which has already been, or may hereafter be propounded. Yet so greatly have some of the Neo-Darwinians misunderstood the teachings of Darwin, that they represent as "Darwinian heresy" any suggestions in the way of factors "supplementary to," or "co-operative with" natural selection. Of course, if these naturalists were to avow themselves followers of Wallace, instead of followers of Darwin, they would be perfectly justified in repudiating any such suggestions as, *ipso facto* heretical. But, as we have now seen, through all his life Darwin differed from Wallace with regard to this very point; and therefore, unlike Wallace, he was always ready to entertain "additional suggestions" regarding the causes of organic evolution—several of which, indeed, he himself supplied. Hence we arrive at this curious state of matters. Those biologists who of late years have been led by Weismann to adopt the opinions of Wallace, represent as anti-Darwinian the opinions of other biologists who still adhere to the unadulterated doctrines of Darwin. Weismann's *Essays on Heredity* (which argue that natural selection is the only possible cause of adaptive modification) and Wallace's work on *Darwinism* (which in all the respects where any charge of "heresy" is concerned directly contradicts the doctrine of Darwin)—these are the writings which are now habitually represented by the Neo-Darwinians as setting forth the views of Darwin in their "pure" form. The result is that, both in conversation and in the press, we habitually meet with complete inversions of the truth, which show the state of confusion into which a very simple matter has been wrought by the eagerness of certain naturalists to identify the views of Darwin with those of Wallace and Weismann. But we may easily escape this confusion, if we remember that wherever in the writings of these naturalists there occur such phrases as "pure Darwinism" we are to understand pure *Wallaceism*, or the pure theory of natural selection to the exclusion of any supplementary theory. Therefore it is that for the sake of clearness I coined, several years ago, the terms "Neo-Darwinian" and "Ultra-Darwinian" whereby to designate the school in question.

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So much, then, for the Darwinism of Darwin, as contrasted with the Darwinism of Wallace, or, what is the same thing, of the Neo-Darwinian school of Weismann. Next we may turn, by way of antithesis, to the so-called "Neo-Lamarckian" school of the United States. For, by a curious irony of fate, while the Neo-Darwinian school is in Europe seeking to out-Darwin Darwin by assigning an exclusive prerogative to natural selection in both kingdoms of animate nature, the Neo-Lamarckian school is in America endeavouring to reform Darwinism in precisely the opposite direction—viz. by transferring the sovereignty from

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natural selection to the principles of Lamarck. Without denying to natural selection a more or less important part in the process of organic evolution, members of this school believe that much greater importance ought to be assigned to the inherited effects of use and disuse than was assigned to these agencies by Darwin. Perhaps this noteworthy state of affairs, within a decade of Darwin's death, may lead us to anticipate that his judgement—standing, as it does, between these two extremes—will eventually prove the most accurate of all, with respect to the relative importance of these factors of evolution. But, be this as it may, I must now offer a few remarks upon the present position of the matter.

In the first place, to any one who (with Darwin and against Weismann) admits not only the abstract possibility, but an actual working, of the Lamarckian factors, it becomes difficult to determine, even approximately, the degrees of value which ought to be ascribed to them and to natural selection respectively. For, since the results are in both cases identical in kind (as, adaptive changes of organic types), where both sets of causes are supposed to be in operation together, we have no means of estimating the relative shares which they have had in bringing about these results. Of course there are large numbers of cases where it cannot possibly be supposed that the Lamarckian factors have taken any part at all in producing the observed effects; and therefore in such cases there is almost full agreement among evolutionists in theoretically ascribing such effects to the exclusive agency of natural selection. Of such, for instance, are the facts of protective colouring, of mimicry, of the growth of parts which, although *useful*, are never *active* (e.g. shells of mollusks, hard coverings of seeds), and so on. But in the majority of cases where adaptive structures are concerned, there is no means of discriminating between the influences of the Lamarckian and the Darwinian factors. Consequently, if by the Neo-Lamarckian school we understand all those naturalists who assign any higher importance to the Lamarckian factors than was assigned to them by Darwin, we may observe that members of this school differ very greatly among themselves as to the degree of importance that ought to be assigned. On the one hand we have, in Europe, Giard, Perrier, and Eimer, who stand nearer to Darwin than do a number of the American representatives—of whom the most prominent are Cope, Osborn, Packard, Hyatt, Brooks, Ryder, and Dall. The most extreme of these is Professor Cope, whose collection of essays entitled *The Origin of the Fittest*, as well as his more recent and elaborate monograph on *The Development of the Hard Parts of the Mammalia*, represent what appears even to some other members of his school an extravagant estimate of the importance of Lamarckian principles.

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But the most novel, and in many respects the most remarkable school of what may be termed Anti-selectionists is one which is now (1894) rapidly increasing both in numbers and in weight, not only in the New World, but also in Germany, and to a lesser extent, in Great Britain.

This school, without being either Lamarckian or Darwinian (for its individual members differ widely from one another in these respects) maintains a principle which it deems of more importance than either use-inheritance or natural selection. This principle it calls Self-adaptation. It is chiefly botanists who constitute this school, and its principal representatives, in regard to authority, are Sachs, Pfeffer and Henslow.

Apart from topics which are to be dealt with in subsequent chapters, the only matters of much importance which have been raised in the Post-Darwinian period are those presented by the theories of Geddes, Cope, Hyatt, and others, and certain more or less novel ideas set forth in Wallace's *Darwinism*.

Mr. Geddes has propounded a new theory of the origin of species, which in his judgement supersedes to a large extent the theory of natural selection. He has also, in conjunction with Mr. Thomson, propounded a theory of the origin of sex. For my own part, I cannot see that these views embody any principles or suggestions of a sufficiently definite kind to constitute them theories at all. In this respect the views of Mr. Geddes resemble those of

Professors Cope, Hyatt, and others, on what they term "the law of acceleration and retardation." In all these cases, so far as I can see, the so-called explanations are not in fact any explanations; but either a mere re-statement of the facts, or else an enunciation of more or less meaningless propositions. Thus, when it is said that the evolution of any given type has been due to the "acceleration of growth-force" with respect to some structures, and the "retardation of growth-force" with respect to others, it appears evident that we have not any real explanation in terms of causality; we have only the form of an explanation in the terms of a proposition. All that has been done is to express the fact of evolution in somewhat obscure phraseology, since the very thing we want to know about this fact is—What are the causes of it as a fact, or the reasons which have led to the increase of some of the parts of any given type, and the concomitant decrease of others? It is merely the facts themselves that are again presented by saying that the development has been in the one case accelerated, while in the other it has been retarded^[10]. [Pg 16]

So much for what may be termed this New World theory of the origin of species: it is a mere re-statement of the facts. Mr. Geddes' theory, on the other hand, although more than a mere re-statement of the facts, appears to me too vague to be of any explanatory service. His view is that organic evolution has everywhere depended upon an antagonism, within the limits of the same organism, between the processes of nutrition and those of reproduction. But although he is thus able hypothetically to explain certain facts—such as the shortening of a flower-spike into a composite flower—the suggestion is obviously inadequate to meet, even hypothetically, most of the facts of organic evolution, and especially the development of *adaptive* structures. Therefore, it seems to me, we may dismiss it even as regards the comparatively few facts which it might conceivably explain—seeing that these same facts may be equally well explained by the causes which are already known to operate in other cases. For it is the business of natural selection to ensure that there shall nowhere be any needless expenditure of vital energy, and, consequently, that everywhere the balance between nutrition and reproduction shall be most profitably adjusted. [Pg 17]

Similarly with respect to the theory of the *Origin of Sex*, I am unable to perceive even this much of scientific relevancy. As stated by its authors the theory is, that the female is everywhere "anabolic," as compared with the male, which is "katabolic." By anabolic is meant comparative inactivity of protoplasmic change due to a nutritive winding up of molecular constitution, while by katabolic is meant the opposite condition of comparative activity due to a dynamic running down of molecular constitution. How, then, can the *origin* of sex be explained, or the *causes* which led to the differentiation of the sexes be shown by saying that the one sex is anabolic and the other katabolic? In so far as these verbal statements serve to express what is said to be a general fact—namely, that the female sexual elements are less mobile than the male—they merely serve to re-state this general fact in terminology which, as the authors themselves observe, is "unquestionably ugly." But in so far as any question of *origin* or *causality* is concerned, it appears to me that there is absolutely no meaning in such statements. They belong to the order of merely formal explanations, as when it is said that the toxic qualities of morphia are due to this drug possessing a soporific character. [Pg 18]

Much the same, in my opinion, has to be said of the Rev. G. Henslow's theory of the origin of species by what he terms "self-adaptation." Stated briefly his view is that there is no sufficient evidence of natural selection as a *vera causa*, while there is very abundant evidence of adjustments occurring without it, first in individual organisms, and next, by inheritance of acquired characters, in species. Now, much that he says in criticism of the selection theory is of considerable interest as such; but when we pass from the critical to the constructive portions of his books and papers, we again meet with the want of clearness in thought between a statement of facts in terms of a proposition, and an explanation of them in those of causality. Indeed, I understand from private correspondence, that Mr. Henslow himself admits the validity of this criticism; for in answer to my questions,—“How does

Self-adaptation work in each case, and why should protoplasm be able to *adapt itself* into the millions of diverse mechanisms in nature?"—he writes. "Self-adaptation does not profess to be a *vera causa* at all; for the true causes of variation can only be found in the answer to your [above] questions, and I must say at once, *these questions cannot be answered*." That is, they cannot be answered on the hypothesis of self-adaptation, which is therefore a statement of the facts of adaptation as distinguished from an explanation of them. Nevertheless, two things have here to be noted. In the first place, the statement of facts which Mr. Henslow has collected is of considerable theoretical importance as tending to show that there are probably causes of an internal kind (i. e. other than natural selection) which have been largely concerned in the adaptive modification of plants. And, in the second place, it is not quite true that the theory of self-adaptation is, as its author says in the sentences above quoted, a mere statement of the facts of adaptation, without any attempt at explaining their causes. For in his published words he does attempt to do so^[11]. And, although I think his attempt is a conspicuous failure, I ought in fairness to give examples of it. His books are almost exclusively concerned in an application of his theory to the mechanisms of flowers for securing their own fertilization. These mechanisms he ascribes, in the case of entomophylous flowers, to the "thrusts," "strains," and other "irritations" supplied to the flowers by their insect visitors, and consequent "reactions" of the vegetable "protoplasm." But no attempt is made to show why these "reactions" should be of an *adaptive* kind, so as to build up the millions of diverse and often elaborate mechanisms in question—including not only forms and movements, but also colours, odours, and secretions. For my own part I confess that, even granting to an ultra-Lamarckian extent the inheritance of acquired characters, I could conceive of "self-adaptation" alone producing all such innumerable and diversified adjustments only after seeing, with Cardinal Newman, an angel in every flower. Yet Mr. Henslow somewhat vehemently repudiates any association between his theory and that of teleology. [Pg 19] [Pg 20]

On the whole, then, I regard all the works which are here classed together (those by Cope, Geddes, and Henslow), as resembling one another both in their merits and defects. Their common merits lie in their erudition and much of their criticism, while their common defects consist on the one hand in not sufficiently distinguishing between mere statements and real explanations of facts, and, on the other, in not perceiving that the theories severally suggested as substitutes for that of natural selection, even if they be granted true, could be accepted only as co-operative factors, and by no stretch of logic as substitutes.

Turning now to Mr. Wallace's work on *Darwinism*, we have to notice, in the first place, that its doctrine differs from "Darwinism" in regard to the important dogma which it is the leading purpose of that work to sustain—namely, that "the law of utility" is, to all intents and purposes, universal, with the result that natural selection is virtually the only cause of organic evolution. I say "to all intents and purposes," or "virtually," because Mr. Wallace does not expressly maintain the abstract impossibility of laws and causes other than those of utility and natural selection; indeed, at the end of his treatise, he quotes with approval Darwin's judgement, that "natural selection has been the most important, but not the exclusive means of modification." Nevertheless, as he nowhere recognizes any other law or cause of adaptive evolution^[12], he practically concludes that, on inductive or empirical grounds, there *is* no such other law or cause to be entertained—until we come to the particular case of the human mind. But even in making this one particular exception—or in representing that some other law than that of utility, and some other cause than that of natural selection, must have been concerned in evolving the mind of man—he is not approximating his system to that of Darwin. On the contrary, he is but increasing the divergence, for, of course, it was Darwin's view that no such exception could be legitimately [Pg 21]

drawn with respect to this particular instance. And if, as I understand must be the case, his expressed agreement with Darwin touching natural selection not being the only cause of adaptive evolution has reference to this point, the quotation is singularly inapt.

Looking, then, to these serious differences between his own doctrine of evolution—both organic and mental—and that of Darwin, I cannot think that Mr. Wallace has chosen a suitable title for his book; because, in view of the points just mentioned, it is unquestionable that *Darwinism* differs more widely from the *Origin of Species* than does the *Origin of Species* from the writings of the Neo-Lamarckians. But, passing over this merely nominal matter, a few words ought to be added on the very material question regarding the human mind. In subsequent chapters the more general question, or that which relates to the range of utility and natural selection elsewhere will be fully considered.

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Mr. Wallace says,—

"The immense interest that attaches to the origin of the human race, and the amount of misconception which prevails regarding the essential teachings of Darwin's theory on the question, as well as regarding my own special views upon it, induce me to devote a final chapter to its discussion."

Now I am not aware that there is any misconception in any quarter as to the essential teachings of Darwin's theory on this question. Surely it is rather the case that there is a very general and very complete understanding on this point, both by the friends and the foes of Darwin's theory—so much so, indeed, that it is about the only point of similar import in all Darwin's writings of which this can be said. Mr. Wallace's "special views" on the other hand are, briefly stated, that certain features, both of the morphology and the psychology of man, are inexplicable by natural selection—or indeed by any other cause of the kind ordinarily understood by the term natural: they can be explained only by supposing "the intervention of some distinct individual intelligence," which, however, need not necessarily be "one Supreme Intelligence," but some other order of Personality standing anywhere in "an infinite chasm between man and the Great Mind of the universe^[13]." Let us consider separately the corporeal and the mental peculiarities which are given as justifying this important conclusion.

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The bodily peculiarities are the feet, the hands, the brain, the voice, and the naked skin.

As regards the feet Mr. Wallace writes, "It is difficult to see why the prehensile power [of the great toe] should have been taken away," because, although "it may not be compatible with perfectly easy erect locomotion," "how can we conceive that early man, *as an animal*, gained anything by purely erect locomotion^[14]?" But surely it is not difficult to conceive this. In the proportion that our simian progenitors ceased to be arboreal in their habits (and there may well have been very good utilitarian reasons for such a change of habitat, analogous to those which are known to have occurred in the phylogenesis of countless other animals), it would clearly have been of advantage to them that their already semi-erect attitude should have been rendered more and more erect. To name one among several probabilities, the more erect the attitude, and the more habitually it was assumed, the more would the hands have been liberated for all the important purposes of manipulation. The principle of the physiological division of labour would thus have come more and more into play: natural selection would therefore have rendered the upper extremities more and more suited to the execution of these purposes, while at the same time it would have more and more adapted the lower ones to discharging the sole function of locomotion. For my own part, I cannot perceive any difficulty about this: in fact, there is an admirable repetition of the process in the ontogeny of our own children^[15].

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Next, with regard to the hand, Mr. Wallace says, that it "contains latent capacities which are unused by savages, and must have been even less used by palaeolithic man and his still ruder predecessors." Thus, "it has all the appearance of an organ prepared for the use of civilized man^[16]." Even if this be true, however, it would surely be a dangerous argument to rely upon, seeing that we cannot say of how much importance it may have been for early man—or even apes—to have had their power of manipulation progressively improved. But is the statement true? It appears to me that if Mr. Wallace had endeavoured to imitate the manufactures that were practised by "palaeolithic man," he would have found the very best of reasons for cancelling his statement. For it is an extremely difficult thing to chip a flint into the form of an arrow-head: when made, the suitable attachment of it to a previously prepared arrow is no easy matter: neither a bow nor a bow-string could have been constructed by hands of much less perfection than our own: and the slaying of game with the whole apparatus, when it has been constructed, requires a manual dexterity which we may be perfectly certain that Mr. Wallace—unless he has practised the art from boyhood— [Pg 25] does not possess.

So it is with his similar argument that the human voice is more "powerful," more "flexible," and presents a greater "range" and "sweetness" than the needs of savage life can be held to require. The futility of this argument is self-evident as regards "power." And although its weakness is not so obvious with respect to the other three qualities which are named, need we go further than the closely analogous case of certain birds to show the precariousness of arguing from such facts of organic nature to the special operation of "a superior intelligence"? I can hardly suppose that Mr. Wallace will invoke any such agency for the purpose of explaining the "latent capacities" of the voice of a parrot. Yet, in many respects, these are even more wonderful than those of the human voice, albeit in a wild state they are "never required or used^[17]."

Once more, with regard to the naked skin, it seems sufficient to quote the following passage from the first edition of the *Descent of Man*.

"The Rev. T. R. Stebbing, in commenting on this view, remarks, that had Mr. Wallace 'employed his usual ingenuity on the question of man's hairless skin, he might have seen the possibility of its selection through its superior beauty, or the health attaching to superior cleanliness. At any rate it is surprising that he should picture to himself a superior intelligence plucking the hair from the backs of savage men (to whom, according to his own account, it would have been useful and beneficial), in order that the descendants of the poor shorn wretches might, after many deaths from cold and damp in the course of many generations,' have been forced to raise themselves in the scale of civilization through the practice of various arts, in the manner indicated by Mr. Wallace^[18].'" [Pg 26]

To this it may be added that the Chimpanzee "Sally" was largely denuded of hair, especially on the back, or the part of "man's organization" on which Mr. Wallace lays special stress, as being in this respect out of analogy with other mammalia^[19].

Lastly, touching his statement that the brain of savage man is both quantitatively and qualitatively in advance of his requirements, it is here also sufficient to refer to Darwin's answer, as given in the *Descent of Man*. Mr. Wallace, indeed, ignores this answer in his recent re-publication of the argument; but it is impossible to understand why he should have done so. To me, at all events, it seems that one out of several considerations which Darwin advances is alone sufficient to show the futility of this argument. I allude to the consideration that the power of forming abstract ideas with the complex machinery of language as the vehicle of their expression, is probably of itself enough to account for both

the mass and the structure of a savage's brain. But this leads us to the second division of Mr. Wallace's argument, or that derived from the mental endowments of mankind.

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Here the peculiarities called into evidence are, "the Mathematical Faculty," "the Artistic Faculties," and "the Moral Sense." With regard to the latter, he avows himself a member of the intuitional school of ethics; but does not prove a very powerful advocate as against the utilitarian^[20].

It comes, then, to this. According to Mr. Wallace's eventual conclusion, man is to be separated from the rest of organic nature, and the steady progress of evolution by natural causes is to be regarded as stopped at its final stage, because the human mind presents the faculties of mathematical calculation and aesthetic perception. Surely, on antecedent grounds alone, it must be apparent that there is here no kind of proportion between the conclusion and the *data* from which it is drawn. That we are not confined to any such grounds, I will now try to show.

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Let it be remembered, however, that in the following brief criticism I am not concerned with the issue as to whether, or how far, the "faculties" in question have owed their origin or their development to *natural selection*. I am concerned only with the doctrine that in order to account for such and such particular "faculty" of the human mind, some order of causation must be supposed other than what we call natural. I am not a Neo-Darwinist, and so have no desire to make "natural selection" synonymous with "natural causation" throughout the whole domain of life and of mind. And I quite agree with Mr. Wallace that, at any rate, the "aesthetic faculty" cannot conceivably have been produced by natural selection—seeing that it is of no conceivable life-serving value in any of the stages of its growth. Moreover, it appears to me that the same thing has to be said of the play instincts, sense of the ludicrous, and sundry other "faculties" of mind among the lower animals. It being thus understood that I am not differing from Mr. Wallace where he imposes "limits" on the powers of natural selection, but only where he seems to take for granted that this is the same thing as imposing limits on the powers of natural causation, my criticism is as follows.

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In the first place, it is a psychological fallacy to regard the so-called "faculties" of mind as analogous to "organs" of the body. To classify the latter with reference to the functions which they severally perform is to follow a natural method of classification. But it is an artificial method which seeks to partition mental *faculty* into this, that, and the other mental *faculties*. Like all other purely artificial classifications, this one has its practical uses; but, also like them, it is destitute of philosophical meaning. This statement is so well recognized by psychologists, that there is no occasion to justify it. But I must remark that any cogency which Mr. Wallace's argument may appear to present, arises from his not having recognized the fact which the statement conveys. For, had he considered the mind as a whole, instead of having contemplated it under the artificial categories of constituent "faculties," he would probably not have laid any such special stress upon some of the latter. In other words, he would have seen that the general development of the human mind as a whole has presumably involved the growth of those conventionally abstracted parts, which he regards as really separate endowments. Or, if he should find it easier to retain the terms of his metaphor, we may answer him by saying that the "faculties" of mind are "correlated," like "organs" of the body; and, therefore, that any general development of the various other "faculties" have presumably entailed a collateral development of the two in question.

Again, in the second place, it would seem that Mr. Wallace has not sufficiently considered the co-operation of either well-known natural causes, which must have materially assisted the survival of the fittest where these two "faculties" are concerned. For, even if we disregard the inherited effects of use—which, however, if entertained as possible in any degree at all, must have here constituted an important factor,—there remain on the one

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hand, the unquestionable influences of individual education and, on the other hand, of the selection principle operating in the mind itself.

Taking these two points separately, it is surely sufficiently well known that individual education—or special training, whether of mind or body—usually raises congenital powers of any kind to a more or less considerable level above those of the normal type. In other words, whatever doubt there may be touching the *inherited* effects of use, there can be no question touching the immense *developmental* effects thereof in the individual life-time. Now, the conditions of savage life are not such as lead to any deliberate cultivation of the "faculties" either of the mathematical or aesthetic order. Consequently, as might be expected, we find both of them in what Mr. Wallace regards as but a "latent" stage of development. But in just the same way do we find that the marvellous powers of an acrobat when specially trained from childhood—say to curve his spine backwards until his teeth can bite his heels—are "latent" in all men. Or, more correctly, they are *potential in every child*. So it is with the prodigious muscular development of a trained athlete, and with any number of other cases where either the body or the mind is concerned. Why then should Mr. Wallace select the particular instances of the mathematical and aesthetic powers in savages as in any special sense "prophetic" of future development in trained members of civilized races? Although it is true that these "latent capacities and powers are unused by savages," is it not equally true that savages fail to use their latent capacities and powers as tumblers and athletes? Moreover, is it not likewise true that *as* used by savages, or as occurring normally in man, such capacities and powers are no less poorly developed than are those of the "faculties" on which Mr. Wallace lays so much stress? In other words, are not "latent capacities and powers" of all kinds more or less equally in excess of anything that is ever required of them by man in a state of nature? Therefore, if we say that where mathematics and the fine arts are concerned the potential capacities of savage man are in some mystical sense "prophetic" of a Newton or a Beethoven, so in consistency ought we to say that in these same capacities we discern a similar prophecy of those other uses of civilized life which we have in a rope-dancer or a clown.

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Again, and in addition to this, it should be remembered that, even if we do suppose any prophecy of this kind where the particular capacities in question are concerned, we must clearly extend the reference to the lower animals. Not a few birds display aesthetic feelings in a measure fairly comparable with those of savages; while we know that some animals present the germs of a "faculty" of computation^[21]. But, it is needless to add, this fact is fatal to Mr. Wallace's argument as I understand it—viz. that the "faculties" in question have been in some special manner communicated by some superior intelligence to *man*.

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Once more, it is obviously unfair to select such men as a "Newton, a La Place, a Gauss, or a Cayley" for the purpose of estimating the difference between savages and civilized man in regard to the latter "faculty." These men are the picked mathematicians of centuries. Therefore they are men who not only enjoyed all the highest possible benefits of individual culture, but likewise those who have been most endowed with mathematical power congenitally. So to speak, they are the best variations in this particular direction which our race is known to have produced. But had such variations arisen among savages it is sufficiently obvious that they could have come to nothing. Therefore, it is the *normal average* of "mathematical faculty" in civilized man that should be contrasted with that of savage man; and, when due regard is paid to the all-important consideration which immediately follows, I cannot feel that the contrast presents any difficulty to the theory of human evolution by natural causation.

Lastly, the consideration just alluded to is, that civilized man enjoys an advantage over savage man far in advance even of those which arise from a settled state of society, incentives to intellectual training, and so on. This inestimable advantage consists in the art of writing, *and the consequent transmission of the effects of culture from generation to*

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generation. Quite apart from any question as to the hereditary transmission of acquired characters, we have in this *intellectual* transmission of acquired *experience* a means of accumulative cultivation quite beyond our powers to estimate. For, unlike all other cases where we recognize the great influence of individual use or practice in augmenting congenital "faculties" (such as in the athlete, pianist, &c.), in this case the effects of special cultivation do not end with the individual life, but are carried on and on through successive generations *ad infinitum*. Hence, a civilized man inherits mentally, if not physically, the effects of culture for ages past, and this in whatever direction he may choose to profit therefrom. Moreover—and I deem this an immensely important addition—in this unique department of purely intellectual transmission, a kind of non-physical natural selection is perpetually engaged in producing the best results. For here a struggle for existence is constantly taking place among "ideas," "methods," and so forth, in what may be termed a psychological environment. The less fit are superseded by the more fit, and this not only in the mind of the individual, but, through language and literature, still more in the mind of the race. "A Newton, a La Place, a Gauss, or a Cayley," would all alike have been impossible, but for a previously prolonged course of mental evolution due to the selection principle operating in the region of mathematics, by means of continuous survivals of the best products in successive generations. And, of course, the same remark applies to art in all its branches^[22].

Quitting then the last, and in my opinion the weakest chapter of *Darwinism*, the most important points presented by other portions of this work are—to quote its author's own enumeration of them—an attempted "proof that all specific characters are (or once have been) either useful in themselves or correlated with useful characters": an attempted "proof that natural selection can, in certain cases, increase the sterility of crosses": an attempted "proof that the effects of use and disuse, even if inherited, must be overpowered by natural selection": an attempted proof that the facts of variation in nature are in themselves sufficient to meet the difficulty which arises against the theory of natural selection, as held by him, from the swamping effects of free intercrossing: and, lastly, "a fuller discussion on the colour relations of animals, with additional facts and arguments on the origin of sexual differences of colour." As I intend to deal with all these points hereafter, excepting the last, it will be sufficient in this opening chapter to remark, that in as far as I disagree with Mr. Wallace (and agree with Darwin), on the subject of "sexual differences of colour," my reasons for doing so have been already sufficiently stated in Part I. But there is much else in his treatment of this subject which appears to me highly valuable, and therefore presenting an admirable contribution to the literature of Darwinism. In particular, it appears to me that the most important of his views in this connexion probably represents the truth—namely, that, among the higher animals, more or less conspicuous peculiarities of colour have often been acquired for the purpose of enabling members of the same species quickly and certainly to recognize one another. This theory was first published by Mr. J. E. Todd, in 1888, and therefore but a short time before its re-publication by Mr. Wallace. As his part in the matter has not been sufficiently recognized, I should like to conclude this introductory chapter by drawing prominent attention to the merits of Mr. Todd's paper. For not only has it the merit of priority, but it deals with the whole subject of "recognition colours"—or, as he calls them, "directive colours"—in a more comprehensive manner than has been done by any of his successors. In particular, he shows that the principle of recognition-marking is not restricted to facilitating sexual intercourse, but extends also to several other matters of importance in the economy of animal life^[23].

Having thus briefly sketched the doctrines of the sundry Post-Darwinian Schools from a general point of view, I shall endeavour throughout the rest of this treatise to discuss in

appropriate detail the questions which have more specially come to the front in the post-Darwinian period. It can scarcely be said that any one of these questions has arisen altogether *de novo* during this period; for glimmerings, more or less conspicuous, of all are to be met with in the writings of Darwin himself. Nevertheless it is no less true that only after his death have they been lighted up to the full blaze of active discussion^[24]. By far the most important of them are those to which the rest of this treatise will be confined. They are four in number, and it is noteworthy that they are all intimately connected with the great question which Darwin spent the best years of his life in contemplating, and which has therefore, in one form or another, occupied the whole of the present chapter—the question as to whether natural selection has been the sole cause, or but the chief cause of modification. [Pg 36]

The four questions above alluded to appertain respectively to Heredity, Utility, Isolation, and Physiological Selection. Of these the first two will form the subject-matter of the present volume, while the last two will be dealt with in the final instalment of *Darwin, and after Darwin*.

SECTION I *HEREDITY*

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CHAPTER II. CHARACTERS AS HEREDITARY AND ACQUIRED (PRELIMINARY).

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We will proceed to consider, throughout Section I of the present work, the most important among those sundry questions which have come to the front since the death of Darwin. For it was in the year after this event that Weismann published the first of his numerous essays on the subject of Heredity, and, unquestionably, it has been these essays which have given such prominence to this subject during the last decade.

At the outset it is desirable to be clear upon certain points touching the history of the subject; the limits within which our discussion is to be confined; the relation in which the present essay stands to the one that I published last year under the title *An Examination of Weismannism*; and several other matters of a preliminary kind.

The problems presented by the phenomena of heredity are manifold; but chief among them is the hitherto unanswered question as to the transmission or non-transmission of acquired characters. This is the question to which the present Section will be confined.

Although it is usually supposed that this question was first raised by Weismann, such was not the case. Any attentive reader of the successive editions of Darwin's works may perceive that at least from the year 1859 he had the question clearly before his mind; and that during the rest of his life his opinion with regard to it underwent considerable modifications—becoming more and more Lamarckian the longer that he pondered it. But it was not till 1875 that the question was clearly presented to the general public by the independent thought of Mr. Galton, who was led to challenge the Lamarckian factors *in toto* by way of deduction from his theory of Stirp—the close resemblance of which to Professor Weismann's theory of [Pg 40]

Germ-plasm has been shown in my *Examination of Weismannism*. Lastly, I was myself led to doubt the Lamarckian factors still further back in the seventies, by having found a reason for questioning the main evidence which Mr. Darwin had adduced in their favour. This doubt was greatly strengthened on reading, in the following year, Mr. Galton's *Theory of Heredity* just alluded to; and thereupon I commenced a prolonged course of experiments upon the subject, the general nature of which will be stated in future chapters. Presumably many other persons must have entertained similar misgivings touching the inheritance of acquired characters long before the publication of Weismann's first essay upon the subject in 1883. The question as to the inheritance of acquired characters was therefore certainly not first raised by Weismann—although, of course, there is no doubt that it was conceived by him independently, and that he had the great merit of calling general attention to its existence and importance. On the other hand, it cannot be said that he has succeeded in doing very much towards its solution. It is for these reasons that any attempt at dealing with Weismann's fundamental postulate—i.e. that of the non-inheritance of acquired characters—was excluded from my *Examination of Weismannism*. As there stated, he is justified in assuming, for the purposes of his discussion, a negative answer to the question of such inheritance; but evidently the question itself ought not to be included within what we may properly understand by "Weismannism." Weismannism, properly so called, is an elaborate system of theories based on the fundamental postulate just mentioned—theories having reference to the mechanism of heredity on the one hand, and to the course of organic evolution on the other. Now it was the object of the foregoing *Examination* to deal with this system of theories *per se*; and therefore we have here to take a new point of departure and to consider separately the question of fact as to the inheritance or non-inheritance of acquired characters. At first sight, no doubt, it will appear that in adopting this method I am putting the cart before the horse. For it may well appear that I ought first to have dealt with the validity of Weismann's postulate, and not till then to have considered the system of theories which he has raised upon it. But this criticism is not likely to be urged by any one who is well acquainted with the questions at issue. For, in the first place, it is notorious that the question of fact is still open to question; and therefore it ought to be considered separately, or apart from any theories which may have been formed with regard to it. In the second place, our judgement upon this question of fact must be largely influenced by the validity of general reasonings, such as those put forward in the interests of rival theories of heredity; and, as the theory of germ-plasm has been so thoughtfully elaborated by Professor Weismann, I have sought to give it the attention which it deserves as preliminary to our discussion of the question of fact which now lies before us. Thirdly and lastly, even if this question could be definitely answered by proving either that acquired characters are inherited or that they are not, it would by no means follow that Weismann's theory of heredity would be proved wholly false in the one case, or wholly true in the other. That it need not be wholly true, even were its fundamental postulate to be proved so, is evident, because, although the fact might be taken to prove the theory of Continuity, the theory of Germ-plasm is, as above stated, very much more than this. That the theory of Germ-plasm need not be wholly false, even if acquired characters should ever be proved heritable, a little thought may easily show, because, in this event, the further question would immediately arise as to the degrees and the comparative frequency of such inheritance. For my own part, as stated in the *Examination*, I have always been disposed to accept Mr. Galton's theory of Stirp in preference to that of Germ-plasm on this very ground—i. e. that it does not dogmatically exclude the possibility of an occasional inheritance of acquired characters in faint though cumulative degrees. And whatever our individual opinions may be touching the admissibility of such a *via media* between the theories of Pangenesis and Germ-plasm, at least we may all agree on the desirability of fully considering the matter as a preliminary to the discussion of the question of fact.

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As it is not to be expected that even those who may have read my previous essay can now carry all these points in their memories, I will here re-state them in a somewhat fuller form.

The following diagram will serve to give a clearer view of the sundry parts of Professor Weismann's system of theories, as well as of their relations to one another.



**Postulate as to the absolute
non-inheritance of acquired
characters.**

Now, as just explained, the parts of this system which may be properly and distinctively called "Weismannism" are those which go to form the Y-like structure of deductions from the fundamental postulate. Therefore, it was the Y-like system of deductions which were dealt with in the *Examination of Weismannism*, while it is only his basal postulate which has to be dealt with in the following chapters.

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So much, then, for the relations of Weismann's system of theories to one another. It is, however, of even more importance that we should gain a clear view of the relations between his theory of *heredity* to those of Darwin and of Galton, as preliminary to considering the fundamental question of fact.

As we have already seen, the theory of germ-plasm is not only a theory of heredity: it is also, and more distinctively, a theory of evolution, &c. As a theory of heredity it is grounded on its author's fundamental postulate—the *continuity* of germ-plasm. But as a theory of evolution, it requires for its support this additional postulate, that the continuity of germ-plasm has been *absolute* "since the first origin of life." It is clear that this additional postulate is not needed for his theory of heredity, but only for his additional theory of evolution, &c. There have been one or two other theories of heredity, prior to this one, which, like it, have been founded on the postulate of Continuity of the substance of heredity; but it has not been needful for any of these theories to postulate further that this substance has been *always* thus isolated, or even that it is now *invariably* so. For even though the isolation be frequently invaded by influences of body-changes on the congenital characters of this substance, it does not follow that this principle of Continuity may not still be true *in the main*, even although it is supplemented in some degree by that of use-inheritance. Indeed, so far as the phenomena of heredity are concerned, it is conceivable that all congenital characters were originally acquired, and afterwards became congenital on account of their long inheritance. I do not myself advocate this view as biologically probable, but merely state it as logically possible, and in order to show that, so far as the phenomena of heredity are concerned, there appears to be no reason for Weismann's deduction that the principle of Continuity, if true at all, must be *absolute*. And it would

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further appear, the only reason why he makes this deduction (stem of the Y) is in order to provide a foundation for his further theories of evolution, &c. (arms of the Y). It is indeed necessary for these further theories that body-changes should never exercise any hereditary influence on the hereditary endowments of germ-plasm, and therefore it is that he posits the substance of heredity as, not only continuous, but uninterruptably so "since the first origin of life."

Now, this may be made more clear by briefly comparing Weismann's theory with those of Darwin and of Galton. Weismann's theory of heredity, then, agrees with its predecessors which we are considering in all the following respects. The substance of heredity is particulate; is mainly lodged in highly specialized cells; is nevertheless also distributed throughout the general cellular tissues, where it is concerned in all processes of regeneration, repair, and a-sexual reproduction; presents an enormously complex structure, in that every constituent part of a potentially future organism is represented in a fertilized ovum by corresponding particles; is everywhere capable of virtually unlimited multiplication, without ever losing its hereditary endowments; is often capable of carrying these endowments in a dormant state through a long series of generations until at last they reappear in what we recognize as recursions. Thus far all three theories are in agreement. In fact, the only matter of any great importance wherein they disagree has reference to the doctrine of Continuity^[25]. For while Darwin's theory supposes the substance of heredity to be mainly formed anew in each ontogeny, and therefore that the continuity of this substance is for the most part interrupted in every generation^[26], Weismann's theory supposes this substance to be formed only during the phylogeny of each species, and therefore to have been absolutely uninterrupted since the first origin of life.

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But now, Galton's theory of heredity stands much nearer to Weismann's in this matter of Continuity; for it is, as he says, a theory of "modified pangenesis," and the modification consists in allowing very much more for the principle of Continuity than is allowed by Darwin's theory; in fact he expresses himself as quite willing to adopt (on adequate grounds being shown) the doctrine of Continuity as absolute, and therefore propounded, as logically possible, the identical theory which was afterwards and independently announced by Weismann. Or, to quote his own words—

"We might almost reserve our belief that the structural [i. e. somatic] cells can react on the sexual elements at all, and we may be confident that at most they do so in a very faint degree; in other words, that acquired modifications are barely, if at all, *inherited*, in the correct sense of that word^[27]."

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So far Mr. Galton; but for Weismann's further theory of evolution, &c., it is necessary to postulate the additional doctrine in question; and it makes a literally immeasurable difference to any theory of evolution whether or not we entertain this additional postulate. For no matter how faintly or how fitfully the substance of heredity may be modified by somatic tissues, the Lamarckian principles are hypothetically allowed some degree of play. And although this is a lower degree than Darwin supposed, their influence in determining the course of organic evolution may still have been enormous; seeing that their action in any degree must always have been *directive* of variation on the one hand, and *cumulative* on the other.

Thus, by merely laying this theory side by side with Weismann's we can perceive at a glance how a *pure* theory of *heredity* admits of being based on the postulate of Continuity alone, without cumbering itself by any further postulate as to this Continuity being *absolute*. And this, in my opinion is the truly scientific attitude of mind for us to adopt as preliminary to the following investigation. For the whole investigation will be concerned—and concerned only—with this question of Continuity as absolute, or as admitting of degrees. There is, without any question, abundant evidence to prove that the substance of heredity is

at least partly continuous (Gemmules). It may be that there is also abundant evidence to prove this substance much more *largely* continuous than Darwin supposed (Stirp); but be this as it may, it is certain that any such question as to the *degree* of continuity differs, *toto caelo*, from that as to whether there can ever be any continuity at all. [Pg 48]

How, then, we may well ask, is it that so able a naturalist and so clear a thinker as Weismann can have so far departed from the inductive methods as to have not merely propounded the question touching Continuity and its degrees, or even of Continuity as absolute; but to have straightway assumed the latter possibility as a basis on which to run a system of branching and ever-changing speculations concerning evolution, variation, the ultimate structure of living material, the intimate mechanism of heredity, or, in short, such a system of deductive conjectures as has never been approached in the history of science? The answer to this question is surely not far to seek. Must it not be the answer already given? Must it not have been for the sake of rearing this enormous structure of speculation that Weismann has adopted the assumption of Continuity as absolute? As we have just seen, Galton had well shown how a theory of heredity could be founded on the general doctrine of Continuity, without anywhere departing from the inductive methods—even while fully recognizing the possibility of such continuity as absolute. But Galton's theory was a "*Theory of Heredity*," and nothing more. Therefore, while clearly perceiving that the Continuity in question *may* be absolute, he saw no reason, either in fact or in theory, for concluding that it *must* be. On the contrary, he saw that this question is, for the present, necessarily unripe for profitable discussion—and, *a fortiori*, for the shedding of clouds of seed in all the directions of "Weismannism." [Pg 49]

Hence, what I desire to be borne in mind throughout the following discussion is, that it will have exclusive reference to the question of fact already stated, without regard to any superjacent theories; and, still more, that there is a vast distinction between any question touching the degrees in which acquired characters are transmitted to progeny, and the question as to whether they are ever transmitted in any degree at all. Now, the latter question, being of much greater importance than the former, is the one which will mainly occupy our attention throughout the rest of this Section.

We have already seen that before the subject was taken up by Weismann the difference between acquired and congenital characters in respect to transmissibility was generally taken to be one of degree; not one of kind. It was usually supposed that acquired characters, although not so fully and not so certainly inherited as congenital characters, nevertheless were inherited in some lesser degree; so that if the same acquired character continued to be successively acquired in a number of sequent generations, what was at first only a slight tendency to be inherited would become by summation a more and more pronounced tendency, till eventually the acquired character might become as strongly inherited as a congenital one. Or, more precisely, it was supposed that an acquired character, in virtue of such a summation of hereditary influence, would in time become congenital. Now, if this supposition be true, it is evident that more or less assistance must be lent to natural selection in its work of evolving adaptive modifications^[28]. And inasmuch as we know to what a wonderful extent adaptive modifications are secured during individual life-times—by the direct action of the environment on the one hand, and by increased or diminished use of special organs and mental faculties on the other—it becomes obvious of what importance even a small measure of transmissibility on their part would be in furnishing to natural selection ready-made variations in required directions, as distinguished from promiscuous variations in all directions. Contrariwise, if functionally-produced adaptations and adaptations produced by the direct action of the environment are never transmitted in any degree, not only would there be an incalculable waste, so to speak, of adaptive modifications—these being all laboriously and often most delicately built up during life-times of individuals only to be thrown down again as regards the interest of species—but so large an additional burden would be thrown upon the shoulders of natural selection that it [Pg 50]

becomes difficult to conceive how even this gigantic principle could sustain it, as I shall endeavour to show more fully in future chapters. On the other hand, however, Weismann and his followers not only feel no difficulty in throwing overboard all this ready-made machinery for turning out adaptive modifications when and as required; but they even represent that by so doing they are following the logical maxim, *Entia non sunt multiplicanda praeter necessitatem*—which means, in its relation to causality, that we must not needlessly multiply hypothetical principles to explain given results. But when appeal is here made to this logical principle—the so-called Law of Parsimony—two things are forgotten.

In the first place, it is forgotten that the very question in debate is whether causes of the Lamarckian order *are* unnecessary to explain all the phenomena of organic nature. Of course if it could be proved that the theory of natural selection alone is competent to explain all these phenomena, appeal to the logical principle in question would be justifiable. But this is precisely the point which the followers of Darwin refuse to accept; and so long as it remains the very point at issue, it is a mere begging the question to represent that a class of causes which have hitherto been regarded as necessary are, in fact, unnecessary. Or, in other words, when Darwin himself so decidedly held that these causes are necessary as supplements to natural selection, the burden of proof is quite as much on the side of Weismann and his followers to show that Darwin's opinion was wrong, as it is on the side of Darwin's followers to show that it was right. Yet, notwithstanding the elaborate structure of theory which Weismann has raised, there is nowhere one single fact or one single consideration of much importance to the question in debate which was not perfectly well known to Darwin. Therefore I say that all this challenging of Darwinists to justify their "Lamarckian assumptions" really amounts to nothing more than a pitting of opinion against opinion, where there is at least as much call for justification on the one side as on the other.

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Again, when these challenges are thrown down by Weismann and his followers, it appears to be forgotten that the conditions of their own theory are such as to render acceptance of the gauge a matter of great difficulty. The case is very much like that of a doughty knight pitching his glove into the sea, and then defying any antagonist to take it up. That this is the case a very little explanation will suffice to show.

The question to be settled is whether acquired characters are ever transmitted by heredity. Now suppose, for the sake of argument, that acquired characters are transmitted by heredity—though not so fully and not so certainly as congenital characters—how is this fact to be proved to the satisfaction of Weismann and his followers? First of all they answer,—Assuredly by adducing experimental proof of the inheritance of injuries, or mutilations. But in making this answer they appear to forget that Darwin has already shown its inefficiency. That the self-styled Neo-Lamarckians have been much more unguarded in this respect, I fully admit; but it is obviously unfair to identify Darwin's views with those of a small section of evolutionists, who are really as much opposed to Darwin's teaching on one side as is the school of Weismann on the other. Yet, on reading the essays of Weismann himself—and still more those of his followers—one would almost be led to gather that it is claimed by him to have enunciated the distinction between congenital and acquired characters in respect of transmissibility; and therefore also to have first raised the objection which lies against the theory of Pangenesis in respect of the non-transmissibility of mutilations. In point of fact, however, Darwin is as clear and decided on these points as Weismann. And his answer to the obvious difficulty touching the non-transmissibility of mutilations is, to quote his own words, "the long-continued inheritance of a part which has been removed during many generations is no real anomaly, for gemmules formerly derived from the part are multiplied and transmitted from generation to generation^[29]." Therefore, so far as Darwin's theory is concerned, the challenge to produce evidence of the transmission of injuries is irrelevant: it is no more a part of Darwin's theory than it is of Weismann's to maintain that injuries *are* transmitted.

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There is, however, one point in this connexion to which allusion must here be made. Although Darwin did not believe in the transmissibility of mutilations when these consist merely in the amputation of parts of an organism, he did believe in a probable tendency to transmission when removal of the part is followed by gangrene. For, as he says, in that case, all the gemmules of the mutilated or amputated part, as they are gradually attracted to that part (in accordance with the law of affinity which the theory assumes), will be successively destroyed by the morbid process. Now it is of importance to note that Darwin made this exception to the general rule of the non-transmissibility of mutilations, not because his theory of pangenesis required it, but because there appeared to be certain very definite observations and experiments—which will be mentioned later on—proving that when mutilations are followed by gangrene they are apt to be inherited: his object, therefore, was to reconcile these alleged facts with his theory, quite as much as to sustain his theory by such facts.

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So much, then, for the challenge to produce direct evidence of the transmissibility of acquired characters, so far as mutilations are concerned: believers in Darwin's theory, as distinguished from Weismann's, are under no obligation to take up such a challenge. But the challenge does not end here. Show us, say the school of Weismann, a single instance where an acquired character *of any kind* (be it a mutilation or otherwise) has been inherited: this is all that we require: this is all that we wait for: and surely, unless it be acknowledged that the Lamarckian doctrine reposes on mere assumption, at least one such case ought to be forthcoming. Well, nothing can sound more reasonable than this in the first instance; but as soon as we begin to cast about for cases which will satisfy the Neo-Darwinians, we find that the structure of their theory is such as to preclude, in almost every conceivable instance, the possibility of meeting their demand. For their theory begins by assuming that natural selection is the one and only cause of organic evolution. Consequently, what their demand amounts to is throwing upon the other side the burden of disproving this assumption—or, in other words, of proving the negative that in any given case of transmitted adaptation natural selection has *not* been the sole agent at work. Now, it must obviously be in almost all cases impossible to prove this negative among species in a state of nature. For, even supposing that among such species Lamarckian principles have had a large share in the formation of hereditary and adaptive characters, how would Weismann himself propose that we should set about the proof of such a fact, where the proof demanded by his assumption is, that the *abstract possibility* of natural selection having had anything to do with the matter must be excluded? Obviously this is impossible in the case of inherited characters which are also *adaptive* characters. How then does it fare with the case of inherited characters which are not also adaptive? Merely that this case is met by another and sequent assumption, which constitutes an integral part of the Neo-Darwinian creed—namely, that in nature there *can be no such characters*. Seeing that natural selection is taken to be the only possible cause of change in species, it follows that all changes occurring in species must necessarily be adaptive, whether or not we are able to perceive the adaptations. In this way apparently useless characters, as well as obviously useful ones, are ruled out of the question: that is to say, *all* hereditary characters of species in a state of nature are *assumed* to be due to natural selection, and then it is demanded that the validity of this assumption should be disproved by anybody who doubts it. Yet Weismann himself would be unable to suggest any conceivable method by which it can be disproved among species in a state of nature—and this even supposing that the assumption is entirely false^[30].

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Consequently, the only way in which these speciously-sounding challenges can be adequately met is by removing some individuals of a species from a state of nature, and so from all known influences of natural selection; then, while carefully avoiding artificial selection, causing these individuals and their progeny through many generations unduly to exercise some parts of their bodies, or unduly to fail in the exercise of others. But, clearly, such an experiment is one that must take years to perform, and therefore it is now too early

in the day to reproach the followers of Darwin with not having met the challenges which are thrown down by the followers of Weismann^[31].

Probably enough has now been said to show that the Neo-Darwinian assumption precludes the possibility of its own disproof from any of the facts of nature (as distinguished from domestication)—and this even supposing that the assumption be false. On the other hand, of course, it equally precludes the possibility of its own proof; and therefore it is as idle in Darwinists to challenge Weismann for proof of his negative (i. e. that acquired characters are not transmitted), as it is in Weismann to challenge Darwinists for proof of the opposite negative (i. e. that all seeming cases of such transmission are not due to natural selection). This dead-lock arises from the fact that in nature it is beyond the power of the followers of Darwin to exclude the abstract possibility of natural selection in any given case, while it is equally beyond the power of the followers of Weismann to exclude the abstract possibility of Lamarckian principles. Therefore at present the question must remain for the most part a matter of opinion, based upon general reasoning as distinguished from special facts or crucial experiments. The evidence available on either side is presumptive, not demonstrative^[32]. But it is to be hoped that in the future, when time shall have been allowed for the performance of definite experiments on a number of generations of domesticated plants or animals, intentionally shielded from the influences of natural selection while exposed to those of the Lamarckian principles, results will be gained which will finally settle the question one way or the other. [Pg 57] [Pg 58]

Meanwhile, however, we must be content with the evidence as it stands; and this will lead us to the second division of our subject. That is to say, having now dealt with the antecedent, or merely logical, state of the question, we have next to consider what actual, or biological, evidence there is at present available on either side of it. Thus far, neither side in the debate has any advantage over the other. On grounds of general reasoning alone they both have to rely on more or less dogmatic assumptions. For it is equally an unreasoned statement of opinion whether we allege that all the phenomena of organic evolution can be, or can not be, explained by the theory of natural selection alone. We are at present much too ignorant touching the causes of organic evolution to indulge in dogmatism of this kind; and if the question is to be referred for its answer to authority, it would appear that, both in respect of number and weight, opinions on the side of having provisionally to retain the Lamarckian factors are more authoritative than those *per contra*^[33].

Turning then to the question of fact, with which the following chapters are concerned, I will conclude this preliminary one with a few words on the method of discussion to be adopted.

First I will give the evidence in favour of Lamarckianism; this will occupy the next two chapters. Then, in Chapter V, I will similarly give the evidence *per contra*, or in favour of Continuity as absolute. Lastly, I will sum up the evidence on both sides, and give my own judgement on the whole case. But on whichever side I am thus acting as special pleader for the time being, I will adduce only such arguments as seem to me valid—excluding alike from both the many irrelevant or otherwise invalid reasonings which have been but too abundantly published. Moreover, I think it will be convenient to consider all that has been said—or may be said—in the way of criticism to each argument by the opposite side while such argument is under discussion—i. e. not to wait till all the special pleading on one side shall have been exhausted before considering the exceptions which have been (or admit of being) taken to the arguments adduced, but to deal with such exceptions at the time when each of these arguments shall have been severally stated. Again, and lastly, I will arrange the evidence in each case—i. e. on both sides—under three headings, viz. (A) Indirect, (B) Direct, and (C) Experimental^[34].] [Pg 59]

CHAPTER III.

CHARACTERS AS HEREDITARY AND ACQUIRED (continued).

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(A.)

Indirect Evidence in favour of the Inheritance of Acquired Characters.

Starting with the evidence in favour of the so-called Lamarckian factors, we have to begin with the Indirect—and this without any special reference to the theories, either of Weismann or of others.

It has already been shown, while setting forth in the preceding chapter the antecedent standing of the issue, that in this respect the *prima facie* presumption is wholly on the side of the transmission, in greater degree or less, of acquired characters. Even Weismann allows that all "*appearances*" point in this direction, while there is no inductive evidence of the action of natural selection in any one case, either as regards germs or somas, and therefore, *a fortiori*, of the "all-sufficiency" of this cause^[35]. It is true that in some of his earlier essays he has argued that there is no small weight of *prima facie* evidence in favour of his own views as to the non-inheritance of acquired characters. This, however, will have to be considered in its proper place further on. Meanwhile I shall say merely in general terms that it arises almost entirely from a confusion of the doctrine of Continuity as absolute with that of Continuity as partial, and therefore, as admitting of degrees in different cases—which, as already explained, are doctrines wide as the poles asunder. But, leaving aside for the present such *prima facie* evidence as Weismann has adduced on his side of the issue, I may quote him as a hostile witness to the weight of this kind of evidence *per contra*, in so far as it has already been presented in the foregoing chapter. Indeed, Weismann is much too logical a thinker not to perceive the cogency of the "appearances" which lie against his view of Continuity as absolute—although he has not been sufficiently careful in distinguishing between such Continuity and that which admits of degrees.

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We may take it, then, as agreed on all hands that whatever weight merely *prima facie* evidence may in this matter be entitled to, is on the side of what I have termed moderated Lamarckianism: first sight "appearances" are against the Neo-Darwinian doctrine of the absolute non-inheritance of acquired characters.

Let us now turn to another and much more important line of indirect evidence in favour of moderated Lamarckianism.

The difficulty of *excluding the possibility* of natural selection having been at work in the case of wild plants and animals has already been noticed. Therefore we may now appreciate the importance of all facts or arguments which *attenuate the probability* of natural selection having been at work. This may be done by searching for cases in nature where a congenital structure, although unquestionably adaptive, nevertheless presents so small an amount of adaptation, that we can scarcely suppose it to have been arrived at by natural selection in the struggle for existence, as distinguished from the inheritance of functionally-produced modifications. For if functionally-produced modifications are ever transmitted at all, there is no limit to the minuteness of adaptive values which may thus become congenital; whereas, in order that any adaptive structure or instinct should be seized upon and accumulated by

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natural selection, it must from the very first have had an adaptive value sufficiently great to have constituted its presence a matter of life and death in the struggle for existence. Such structures or instincts must not only have always presented some measure of adaptive value, but this must always have been sufficiently great to reach what I have elsewhere called a selection-value. Hence, if we meet with cases in nature where adaptive structures or instincts present so low a degree of adaptive value that it is difficult to conceive how they could ever have exercised any appreciable influence in the battle for life, such cases may fairly be adduced in favour of the Lamarckian theory. For example, the Neo-Lamarckian school of the United States is chiefly composed of palaeontologists; and the reason of this seems to be that the study of fossil forms—or of species in process of formation—reveals so many instances of adaptations which in their nascent condition present such exceedingly minute degrees of adaptive value, that it seems unreasonable to attribute their development to a survival of the fittest in the complex struggle for existence. But as this argument is in my opinion of greatest force when it is applied to certain facts of physiology with which I am about to deal, I will not occupy space by considering any of the numberless cases to which the Neo-Lamarckians apply it within the region of palaeontology^[36].

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Turning then to inherited actions, it is here that we might antecedently expect to find our best evidence of the Lamarckian principles, if these principles have really had any share in the process of adaptive evolution. For we know that in the life-time of individuals it is action, and the cessation of action, which produce nearly all the phenomena of acquired adaptation—use and disuse in animals being merely other names for action and the cessation of action. Again, we know that it is where neuro-muscular machinery is concerned that we meet with the most conclusive evidence of the remarkable extent to which action is capable of co-ordinating structures for the ready performance of particular functions; so that even during the years of childhood "practice makes perfect" to the extent of organizing neuro-muscular adjustments, so elaborate and complete as to be indistinguishable from those which in natural species we recognized as reflex actions on the one hand, and instinctive actions on the other. Hence, if there be any such thing as "use-inheritance" at all, it is in the domain of reflex actions and instinctive actions that we may expect to find our best evidence of the fact. Therefore I will restrict the present line of evidence—(A)—to these two classes of phenomena, as together yielding the best evidence obtainable within this line of argument.

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The evidence in favour of the Lamarckian factors which may be derived from the phenomena of reflex action has never, I believe, been pointed out before; but it appears to me of a more cogent nature than perhaps any other. In order to do it justice, I will begin by re-stating an argument in favour of these factors which has already been adduced by previous writers, and discussed by myself in published correspondence with several leaders of the ultra-Darwinian school.

Long ago Professor Broca and Mr. Herbert Spencer pointed to the facts of co-adaptation, or co-ordination within the limits of the same organism, as presenting good evidence of Lamarckian principles, working in association with natural selection. Thus, taking one of Lamarck's own illustrations, Mr. Spencer argued that there must be numberless changes—extending to all the organs, and even to all the tissues, of the animal—which in the course of many generations have conspired to convert an antelope into a giraffe. Now the point is, that throughout the entire history of these changes their utility must always have been dependent on their association. It would be useless that an incipient giraffe should present the peculiar form of the hind-quarters which we now perceive, unless at the same time it presented the correspondingly peculiar form of the fore-quarters; and as each of these great modifications entails innumerable subordinate modifications throughout both halves of the creature

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concerned, the chances must have been infinitely great against the required association of so many changes happening to have arisen congenitally in the same individuals by way of merely fortuitous variation. Yet, if we exclude the Lamarckian interpretation, which gives an intelligible *cause* of co-ordination, we are required to suppose that such a happy concurrence of innumerable independent variations must have occurred by mere accident—and this on innumerable different occasions in the bodies of as many successive ancestors of the existing species. For at each successive stage of the improvement natural selection (if working alone) must have needed all, or at any rate most, of the co-ordinated parts to occur in the same individual organisms^[37].

In alluding to what I have already published upon the difficulty which thus appears to be presented to his theory, Weismann says, "At no distant time I hope to be able to consider this objection, and to show that the apparent support given to the old idea [i. e. of the transmission of functionally-produced modifications] is really insecure, and breaks down as soon as it is critically examined^[38]."

So much for what Weismann has said touching this matter. But the matter has also been dealt with both by Darwin and by Wallace. Darwin very properly distinguishes between the fallacy that "with animals such as the giraffe, of which the whole structure is admirably co-ordinated for certain purposes, it has been supposed that all the parts must have been simultaneously modified^[39]," and the sound argument that the co-ordination itself cannot have been due to natural selection alone. This important distinction may be rendered more clear as follows. [Pg 66]

The facts of artificial selection prove that immense modifications of structure may be caused by a cumulative blending in the same individuals of characters which were originally distributed among different individuals. Now, in the parallel case of natural selection the characters thus blended will usually—if not invariably—be of an adaptive kind; and their eventual blending together in the same individuals will be due to free intercrossing of the most fit. But this *blending of adaptations* is quite a different matter from the *occurrence of co-ordination*. For it belongs to the essence of co-ordination that each of the co-ordinated parts should be destitute of adaptive value *per se*: the adaptation only begins to arise if all the parts in question occur associated together in the same individuals *from the very first*. In this case it is obvious that the analogy of artificial selection can be of no avail in explaining the facts, since the difficulty presented has nothing to do with the blending in single individuals of adaptations previously distributed among different individuals; it has to do with the simultaneous appearance in single individuals of a co-adaptation of parts, none of which could ever have been of any adaptive value had it been previously distributed among different individuals. Consequently, where Darwin comes to consider this particular case (or the case of co-adaptation as distinguished from the blending of adaptations), he freely invokes the aid of the Lamarckian principles^[40]. [Pg 67]

Wallace, on the other hand, refuses to do this, and says that "the best answer to the difficulty" of supposing natural selection to have been the only cause of co-adaptation may be "found in the fact that the very thing said to be impossible by variation and natural selection, has been again and again affected by variation and artificial selection^[41]." This analogy (which Darwin had already and very properly adduced with regard to the *blending of adaptations*) he enforces by special illustrations; but he does not appear to perceive that it misses the whole and only point of the "difficulty" against which it is brought. For the case which his analogy sustains is not that which Darwin, Spencer, Broca and others, mean by *co-adaptation*: it is the case of a blending of *adaptations*. It is not the case where adaptation is *first initiated in spite of intercrossing*, by a fortuitous concurrence of variations each in itself being without adaptive value: it is the case where adaptation is *afterwards increased*

by means of intercrossing, through the blending of variations each of which has always been in itself of adaptive value. [Pg 68]

From this I hope it will be apparent that the only way in which the "difficulty" from co-adaptation can be logically met by the ultra-Darwinian school, is by denying that the phenomenon of co-adaptation (as distinguished from the blending of adaptations) is ever to be really met with in organic nature. It may be argued that in all cases where co-adaptation *appears* to occur, closer examination will show that the facts are really due to a blending of adaptations. The characters A + B + C + D, which are now found united in the same organism, and, as thus united, all conspiring to a common end, may originally have been distributed among different organisms, where they *severally* subserved some other ends—or possibly the same end, though in a less efficient manner. Obviously, however, in this case their subsequent combination in the same organism would not be an instance of co-adaptation, but merely of an advantageous blending together of already existing adaptations. This argument, or rejoinder, has in point of fact been adopted by Professor Meldola, he believes that all cases of seeming co-adaptation are thus due to a mere blending of adaptations^[42]. Of course, if this position can be maintained, the whole difficulty from co-adaptation would lapse. But even then it would lapse on the ground of *fact*. It would not have been overturned, or in any way affected, by Wallace's *argument* from artificial selection. For, in that event, no such argument would be required, and, if adduced, would be irrelevant, since no one has ever alleged that there is any difficulty in understanding the mere confluence of adaptations by free-intercrossing of the best adapted. [Pg 69]

Now, if we are agreed that the only question in debate is the question of fact whether or not co-adaptation ever occurs in nature, it appears to me that the best field for debating the question is furnished by the phenomena of reflex action. I can well perceive that the instances adduced by Broca and Spencer in support of their common argument—such as the giraffe, the elk, &c.—are equivocal. But I think that many instances which may be adduced of reflex action are much more to the point. *For it belongs to the very nature of reflex action that it cannot work unless all parts of the machinery concerned are already present, and already co-ordinated, in the same organism.* It would be useless, in so far as such action is concerned if the afferent and efferent nerves, the nerve-centre, and the muscles organically grouped together, were not all present from the very first in the same individuals, and from the very first were not co-ordinated as a definite piece of organic machinery.

With respect to reflex actions, therefore, it is desirable to begin by pointing out how widely the adaptations which they involve differ from those where no manufacture, so to speak, of special machinery is required. Thus, it is easy to understand how natural selection alone is capable of gradually accumulating congenital variations in the direction of protective colouring; of mimicry; of general size, form, mutual correlation of parts as connected with superior strength, fleetness, agility, &c.; of greater or less development of particular parts, such as legs, wings, tails, &c. For in all such cases the adaptation which is in process of accumulation is from its very commencement and throughout each of its subsequent stages, of *use* in the struggle for existence. And inasmuch as all the individuals of each successive generation vary round the specific mean which characterized the preceding generation, there will always be a sufficient number of individuals which present congenital variations of the kind required for natural selection to seize upon, without danger of their being swamped by free intercrossing—as Mr. Wallace has very ably shown in his *Darwinism*. But this law of averages can apply only to cases where single structures—or a single group of correlated structures—are already present, and already varying round a specific mean. The case is quite different where a *co-ordination* of structures is required for the performance of a *previously non-existent* reflex action. For some, at least, of these structures must be *new*, as must also be the function which all of them first conspire to perform. Therefore, neither the new elements of structure, nor the new combination of structures, can have been previously given as varying round a specific mean. On the contrary, a very definite piece of machinery, [Pg 70]

consisting of many co-ordinated parts, must somehow or other be originated in a high degree of working efficiency, before it can be capable of answering its purpose in the prompt performance of a particular action under particular circumstances of stimulation. Lastly, such pieces of machinery are always of a highly delicate character, and usually involve so immensely complex a co-ordination of mutually dependent parts, that it is only a physiologist who can fully appreciate the magnitude of the distinction between "adaptations" of this kind, and "adaptations" of the kind which arise through natural selection seizing upon congenital variations as these oscillate round a specific mean. [Pg 71]

Or the whole argument may be presented in another form, under three different headings, thus:—

In the first place, it will be evident from what has just been said, that such a piece of machinery as is concerned in even the simplest reflex action cannot have occurred in any considerable number of individuals of a species, *when it first began to be constructed*. On the contrary, if its *origin* were dependent on congenital variations alone, the needful co-adaptation of parts which it requires can scarcely have happened to occur in more than a very small percentage of cases—even if it be held conceivable that by such means alone it should ever have occurred at all. Hence, instead of preservation and subsequent improvement having taken place *in consequence of* free intercrossing among all individuals of the species (as in the cases of protective colouring, &c., where adaptation has no reference to any mechanical co-adaptation of parts), they must have taken place *in spite of* such intercrossing.

In the second place, adaptations due to organic machineries of this kind differ in another all-important respect from those due to a summation of adaptive characters which are already present and already varying round a specific mean. The latter depend for their summation upon the fact—not merely, as just stated, that they are already present, already varying round a specific mean, and therefore owe their progressive evolution to free intercrossing, but also—that *they admit of very different degrees of adaptation*. It is only because the degree of adaptation in generation B is superior to that in generation A that *gradual improvement* in respect of adaptation is here possible. In the case of protective resemblance, for example, a very imperfect and merely accidental resemblance to a leaf, to another insect, &c., may at the first start have conferred a sufficient degree of adaptive imitation to count for something in the struggle for life; and, if so, the basis would be given for a progressive building up by natural selection of structures and colours in ever-advancing degrees of adaptive resemblance. There is here no necessity to suppose—nor in point of fact is it ever supposed, since the supposition would involve nothing short of a miracle—that such extreme perfection in this respect as we now so frequently admire has originated suddenly in a single generation, as a collective variation of a congenital kind affecting simultaneously a large proportional number of individuals. But in the case of a reflex mechanism—which may involve even greater marvels of adaptive adjustment, and *all* the parts of which must occur in the same *individuals* to be of any use—it *is* necessary to suppose some such sudden and collective origin in some very high degree of efficiency, if natural selection has been the only principle concerned in afterwards perfecting the mechanism. For it is self-evident that a reflex action, from its very nature, cannot admit of any great differences in its degrees of adaptation: if it is to work at all, so as to count for anything in the struggle for life, it must already be given in a state of working efficiency. So that, unless we invoke either the doctrine of "prophetic types" or the theory of sudden creations, I confess I do not see how we are to explain either the origin, or the development, of a reflex mechanism by means of natural selection alone. [Pg 72]

Lastly, in the third place, *even when reflex mechanisms have been fully formed*, it is often beyond the power of sober credence to believe that they now are, or ever can have been, of selective value in the struggle for existence, as I will show further on. And such cases go to [Pg 73]

fortify the preceding argument. For if not conceivably of selective value even when completely evolved, much less can they conceivably have been so through all the stages of their complex evolution back to their very origin. Therefore, supposing for the present that there are such cases of reflex action in nature, neither their origin nor their development can conceivably have been due to natural selection alone. The Lamarckian factors, however, have no reference to degrees of adaptation, any more than they have to degrees of complexity. No question of value, as selective or otherwise, can obtain in their case: neither in their case does any difficulty obtain as regards the co-adaptation of severally useless parts.

Now, if all these distinctions between the Darwinian and Lamarckian principles are valid— [Pg 74] and I cannot see any possibility of doubt upon this point—strong evidence in favour of the latter would be furnished by cases (if any occur) where structures, actions, instincts, &c., although of some adaptive value, are nevertheless plainly not of selective value. According to the ultra-Darwinian theory, no such cases ought ever to occur: according to the theory of Darwin himself, they ought frequently to occur. Therefore a good test, or criterion, as between these different theories of organic evolution is furnished by putting the simple question of fact—Can we, or can we not, show that there are cases of adaptation where the degree of adaptation is so small as to be incompatible with the supposition of its presenting a selective value? And if we put the wider question—Are there any cases where the co-adaptation of severally useless parts has been brought about, when even the resulting whole does not present a selective value?—then, of course, we impose a still more rigid test.

Well, notwithstanding the difficulty of proving such a negative as the absence of natural selection where adaptive development is concerned, I believe that there are cases which conform to both these tests simultaneously; and, moreover, that they are to be found in most abundance where the theory of use-inheritance would most expect them to occur—namely, in the province of reflex action. For the very essence of this theory is the doctrine, that constantly associated use of the same parts for the performance of the same action will progressively organize those parts into a reflex mechanism—no matter how high a degree of co-adaptation may thus be reached on the one hand, or how low a degree of utilitarian value on the other. [Pg 75]

Having now stated the general or abstract principles which I regard as constituting a defence of the Lamarckian factors, so far as this admits of being raised on grounds of physiology, we will now consider a few concrete cases by way of illustration. It is needless to multiply such cases for the mere purpose of illustration. For, on reading those here given, every physiologist will at once perceive that they might be added to indefinitely. The point to observe is, the relation in which these samples of reflex action stand to the general principles in question; for there is nothing unusual in the samples themselves. On the contrary, they are chosen because they are fairly typical of the phenomena of reflex action in general.

In our own organization there is a reflex mechanism which ensures the prompt withdrawal of the legs from any source of irritation supplied to the feet. For instance, even after a man has broken his spine in such a manner as totally to interrupt the functional continuity of his spinal cord and brain, the reflex mechanism in question will continue to retract his legs when his feet are stimulated by a touch, a burn, &c. This responsive action is clearly an adaptive action, and, as the man neither feels the stimulation nor the resulting movement, it is as clearly a reflex action. The question now is as to the mode of its origin and development.

I will not here dwell upon the argument from co-adaptation, because this may be done more effectually in the case of more complicated reflex actions, but will ask whether we can [Pg 76] reasonably hold that this particular reflex action—comparatively simple though it is—has ever been of selective value to the human species, or to the ancestors thereof? Even in its

present fully-formed condition it is fairly questionable whether it is of any adaptive *value* at all. The movement performed is no doubt an adaptive *movement*; but is there any occasion upon which the reflex mechanism concerned therein can ever have been of adaptive *use*? Until a man's legs have been paralyzed as to their voluntary motion, he will always promptly withdraw his feet from any injurious source of irritation by means of his conscious intelligence. True, the reflex mechanism secures an almost inappreciable saving in the time of response to a stimulus, as compared with the time required for response by an act of will; but the difference is so exceedingly small, that we can hardly suppose the saving of it in this particular case to be a matter of any adaptive—much less selective—importance. Nor is it more easy to suppose that the reflex mechanism has been developed by natural selection for the purpose of replacing voluntary action when the latter has been destroyed or suspended by grave spinal injury, paralysis, coma, or even ordinary sleep. In short, even if for the sake of argument we allow it to be conceivable that any single human being, ape, or still more distant ancestor, has ever owed its life to the possession of this mechanism, we may still be certain that not one in a million can have done so. And, if this is the case with regard to the mechanism as now fully constructed, still more must it have been the case with regard to all the previous stages of construction. For here, without elaborating the point, it would appear that a process of construction by survival of the fittest alone is incomprehensible.

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On the other hand, of course, the theory of use-inheritance furnishes a fully intelligible—whether or not a true—explanation. For those nerve-centres in the spinal cord which co-ordinate the muscles required for retracting the feet are the centres used by the will for this purpose. And, by hypothesis, the frequent use of them for this purpose under circumstances of stimulation which render the muscular response appropriate, will eventually establish an organic connexion between such response and the kind of stimulation to which it is appropriate—even though there be no utilitarian reason for its establishment^[43]. To invert a phrase of Aristotle, we do not frequently use this mechanism because we have it (seeing that in our normal condition there is no necessity for such use); but, by hypothesis, we have it because we have frequently used its several elements in appropriate combination.

I will adduce but one further example in illustration of these general principles—passing at once from the foregoing case of comparative simplicity to one of extreme complexity.

There is a well-known experiment on a brainless frog, which reveals a beautiful reflex mechanism in the animal, whereby the whole body is enabled continually to readjust its balance on a book (or any other plane surface), as this is slowly rotated on a horizontal axis. So long as the book is lying flat, the frog remains motionless; but as soon as the book is tilted a little, so that the frog is in danger of slipping off, all the four feet begin to crawl up the hill; and the steeper the hill becomes, the faster they crawl. When the book is vertical, the frog has reached the now horizontal back, and so on. Such being the facts, the question is—How can the complicated piece of machinery thus implied have been developed by natural selection? Obviously it cannot have been so by any of the parts concerned having been originally distributed among different individuals, and afterwards united in single individuals by survival (i.e. free intercrossing) of the fittest. In other words, the case is obviously one of co-adaptation, and not one of the blending of adaptations. Again, and no less obviously, it is impossible that the co-adaptation can have been *gradually developed* by natural selection, because, in order to have been so, it must by hypothesis have been of some degree of use in every one of its stages; yet it plainly cannot have been until it had been fully perfected in all its astonishing complexity^[44].

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Lastly, not only does it thus appear impossible that during all stages of its development—or while as yet incapable of performing its intricate function—this nascent mechanism can have had any adaptive value; but even as now fully developed, who will venture to maintain that it presents any selective value? As long as the animal preserves its brain, it will likewise preserve its balance, by the exercise of its intelligent volition. And, if the brain

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were in some way destroyed, the animal would be unable to breed, or even to feed; so that natural selection can never have had any *opportunity*, so to speak, of developing this reflex mechanism in brainless frogs. On the other hand, as we have just seen, we cannot perceive how there can ever have been any *raison d'être* for its development in normal frogs—even if its development were conceivably possible by means of this agency. But if practice makes perfect in the race, as it does in the individual, we can immediately perceive that the constant habit of correctly adjusting its balance may have gradually developed, in the batrachian organization, this non-necessary reflex^[45].

And, of course, this example—like that of withdrawing the feet from a source of stimulation, which a frog will do as well as a man—does not stand alone. Without going further a-field than this same animal, any one who reads, from our present point of view, Goltz's work on the reflex actions of the frog, will find that the great majority of them—complex and refined though most of them are—cannot conceivably have ever been of any use to any frog that was in undisturbed possession of its brain. [Pg 80]

Hence, not to occupy space with a reiteration of facts all more or less of the same general kind, and therefore all presenting identical difficulties to ultra-Darwinian theory, I shall proceed to give two others which appear to me of particular interest in the present connexion, because they furnish illustrations of reflex actions in a state of only partial development, and are therefore at the present moment demonstrably useless to the animal which displays them.

Many of our domesticated dogs, when we gently scratch their sides and certain other parts of the body, will themselves perform scratching movements with the hind leg of the same side as that upon which the irritation is being supplied. According to Goltz^[46], this action is a true reflex; for he found that it is performed equally well in a dog which has been deprived of its cerebral hemispheres, and therefore of its normal volition. Again, according to Haycraft^[47], this reflex is congenital, or not acquired during the life-time of each individual dog. Now, although the action of scratching is doubtless adaptive, it appears to me incredible that it could ever have become organized into a congenital reflex by natural selection. For, in order that it should, the scratching away fleas would require to have been a function of selective value. Yet, even if the irritation caused by fleas were supposed to be so far fatal in the struggle for existence, it is certain that they would always be scratched away by the conscious intelligence of each individual dog; and, therefore, that no advantage could be gained by organizing the action into a reflex. On the other hand, if acquired characters are ever in any degree transmitted, it is easy to understand how so frequently repeated an action should have become, in numberless generations of dogs, congenitally automatic. [Pg 81]

So much for the general principle of selective value as applied to this particular case. And similarly, of course, we might here repeat the application of all the other general principles, which have just been applied in the two preceding cases. But it is only one of these other general principles which I desire in the present case specially to consider, for the purpose of considering more closely than hitherto the difficulty which this principle presents to ultra-Darwinian theory. [Pg 82]

The difficulty to which I allude is that of understanding how all the stages in the *development* of a reflex action can have been due to natural selection, seeing that, before the reflex mechanism has been sufficiently elaborated to perform its function, it cannot have presented any degree of utility. Now the particular force of the present example, the action of scratching—as also of the one to follow—consists in the fact that it is a case where a reflex action is not yet completely organized. It appears to be only in course of construction, so that it is neither invariably present, nor, when it is present, is it ever fully adapted to the performance of its function.

That it is not invariably present (when the brain is so) may be proved by trying the simple experiment on a number of puppies—and also of full-grown dogs. Again, that even when it is present it is far from being fully adapted to the performance of its function, may be proved by observing that only in rare instances does the scratching leg succeed in scratching the place which is being irritated. The movements are made more or less at random, and as often as not the foot fails to touch the body at any place at all. Hence, although we have a "prophecy" of a reflex action well designed for the discharge of a particular function, at present the machinery is not sufficiently perfected for the adequate discharge of that function. In this important respect it differs from the otherwise closely analogous reflex action of the frog, whereby the foot of the hind leg is enabled to localize with precision a seat of irritation on the side of the body. But this beautiful mechanism in the frog cannot have sprung into existence ready formed at any historical moment in the past history of the phyla. It must have been the subject of a more or less prolonged evolution, in some stage of which it must presumably have resembled the now nascent scratching reflex of the dog, in making merely abortive attempts at localizing the seat of irritation—supposing, of course, that some physiologist had been there to try the experiment by first removing the brain. Now, even if one could imagine it to be, either in the frog or in the dog, a matter of selective importance that so exceedingly refined a mechanism should have been developed for the sole purpose of inhibiting the bites of parasites—which in every normal animal would certainly be discharged by an *intentional* performance of the movements in question,—even if, in order to save an hypothesis at all costs, we make so violent a supposition as this, still we should do so in vain. For it would still remain undeniably certain that the reflex mechanism is *not* of any selective value. Even now the mechanism in the dog is not sufficiently precise to subserve the only function which occasionally and abortively it attempts to perform. Thus it has all the appearance of being but an imitating shadow of certain neuro-muscular adjustments, which have been habitually performed in the canine phyla by a volitional response to cutaneous irritation. Were it necessary, this argument might be strengthened by observing that the reflex action is positively *improved* by removal of the brain.

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The second example of a nascent reflex in dogs which I have to mention is as follows.

Goltz found that his brainless dogs, when wetted with water, would shake themselves as dry as possible, in just the same way as normal dogs will do under similar circumstances. This, of course, proves that the shaking movements may be performed by a reflex mechanism, which can have no other function to perform in the organization of a dog, and which, besides being of a highly elaborate character, will respond only to a very special kind of stimulation. Now, here also I find that the mechanism is congenital, or not acquired by individual experience. For the puppies on which I experimented were kept indoors from the time of their birth—so as never to have had any experience of being wetted by rain, &c.—till they were old enough to run about with a full power of co-ordinating their general movements. If these young animals were suddenly plunged into water, the shock proved too great: they would merely lie and shiver. But if their feet alone were wetted, by being dipped in a basin of water, the puppies would soon afterwards shake their heads in the peculiar manner which is required for shaking water off the ears, and which in adult dogs constitutes the first phase of a general shaking of the whole body.

Here, then, we seem to have good evidence of all the same facts which were presented in the case of the scratching reflex. In the first place, co-adaptation is present in a very high degree, because this shaking reflex in the dog, unlike the skin-twitching reflex in the horse, does not involve only a single muscle, or even a single group of muscles; it involves more or less the co-ordinated activity of many voluntary muscles all over the body. Such, at any rate, is the case when the action is performed by the intelligent volition of an adult dog; and if a brainless dog, or a young puppy, does not perform it so extensively or so vigorously, this only goes to prove that the reflex has not yet been sufficiently developed to serve as a

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substitute for intelligent volition—i.e. that it is *useless*, or a mere organic shadow of the really adaptive substance. Again, even if this nascent reflex had been so far developed as to have been capable of superseding voluntary action, still we may fairly doubt whether it could have proved of selective value. For it is questionable whether the immediate riddance of water after a wetting is a matter of life and death to dogs in a state of nature. Moreover, even if it were, every individual dog would always have got rid of the irritation, and so of the danger, by means of a *voluntary* shake—with the double result that natural selection has never had any opportunity of gradually building up a special reflex mechanism for the purpose of securing a shake, and that the canine race have not had to wait for any such unnecessary process. Lastly, such a process, besides being unnecessary, must surely have been, under any circumstances, impossible. For even if we were to suppose—again for the sake of saving an hypothesis at any cost—that the presence of a fully-formed shaking reflex is of selective value in the struggle for existence, it is perfectly certain that all the stages through which the construction of so elaborate a mechanism must have passed could not have been, under any circumstances, of any such value. [Pg 86]

But, it is needless to repeat, according to the hypothesis of use-inheritance, there is no necessity to suppose that these incipient reflex mechanisms *are* of any value. If function produces structure in the race as it does in the individual, the voluntary and frequently repeated actions of scratching and shaking may very well have led to an organic integration of the neuro-muscular mechanisms concerned. Their various parts having been always co-ordinated for the performance of these actions by the intelligence of innumerable dogs in the past, their co-adapted activity in their now automatic responses to appropriate stimuli presents no difficulty. And the consideration that neither in their prospectively more fully developed condition, nor, *a fortiori*, in their present and all previous stages of evolution, can these reflex mechanisms be regarded as presenting any selective—or even so much as any adaptive—value, is neither more nor less than the theory of use-inheritance would expect.

Thus, with regard to the phenomena of reflex action in general, all the facts are such as this theory requires, while many of the facts are such as the theory of natural selection alone cannot conceivably explain. Indeed, it is scarcely too much to say, that most of the facts are such as directly contradict the latter theory in its application to them. But, be this as it may, at present there are only two hypotheses in the field whereby to account for the facts of adaptive evolution. One of these hypotheses is universally accepted, and the only question is whether we are to regard it as *alone* sufficient to explain *all* the facts. The other hypothesis having been questioned, we can test its validity only by finding cases which it is fully capable of explaining, and which do not admit of being explained by its companion hypothesis. I have endeavoured to show that we have a large class of such cases in the domain of reflex action, and shall next endeavour to show that there is another large class in the domain of instinct. [Pg 87]

If instinct be, as Professor Hering, Mr. Samuel Butler, and others have argued, "hereditary habit"—i. e. if it comprises an element of transmitted experience—we at once find a complete explanation of many cases of the display of instinct which otherwise remain inexplicable. For although a large number—or even, as I believe, a large majority—of instincts are explicable by the theory of natural selection alone, or by supposing that they were gradually developed by the survival of fortuitous variations in the way of advantageous psychological peculiarities, this only applies to comparatively simple instincts, such as that of a protectively coloured animal exhibiting a preference for the surroundings which it resembles, or even adopting attitudes in imitation of objects which occur in such surroundings. But in all cases where instincts become complex and refined,

we seem almost compelled to accept Darwin's view that their origin is to be sought in consciously intelligent adjustments on the part of ancestors. [Pg 88]

Thus, to give only one example, a species of *Sphex* preys upon caterpillars, which it stings in their nerve-centres for the purpose of paralyzing, without killing them. The victims, when thus rendered motionless, are then buried with the eggs of the *Sphex*, in order to serve as food for her larvae which subsequently develop from these eggs. Now, in order thus to paralyze a caterpillar, the *Sphex* has to sting it successively in nine minute and particular points along the ventral surface of the animal—and this the *Sphex* unerringly does, to the exclusion of all other points of the caterpillar's anatomy. Well, such being the facts—according to M. Fabre, who appears to have observed them carefully—it is conceivable enough, as Darwin supposed^[48], that the ancestors of the *Sphex*, being like many other hymenopterous insects highly intelligent, should have observed that on stinging caterpillars in these particular spots a greater amount of effect was produced than could be produced by stinging them anywhere else; and, therefore, that they habitually stung the caterpillars in these places only, till, in course of time, this originally intelligent habit became by heredity instinctive. But now, on the other hand, if we exclude the possibility of this explanation, it appears to me incredible that such an instinct should ever have been evolved at all; for it appears to me incredible that natural selection, unaided by originally intelligent action, could ever have developed such an instinct out of merely fortuitous variations—there being, by hypothesis, nothing to *determine* variations of an insect's mind in the direction of stinging caterpillars only in these nine intensely localized spots^[49]. [Pg 89]

Again, there are not a few instincts which appear to be wholly useless to their possessors, and others again which appear to be even deleterious. The dusting over of their excrement by certain freely-roaming carnivora; the choice by certain herbivora of particular places on which to void their urine, or in which to die; the howling of wolves at the moon; purring of cats, &c., under pleasurable emotion; and sundry other hereditary actions of the same apparently unmeaning kind, all admit of being readily accounted for as useless habits originally acquired in various ways, and afterwards perpetuated by heredity, because not sufficiently deleterious to have been stamped out by natural selection^[50]. But it does not seem possible to explain them by survival of the fittest in the struggle for existence.

Finally, in the case of our own species, it is self-evident that the aesthetic, moral, and religious instincts admit of a natural and easy explanation on the hypothesis of use-inheritance, while such is by no means the case if that hypothesis is rejected. Our emotions of the ludicrous, of the beautiful, and of the sublime, appear to be of the nature of hereditary instincts; and be this as it may, it would further appear that, whatever else they may be, they are certainly not of a life-preserving character. And although this cannot be said of the moral sense when the theory of natural selection is extended from the individual to the tribe, still, when we remember the extraordinary complexity and refinement to which they have attained in civilized man, we may well doubt whether they can have been due to natural selection alone. But space forbids discussion of this large and important question on the present occasion. Suffice it therefore to say, that I doubt not Weismann himself would be the first to allow that his theory of heredity encounters greater difficulties in the domain of ethics than in any other—unless, indeed, it be that of religion^[51]. [Pg 90]

I have now given a brief sketch of the indirect evidence in favour of the so-called Lamarckian factors, in so far as this appears fairly deducible from the facts of reflex action and of instinct. It will now be my endeavour to present as briefly what has to be said against this evidence.

As previously observed, the facts of reflex action have not been hitherto adduced in the present connexion. This has led me to occupy considerably more space in the treatment of them than those of instinct. On this account, also, there is here nothing to quote, or to consider, *per contra*. On the other hand, however, Weismann has himself dealt with the phenomena of instinct in animals, though not, I think, in man—if we except his brilliant essay on music. Therefore let us now begin this division of our subject by briefly stating, and considering, what he has said upon the subject. [Pg 91]

The answer of Weismann to difficulties which arise against the ultra-Darwinian theory in the domain of instinct, is as follows:—

"The necessity for extreme caution in appealing to the supposed hereditary effects of use, is well shown in the case of those numerous instincts which only come into play once in a life-time, and which do not therefore admit of improvement by practice. The queen-bee takes her nuptial flight only once, and yet how many and complex are the instincts and the reflex mechanisms which come into play on that occasion. Again, in many insects the deposition of eggs occurs but once in a life-time, and yet such insects always fulfil the necessary conditions with unfailing accuracy^[52]."

But in this rejoinder the possibility is forgotten, that although such actions are *now* performed only once in the individual life-time, *originally*—i.e. when the instincts were being developed in a remote ancestry—they may have been performed on many frequent and successive occasions during the individual life-time. In all the cases quoted by Weismann, instincts of the kind in question bear independent evidence of high antiquity, by occurring in whole genera (or even families), by being associated with peculiar and often highly evolved structures required for their performance, and so on. Consequently, in these cases ample time has been allowed for subsequent changes of habit, and of seasonal alterations with respect to propagation—both these things being of frequent and facile occurrence among animals of all kinds, even within periods which fall under actual observation. Nevertheless, I do not question that there are instinctive activities which, as far as we are able to see, can never have been performed more than once in each individual life-time^[53]. The fact, however, only goes to show what is fully admitted—that some instincts (and even highly complex instincts) have apparently been developed by natural selection alone. Which, of course, is not equivalent to showing that all instincts must have been developed by natural selection alone. The issue is not to be debated on general grounds like this, but on those of particular cases. Even if it were satisfactorily proved that the instincts of a queen-bee have been developed by natural selection, it would not thereby be proved that such has been the case with the instincts of a *Sphex* wasp. One can very well understand how the nuptial flight of the former, with all its associated actions, may have been brought about by natural selection alone; but this does not help us to understand how the peculiar instincts of the latter can have been thus caused. [Pg 92]

Strong evidence in favour of Weismann's views does, however, at first sight seem to be furnished by social hymenoptera in other respects. For not only does the queen present highly specialized and altogether remarkable instincts; but the neuters present totally different and even still more remarkable instincts—which, moreover, are often divided into two or more classes, corresponding with the different "castes." Yet the neuters, being barren females, never have an opportunity of bequeathing their instincts to progeny. Thus it appears necessary to suppose that the instincts of all the different castes of neuters are latent in the queen and drones, together with the other instincts which are patent in both. Lastly, it seems necessary to suppose that all this wonderful organization of complex and segregated instincts must have been built up by natural selection acting exclusively on the queens and drones—seeing that these exercise their own instincts only once in a life-time, while, as just observed, the neuters cannot possibly bequeath their individual experience to progeny. [Pg 93]

Obviously, however, natural selection must here be supposed to be operating at an immense disadvantage; for it must have built up the often diverse and always complex instincts of neuters, not directly, but indirectly through the queens and drones, which never manifest any of these instincts themselves.

Now Darwin fully acknowledged the difficulty of attributing these results to the unaided influence of natural selection; but the fact of neuter insects being unable to propagate seemed to him to leave no alternative. And so it seems to Weismann, who accordingly quotes these instincts in support of his views. And so it seemed to me, until my work on *Animal Intelligence* was translated into French, and an able Preface was supplied to that translation by M. Perrier. In this Preface it is argued that we are not necessarily obliged to exclude the possibility of Lamarckian principles having operated in the original formation of these instincts. On the contrary, if such principles ever operate at all, Perrier shows that here we have a case where it is virtually certain that they must have operated. For although neuter insects are now unable to propagate, their organization indicates—if it does not actually prove—that they are descended from working insects which were able to propagate. Thus, in all probability, what we now call a "hive" was originally a society of sexually mature insects, all presenting the same instincts, both as to propagation and to co-operation. When these instincts, thus common to all individuals composing the hive, had been highly perfected, it became of advantage in the struggle for existence (between different hives or communities) that the functions of reproduction should devolve more upon some individuals, while those of co-operation should devolve more upon others. Consequently, this division of labour began, and gradually became complete, as we now find it in bees and ants. Perrier sustains the hypothesis thus briefly sketched by pointing to certain species of social hymenoptera where we may actually observe different stages of the process—from cases where all the females of the hive are at the same time workers and breeders, up to the cases where the severance between these functions has become complete. Therefore, it seems to me, it is no longer necessary to suppose that in these latter cases all the instincts of the (now) barren females can only have been due to the unaided influence of natural selection.

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Nevertheless, although I think that Perrier has made good his position thus far, that his hypothesis fails to account for some of the instincts which are manifested by neuter insects, such as those which, so far as I can see, must necessarily be supposed to have originated after the breeding and working functions had become separated—seeing that they appear to have exclusive reference to this peculiar state of matters. Possibly, however, Perrier might be able to meet each of these particular instincts, by showing how they could have arisen out of simpler beginnings, prior to the separation of the two functions in question. There is no space to consider such possibilities in detail; but, until this shall have been done, I do not think we are entitled to conclude that the phenomena of instinct as presented by neuter insects are demonstrably incompatible with the doctrines of Lamarck—or, that these phenomena are available as a logical proof of the unassisted agency of natural selection in the case of instincts in general^[54].

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(B.)

Inherited Effects of Use and of Disuse.

There is no doubt that Darwin everywhere attaches great weight to this line of evidence. Nevertheless, in my opinion, there is equally little doubt that, taken by itself, it is of immeasurably less weight than Darwin supposed. Indeed, I quite agree with Weismann that the whole of this line of evidence is practically worthless; and for the following reasons.

The evidence on which Darwin relied to prove the inherited effects of use and disuse was derived from his careful measurements of the increase or decrease which certain bones of

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our domesticated animals have undergone, as compared with the corresponding bones of ancestral stocks in a state of nature. He chose domesticated animals for these investigations, because, while yielding unquestionable cases of increased or diminished use of certain organs over a large number of sequent generations, the results were not complicated by the possible interference of natural selection on the one hand, or by that of the economy of nutrition on the other. For "with highly-fed domesticated animals there seems to be no economy of growth, or any tendency to the elimination of superfluous details^[55];" seeing that, among other considerations pointing in the same direction, "structures which are rudimentary in the parent species, sometimes become partially re-developed in our domesticated productions^[56]."

The method of Darwin's researches in this connexion was as follows. Taking, for example, the case of ducks, he carefully weighed and measured the wing-bones and leg-bones of wild and tame ducks; and he found that the wing-bones were smaller, while the leg-bones were larger, in the tame than in the wild specimens. These facts he attributed to many generations of tame ducks using their wings less, and their legs more, than was the case with their wild ancestry. Similarly he compared the leg-bones of wild rabbits with those of tame ones, and so forth—in all cases finding that where domestication had led to increased use of a part, that part was larger than in the wild parent stock; while the reverse was the case with parts less used. Now, although at first sight these facts certainly do seem to yield good evidence of the inherited effects of use and disuse, they are really open to the following very weighty objections.

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First of all, there is no means of knowing how far the observed effects may have been due to increased or diminished use during only the individual life-time of each domesticated animal. Again, and this is a more important point, in all Darwin's investigations the increase or decrease of a part was estimated, not by directly comparing, say the wing-bones of a domesticated duck with the wing-bones of a wild duck, but by comparing the *ratio* between the wing and leg bones of a tame duck with the *ratio* between the wing and leg bones of a wild duck. Consequently, if there be any reason to doubt the supposition that a really inherited decrease in the size of a part thus estimated is due to the inherited effects of disuse, such a doubt will also extend to the evidence of increased size being due to the inherited effects of use. Now there is the gravest possible doubt lying against the supposition that any really inherited decrease in the size of a part is due to the inherited effects of disuse. For it may be—and, at any rate to some extent, must be—due to another principle, which it is strange that Darwin should have overlooked. This is the principle which Weismann has called Panmixia, and which cannot be better expressed than in his own words:—

"A goose or a duck must possess strong powers of flight in the natural state, but such powers are no longer necessary for obtaining food when it is brought into the poultry-yard; so that a rigid selection of individuals with well-developed wings at once ceases among its descendants. Hence, in the course of generations, a deterioration of the organs of flight must necessarily ensue^[57]."

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Or, to state the case in another way: if any structure which was originally built up by natural selection on account of its use, ceases any longer to be of so much use, in whatever degree it ceases to be of use, in that degree will the premium before set upon it by natural selection be withdrawn. And the consequence of this withdrawal of selection as regards that particular part will be to allow the part to degenerate in successive generations. Such is the principle which Weismann calls Panmixia, because, by the withdrawal of selection from any particular part, promiscuous breeding ensues with regard to that part. And it is easy to see that this principle must be one of very great importance in nature; because it must necessarily come into operation in all cases where any structure or any instinct has, through

any change in the environment or in the habits of a species, ceased to be useful. It is likewise easy to see that its effect must be the same as that which was attributed by Darwin to the inherited effect of disuse; and, therefore, that the evidence on which he relied in proof of the inherited effects both of use and of disuse is vitiated by the fact that the idea of Panmixia did not occur to him.

Here, however, it may be said that the idea first occurred to me^[58] just after the publication of the last edition of the *Origin of Species*. I called the principle the Cessation of Selection [Pg 99]—which I still think a better, because a more descriptive, term than Panmixia; and at that time it appeared to me, as it now appears to Weismann, entirely to supersede the necessity of supposing that the effect of disuse is ever inherited in any degree at all. Thus it raised the whole question as to the admissibility of Lamarckian principles in general; or the question on which we are now engaged touching the possible inheritance of acquired, as distinguished from congenital, characters. But on discussing the matter with Mr. Darwin, he satisfied me that the larger question was not to be so easily closed. That is to say, although he fully accepted the principle of the Cessation of Selection, and as fully acknowledged its obvious importance, he convinced me that there was independent evidence for the transmission of acquired characters, sufficient in amount to leave the general structure of his previous theory unaffected by what he nevertheless recognized as a factor which must necessarily be added. All this I now mention in order to show that the issue which Weismann has raised since Darwin's death was expressly contemplated during the later years of Darwin's life. For if the idea of Panmixia—in the absence of which Weismann's entire system would be impossible—had never been present to Darwin's mind, we should have been left in uncertainty how he would have regarded this subsequent revolt against what are generally called the Lamarckian principles^[59].

Moreover, in this connexion we must take particular notice that the year after I had [Pg 100] published these articles on the Cessation of Selection, and discussed with Mr. Darwin the bearing of this principle on the question of the transmission of acquired characters, Mr. Galton followed with his highly important essay on Heredity. For in this essay Mr. Galton fully adopted the principle of the Cessation of Selection, and was in consequence the first publicly to challenge the Lamarckian principles—pointing out that, if it were thus possible to deny the transmission of acquired characters *in toto*, "we should be relieved from all further trouble"; but that, if such characters are transmitted "in however faint a degree, a complete theory of heredity must account for them." Thus the question which, in its revived condition, is now attracting so much attention, was propounded in all its parts some fifteen or sixteen years ago; and no additional facts or new considerations of any great importance bearing upon the subject have been adduced since that time. In other words, about a year after my own conversations with Mr. Darwin, the whole matter was still more effectively brought before his notice by his own cousin. And the result was that he still retained his belief in the Lamarckian factors of organic evolution, even more strongly than it was retained either by Mr. Galton or myself^[60].

We have now considered the line of evidence on which Darwin chiefly relied in proof of the transmissibility of acquired characters; and it must be allowed that this line of evidence is practically worthless. What he regarded as the inherited effects of use and of disuse may be [Pg 101] entirely due to the cessation of selection in the case of our domesticated animals, combined with an active *reversal* of selection in the case of natural species. And in accordance with this view is the fact that the degeneration of disused parts proceeds much further in the case of wild species than it does in that of domesticated varieties. For although it may be said that in the case of wild species more time has been allowed for a greater accumulation of the inherited effects of disuse than can have been the case with domesticated varieties, the alternative explanation is at least as probable—that in the case of wild species the merely negative, or passive, influence of the *cessation* of selection has been continuously and

powerfully assisted by the positive, or active, influence of the *reversal* of selection, through economy of growth and the general advantage to be derived from the abolition of useless parts^[61].

The absence of any good evidence of this direct kind in favour of use-inheritance will be rendered strikingly apparent to any one who reads a learned and interesting work by Professor Semper^[62]. His object was to show the large part which he believed to have been played by external conditions of life in directly modifying organic types—or, in other words, of proving that side of Lamarckianism which refers to the immediate action of the environment, whether with or without the co-operation of use-inheritance and natural selection. Although Semper gathered together a great array of facts, the more carefully one reads his book the more apparent does it become that no single one of the facts is in itself conclusive evidence of the transmission to progeny of characters which are acquired through use-inheritance or through direct action of the environment. Every one of the facts is susceptible of explanation on the hypothesis that the principle of natural selection has been the only principle concerned. This, however, it must be observed, is by no means equivalent to proving that characters thus acquired are not transmitted. As already pointed out, it is impracticable with species in a state of nature to dissociate the distinctively Darwinian from the possibly Lamarckian factors; so that even if the latter are largely operative, we can only hope for direct evidence of the fact from direct experiments on varieties in a state of domestication. To this branch of our subject, therefore, we will now proceed.

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CHAPTER IV. CHARACTERS AS HEREDITARY AND ACQUIRED (*continued*).

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(C.)

Experimental Evidence in favour of the Inheritance of Acquired Characters.

Notwithstanding the fact already noticed, that no experiments have hitherto been published with reference to the question of the transmission of acquired characters^[63], there are several researches which, with other objects in view, have incidentally yielded seemingly good evidence of such transmission. The best-known of these researches—and therefore the one with which I shall begin—is that of Brown-Séquard touching the effects of certain injuries of the nervous system in guinea-pigs.

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During a period of thirty years Brown-Séquard bred many thousands of guinea-pigs as material for his various researches; and in those whose parents had not been operated upon in the ways to be immediately mentioned, he never saw any of the peculiarities which are about to be described. Therefore the hypothesis of coincidence, at all events, must be excluded. The following is his own summary of the results with which we are concerned:—

1st. Appearance of epilepsy in animals born of parents which had been rendered epileptic by an injury to the spinal cord.

2nd. Appearance of epilepsy also in animals born of parents which had been rendered epileptic by section of the sciatic nerve.

3rd. A change in the shape of the ear in animals born of parents in which such a change was the effect of a division of the cervical sympathetic nerve.

4th. Partial closure of the eyelids in animals born of parents in which that state of the eyelids had been caused either by section of the cervical sympathetic nerve, or the removal of the superior cervical ganglion.

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5th. Exophthalmia in animals born of parents in which an injury to the restiform body had produced that protrusion of the eyeball. This interesting fact I have witnessed a good many times, and seen the transmission of the morbid state of the eye continue through four generations. In these animals, modified by heredity, the two eyes generally protruded, although in the parents usually only one showed exophthalmia, the lesion having been made in most cases only on one of the corpora restiformia.

6th. Haematoma and dry gangrene of the ears in animals born of parents in which these ear-alterations had been caused by an injury to the restiform body near the nib of the calamus.

7th. Absence of two toes out of the three of the hind leg, and sometimes of the three, in animals whose parents had eaten up their hind-leg toes which had become anaesthetic from a section of the sciatic nerve alone, or of that nerve and also of the crural. Sometimes, instead of complete absence of the toes, only a part of one or two or three was missing in the young, although in the parent not only the toes but the whole foot were absent (partly eaten off, partly destroyed by inflammation, ulceration, or gangrene.)

8th. Appearance of various morbid states of the skin and hair of the neck and face in animals born of parents having had similar alterations in the same parts, as effects of an injury to the sciatic nerve.

These results^[64] have been independently vouched for by two of Brown-Séquard's former assistants—Dr. Dupuy, and the late Professor Westphal. Moreover, his results with regard to epilepsy have been corroborated also by Obersteiner^[65]. I may observe, in passing, that this labour of testing Brown-Séquard's statements is one which, in my opinion, ought rather to have been undertaken, if not by Weismann himself, at all events by some of his followers. Both he and they are incessant in their demand for evidence of the transmission of acquired characters; yet they have virtually ignored the foregoing very remarkable statements. However, be this as it may, all that we have now to do is to consider what the school of Weismann has had to say with regard to these experiments on the grounds of general reasoning which they have thus far been satisfied to occupy.

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In view of Obersteiner's corroboration of Brown-Séquard's results touching the artificial production and subsequent transmission of epilepsy, Weismann accepts the facts, but, in order to save his theory of heredity, he argues that the transmission may be due to a traumatic introduction of "some unknown microbe" which causes the epilepsy in the parent, and, by invading the ova or spermatozoa as the case may be, also produces epilepsy in the offspring. Here, of course, there would be transmission of epilepsy, but it would not be, technically speaking, an hereditary transmission. The case would resemble that of syphilis, where the sexual elements remain unaffected as to their congenital endowments, although they have been made the vehicles for conveying an organic poison to the next generation.

Now it would seem that this suggestion is not, on the face of it, a probable one. For "some unknown microbe" it indeed must be, which is always on hand to enter a guinea-pig when certain operations are being performed on certain parts of the nervous system, but yet will never enter when operations of any kind are being effected elsewhere. Moreover, Westphal

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has produced the epilepsy *without any incision*, by striking the heads of the animals with a hammer^[66]. This latter fact, it appears to me, entirely abolishes the intrinsically improbable suggestion touching an unknown—and strangely eclectic—microbe. However, it is but fair to state what Weismann himself has made of this fact. The following is what he says:—

"It is obvious that the presence of microbes can have nothing to do with such an attack, but the shock alone must have caused morphological and functional changes in the centre of the pons and medulla oblongata, identical with those produced by microbes in the other cases.... Various stimuli might cause the nervous centres concerned to develop the convulsive attack which, together with its after-effects, we call epilepsy. In Westphal's case, such a stimulus would be given by a powerful mechanical shock (viz. blows on the head with a hammer); in Brown-Séquard's experiments, by the penetration of microbes^[67]."

But from this passage it would seem that Weismann has failed to notice that in "Westphal's case," as in "Brown-Séquard's experiments," the epilepsy was *transmitted to progeny*. That epilepsy may be produced in guinea-pigs by a method which does not involve any cutting (i.e. possibility of inoculation) would no doubt tend to corroborate the suggestion of microbes being concerned in its transmission when it is produced by cutting, *if in the former case there were no such transmission*. But as there *is* transmission in *both* cases, the facts, so far as I can see, entirely abolish the suggestion. For they prove that even when epilepsy is produced in the parents under circumstances which render "it obvious that the presence of microbes can have nothing to do with such an attack," the epileptiform condition is notwithstanding transmitted to the progeny. What, then, is gained by retaining the intrinsically improbable hypothesis of microbes to explain the fact of transmission "in Brown-Séquard's experiments," when this very same fact is proved to occur without the possibility of microbes "in Westphal's case"? [Pg 108]

The only other objection with regard to the seeming transmission of traumatic epilepsy which Weismann has advanced is, that such epilepsy may be produced by two or three very different operations—viz. division of the sciatic nerves (one or both), an injury to the spinal cord, and a stroke on the head. Does not this show, it is asked, that the epileptic condition of guinea-pigs is due to a generally unstable condition of the whole nervous system and is not associated with any particular part thereof? Well, supposing that such is the case, what would it amount to? I cannot see that it would in any way affect the only question in debate—viz. What is the significance of the fact that epilepsy is *transmitted*? Even if it be but "a tendency," "a disposition," or "a diathesis" that is transmitted, it is none the less a case of transmission, in fact quite as much so as if the pathological state were dependent on the impaired condition of any particular nerve-centre. For, it must be observed, there can be no question that it is always produced by an operation of *some* kind. If it were ever to originate in guinea-pigs spontaneously, there might be some room for supposing that its transmission is due to a congenital tendency running through the whole species—although even then it would remain unaccountable, on the ultra-Darwinian view, why this tendency should be congenitally *increased* by means of an operation. But epilepsy does not originate spontaneously in guinea-pigs; and therefore the criticism in question appears to me irrelevant. [Pg 109]

Again, it may be worth while to remark that Brown-Séquard's experiments do not disprove the possibility of its being some one nerve-centre which is concerned in all cases of traumatic epilepsy. And this possibility becomes, I think, a probability in view of Luciani's recent experiments on the dog. These show that the epileptic condition can be produced in this animal by injury to the cortical substance of the hemispheres, and is then transmitted to progeny^[68]. These experiments, therefore, are of great interest—first, as showing that traumatic and transmissible epilepsy is not confined to guinea-pigs; and next, as indicating

that the pathological state in question is associated with the highest nerve-centres, which may therefore well be affected by injury to the lower centres, or even by section of a large nerve trunk.

So much, then, with regard to the case of transmitted epilepsy. But now it must be noted that, even if Weismann's suggestion touching microbes were fully adequate to meet this case, it would still leave unaffected those of transmitted protrusion of the eye, drooping of the eyelid, gangrene of the ear, absence of toes, &c. In all these cases the facts, as stated by Brown-Séguar, are plainly unamenable to any explanation which would suppose them due to microbes, or even to any general neurotic condition induced by the operation. They are much too definite, peculiar, and localized. Doubtless it is on this account that the school of Weismann has not seriously attempted to deal with them, but merely recommends their repetition by other physiologists^[69]. Certain criticisms, however, have been urged by Weismann against the *interpretation* of Brown-Séguar's facts as evidence in favour of the transmission of acquired characters. It does not appear to me that these criticisms present much weight; but it is only fair that we should here briefly consider them^[70].

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First, with regard to Brown-Séguar's results other than the production of transmitted epilepsy, Weismann allows that the hypothesis of microbes can scarcely apply. In order to meet these results, therefore, he furnishes another suggestion—viz. that where the nervous system has sustained "a great shock," the animals are very likely to bear "weak descendants, and such as are readily affected by disease." Then, in answer to the obvious consideration, "that this does not explain why the offspring should suffer from the same disease" as that which has been produced in the parents, he adds—"But this does not appear to have been by any means invariably the case. For 'Brown-Séguar himself says, the changes in the eye of the offspring were of a very variable nature, and were only occasionally exactly similar to those observed in the parents.'"

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Now, this does not appear to me a good commentary. In the first place, it does not apply to the other cases (such as the ears and the toes), where the changes in the offspring, when they occurred at all, *were* exactly similar to those observed in the parents, save that some of them occasionally occurred on the *opposite* side, and frequently also on *both* sides of the offspring. These subordinate facts, however, will not be regarded by any physiologist as making against the more ready interpretation of the results as due to heredity. For a physiologist well knows that homologous parts are apt to exhibit correlated variability—and this especially where variations of a congenital kind are concerned, and also where there is any reason to suppose that the nervous system is involved. Moreover, even in the case of the eye, it was always protrusion that was caused in the parent and transmitted to the offspring as a result of injuring the restiform bodies of the former; while it was always partial closure of the eyelids that was caused and transmitted by section of the sympathetic nerve, or removal of the cervical ganglia. Therefore, if we call such effects "diseases," surely it *was* "the same disease" which in each case appeared in the parents and reappeared in their offspring. Again, the "diseases" were so peculiar, definite, and localized, that I cannot see how they can be reasonably ascribed to a general nervous "shock." Why, for instance, if this were the case, should a protruding eye never result from removal of the cervical ganglia, a drooping eyelid from a puncture of the restiform body, a toeless foot from either or both of these operations, and so on? In view of such considerations I cannot deem these suggestions touching "microbes" and "diseases" as worthy of the distinguished biologist from whom they emanate.

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Secondly, Weismann asks—How can we suppose these results to be instances of the transmission of acquired characters, when from Brown-Séguar's own statement of them it appears that the mutilation itself was not inherited, but only its effects? Neither in the case of the sciatic nerve, the sympathetic nerve, the cervical ganglion, nor the restiform bodies, was there ever any trace of transmitted injury in the corresponding parts of the offspring; so

that, if the "diseases" from which they suffered be regarded as hereditary, we have to suppose that a consequence was in each case transmitted without the transmission of its cause, which is absurd. But I do not think that this criticism can be deemed of much weight by a physiologist as distinguished from a naturalist. For nothing is more certain to a student of physiology, in any of its branches, than that negative evidence, if yielded by the microscope alone, is most precarious. Therefore it does not need a *visible* change in the nervous system to be present, in order that the part affected should be functionally weak or incapable: pathology can show numberless cases of nerve-disorder the "structural" causes of which neither the scalpel nor the microscope can detect. So that, if any peculiar form of nerve-disorder is transmitted to progeny, and if it be certain that it has been caused by injury to some particular part of the nervous system, I cannot see that there is any reason to doubt the transmission of a nervous lesion merely on the ground that it is not visibly discernible. Of course there may be other grounds for doubting it; but I am satisfied that this ground is untenable. Besides, it must be remembered, as regards the particular cases in question, that no one has thus far investigated the histology of the matter by the greatly improved methods which are now at our disposal.

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I have now considered all the criticisms which have been advanced against what may be called the Lamarckian interpretation of Brown-Séguard's results; and I think it will be seen that they present very little force—even if it can be seen that they present any force at all. But it must be remembered that this is a different thing from saying that the Lamarckian interpretation is the true one. The facts alleged are, without question, highly peculiar; and, on this account alone, Brown-Séguard's interpretation of them ought to be deemed provisional. Hence, although as yet they have not encountered any valid criticism from the side of ultra-Darwinian theory, I do not agree with Darwin that, on the supposition of their truth as facts, they furnish positive proof of the transmission of acquired characters. Rather do I agree with Weismann that further investigation is needed in order to establish such an important conclusion on the basis of so unusual a class of facts. This further investigation, therefore, I have undertaken, and will now state the results.

Although this work was begun over twenty years ago, and then yielded negative results, it was only within the last decade that I resumed it more systematically, and under the tutelage of Brown-Séguard himself. During the last two years, however, the experiments have been so much interrupted by illness that even now the research is far from complete. Therefore I will here confine myself to a tabular statement of the results as far as they have hitherto gone, on the understanding that, in so far as they are negative or doubtful, I am not yet prepared to announce them as final.

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We may take Brown-Séguard's propositions in his own order, as already given on page [104](#).

1st. Appearance of epilepsy in animals born of parents which had been rendered epileptic by an injury to the spinal cord.

2nd. Appearance of epilepsy also in animals born of parents which had been rendered epileptic by section of the sciatic nerve.

I did not repeat these experiments with a view to producing epilepsy, because, as above stated, they had been already and sufficiently corroborated in this respect. But I repeated many times the experiments of dividing the sciatic nerve for the purpose of testing the statements made later on in paragraphs 7 and 8, and observed that it almost always had the effect of producing epilepsy in the animal thus operated upon—and this of a peculiar kind, the chief characteristics of which may here be summarized. The epileptiform habit does not supervene until some considerable time after the operation; it is then transitory, lasting only

for some weeks or months. While the habit endures the fits never occur spontaneously, but only as a result of irritating a small area of skin behind the ear on the same side of the body as that on which the sciatic nerve had been divided. Effectual irritation may be either mechanical (such as gentle pinching), electrical, or, though less certainly, thermal. The area of skin in question, soon after the epileptiform habit supervenes, and during all the time that it lasts, swarms with lice of the kind which infest guinea-pigs—i.e. the lice congregate in this area, on account, I think, of the animal being there insensitive, and therefore not disturbing its parasites in that particular spot; otherwise it would presumably throw itself into fits by scratching that spot. On removing the skin from the area in question, no kind or degree of irritation supplied to the subjacent tissue has any effect in producing a fit. A fit never lasts for more than a very few minutes, during which the animal is unconscious and convulsed, though not with any great violence. The epileptiform habit is but rarely transmitted to progeny. Most of these observations are in accordance with those previously made by Brown-Séquard, and also by others who have repeated his experiments under this heading. I can have no doubt that the injury of the sciatic nerve or spinal cord produces a change in some of the cerebral centres, and that it is this change—whatever it is and in whatever part of the brain it takes place—which causes the remarkable phenomena in question. [Pg 115]

3rd. A change in the shape of the ear in animals born of parents in which such a change was the effect of a division of the cervical sympathetic nerve.

4th. Partial closure of the eyelids in animals born of parents in which that state of the eyelids had been caused either by section of the cervical sympathetic nerve, or the removal of the superior cervical ganglion.

I have not succeeded in corroborating these results. It must be added, however, that up to the time of going to press my experiments on this, the easiest branch of the research, have been too few fairly to prove a negative. [Pg 116]

5th. Exophthalmia in animals born of parents in which an injury to the restiform body had produced that protrusion of the eyeball.... In these animals, modified by heredity, the two eyes generally protruded, although in the parents usually only one showed exophthalmia, the lesion having been made in most cases only on one of the corpora restiformia.

I have fully corroborated the statement that injury to a particular spot of the restiform body is quickly followed by a marked protrusion of the eyeball on the same side. I have also had many cases in which some of the progeny of parents thus affected have shown considerable protrusion of the eyeballs on both sides, and this seemingly abnormal protrusion has been occasionally transmitted to the next generation. Nevertheless, I am far from satisfied that this latter fact is anything more than an accidental coincidence. For I have never seen the so-called exophthalmia of progeny exhibited in so high a degree as it occurs in the parents as an immediate result of the operation, while, on examining any large stock of normal guinea-pigs, there is found a considerable amount of individual variation in regard to prominence of eyeballs. Therefore, while not denying that the obviously abnormal amount of protrusion due to the operation may be inherited in lesser degrees, and thus may be the cause of the unusual degree of prominence which is sometimes seen in the eyeballs of progeny born of exophthalmic parents, I am unable to affirm so important a conclusion on the basis supplied by these experiments. [Pg 117]

6th. Haematoma and dry gangrene of the ears in animals born of parents in which these ear-alterations had been caused by an injury to the restiform body.

As regards the animals operated upon (i. e. the parents), I find that the haematoma and dry gangrene may supervene either several weeks after the operation, or at any subsequent time up to many months. When it does supervene it usually affects the upper parts of both ears, and may then eat its way down until, in extreme cases, it has entirely consumed two-thirds of the tissue of both ears. As regards the progeny of animals thus affected, in some cases, but by no means in all, a similarly morbid state of the ears may arise apparently at any time in the life-history of the individual. But I have observed that in cases where two or more individuals *of the same litter* develop this diseased condition, they usually do so at about the same time—even though this be many months after birth, and therefore after the animals are fully grown. But in progeny the morbid process never goes so far as in the parents which have been operated upon, and it almost always affects the *middle* thirds of the ears. In order to illustrate these points, reproductions of two of my photographs are appended. They represent the consequences of the operation on a male and a female guinea-pig. Among the progeny of both these animals there were several in which a portion of each ear was consumed by apparently the same process, where, of course, there had been no operation.

[Pg 118]

FIG. 1.—Reproduction of photographs from life of a male and female guinea-pig, whose left restiform bodies had been injured by a scalpel six months previously. The loss of tissue in both ears was due to haematoma

**and dry gangrene, which, however, had
ceased when the photograph was taken.**

It should be observed that not only is a different *part* of the ear affected in the progeny, but also a very much less *quantity* thereof. Naturally, therefore, the hypothesis of heredity seems less probable than that of mere coincidence on the one hand, or of transmitted microbes on the other. But I hope to have fairly excluded both these alternative explanations. For, as regards merely accidental coincidence, I have never seen this very peculiar morbid process in the ears, or in any other parts, of guinea-pigs which have neither themselves had their restiform bodies injured, nor been born of parents thus mutilated. As regards the hypothesis of microbes, I have tried to inoculate the corresponding parts of the ears of normal guinea-pigs, by first scarifying those parts and then rubbing them with the diseased surfaces of the ears of mutilated guinea-pigs; but have not been able in this way to communicate the disease. [Pg 119]

It will be seen that the above results in large measure corroborate the statements of Brown-Séquard; and it is only fair to add that he told me they are the results which he had himself obtained most frequently, but that he had also met with many cases where the diseased condition of the ears in parents affected the same parts in their progeny, and also occurred in more equal degrees. Lastly, I should like to remark, with regard to these experiments on restiform bodies, and for the benefit of any one else who may hereafter repeat them, that it will be necessary for him to obtain precise information touching the *modus operandi*. For it is only one very localized spot in each restiform body which has to be injured in order to produce any of the results in question. I myself lost two years of work on account of not knowing this exact spot before going to Paris for the purpose of seeing Brown-Séquard himself perform the operation. I had in the preceding year seen one of his assistants do so, but this gentleman had a much more careless method, and one which in my hands yielded uniformly negative results. The exact spot in question in the restiform body is as far forwards as it is possible to reach, and as far down in depth as is compatible with not producing rotatory movements. [Pg 120]

7th. Absence of two toes out of the three of the hind leg, and sometimes of the three, in animals whose parents had eaten up their hind-leg toes which had become anaesthetic from a section of the sciatic nerve alone, or of that nerve and also of the crural. Sometimes, instead of complete absence of the toes, only a part of one or two or three was missing in the young, although in the parent not only the toes but the whole foot were absent.

As I found that the results here described were usually given by division of the sciatic nerve alone—or, more correctly, by excision of a considerable portion of the nerve, in order to prevent regeneration—I did not also divide the crural. But, although I have bred numerous litters from parents thus injured, there has been no case of any inherited deficiency of toes. My experiments in this connexion were carried on through a series of six successive generations, so as to produce, if possible, a cumulative effect. Nevertheless, no effect of any kind was produced. On the other hand, Brown-Séquard informed me that he had observed this inherited absence of toes only in about one or two per cent. of cases. Hence it is possible enough, that my experiments have not been sufficiently numerous to furnish a case. It may be added that there is here no measurable possibility of accidental coincidence (seeing that normal guinea-pigs do not seem ever to produce young with any deficiency of toes), while the only possibility of mal-observation consists in some error with regard to the isolation (or the tabulation) of parents and progeny. Such an error, however, may easily arise. For gangrene of the toes does not set in till some considerable time after division of the sciatic nerve. Hence, if the wound be healed before the gangrene begins, and if any mistake has been made with regard to the isolation (or tabulation) of the animal, it becomes possible that the latter should be recorded as an uninjured, instead of an injured, individual. [Pg 121]

On this account one would like to be assured that Brown-Séquard took the precaution of examining the state of the sciatic nerve in those comparatively few specimens which he alleges to have displayed such exceedingly definite proof of the inheritance of a mutilation. For it is needless to remark, after what has been said in the preceding chapter on the analogous case of epilepsy, that the proof would not be regarded by any physiologist as displaced by the fact that there is no observable deficiency in the sciatic nerve of the toeless young.

8th. Appearance of various morbid states of the skin and hair of the neck and face in animals born of parents having had similar alterations in the same parts, as effects of an injury to the sciatic nerve.

I have not paid any attention to this paragraph, because the facts which it alleges did not seem of a sufficiently definite character to serve as a guide to further experiment.

On the whole, then, as regards Brown-Séquard's experiments, it will be seen that I have not been able to furnish any approach to a full corroboration. But I must repeat that my own experiments have not as yet been sufficiently numerous to justify me in repudiating those of his statements which I have not been able to verify. [Pg 122]

The only other experimental results, where animals are concerned, which seemed to tell on the side of Lamarckianism, are those of Mr. Cunningham, already alluded to. But, as the research is still in progress, the school of Weismann may fairly say that it would be premature to discuss its theoretical bearings.

Passing now from experiments on animals to experiments on plants, I must again ask it to be borne in mind, that here also no researches have been published, which have had for their object the testing of the question on which we are engaged. As in the case of animals, therefore, so in that of plants, we are dependent for any experimental results bearing upon the subject to such as have been gained incidentally during the course of investigations in quite other directions.

Allusion has already been made, in my previous essay, to De Vries' observations on the chromatophores of algae passing from the ovum of the mother to the daughter organism; and we have seen that even Weismann admits, "It appears possible that a transmission of somatogenetic variation has here occurred^[71]." It will now be my object to show that such variations appear to be sometimes transmitted in the case of higher plants, and this under circumstances which carry much less equivocal evidence of the inheritance of acquired characters, than can be rendered by the much more simple organization of an alga. [Pg 123]

I have previously mentioned Hoffmann's experiments on transplantation, the result of which was to show that variations, directly induced by changed conditions of life, were reproduced by seed^[72]. Weismann, however, as we have seen, questions the *somatogenetic* origin of these variations—attributing the facts to a *blastogenetic* change produced in the plants by a direct action of the changed conditions upon the germ-plasm itself^[73]. And he points out that whether he is right or wrong in this interpretation can only be settled by ascertaining whether the observable somatic changes occur in the generation which is first exposed to the changed conditions of life. If they do occur in the first generation, they are somatogenetic changes, which afterwards react on the substance of heredity, so as to transmit the acquired peculiarities to progeny. But if they do not occur till the second (or any later) generation, they are presumably blastogenetic. Unfortunately Hoffmann does not

appear to have attended to this point with sufficient care, but there are other experiments of the same kind where the point has been specially observed.

For instance, M. L. A. Carrière^[74] gathered seed from the wild radish (*Raphanus Raphanistrum*) in France, and sowed one lot in the light dry soil near the Museum of Natural History in Paris, while another lot was sown by him at the same time in heavy soil elsewhere. His object was to ascertain whether he could produce a good cultivated radish by methodical selection; and this he did; in a wonderfully rapid manner, during the course of a very few generations. But the point for us is, that *from the first* the plants grown in the light soil of Paris presented sundry marked differences from those grown in the heavy soil of the country; and that these points of difference had nothing to do with the variations on which his artificial selection was brought to bear. For while his artificial selection was directed to increasing the *size* of the "root," the differences in question had reference to its *form* and *colour*. In Paris an elongated form prevailed, which presented either a white or a rose colour: in the country the form was more rounded, and the colour violet, dark brown, or "almost black." Now, as these differences were strongly apparent in the first generation, and were not afterwards made the subject of selection, both in origin and development they must have been due to "climatic" influences acting on the somatic tissues. And although the author does not appear to have tested their hereditary characters by afterwards sowing the seed from the Paris variety in the country, or *vice versa*, we may fairly conclude that these changes must have been hereditary—1st, from the fact of their intensification in the course of the five sequent generations over which the experiment extended, and, 2nd, from the very analogous results which were similarly obtained in the following case with another genus, where both the somatogenetic and the hereditary characters of the change were carefully and specially observed. This case is as follows. [Pg 124]

The late Professor James Buckman, F.R.S., saved some seed from wild parsnips (*P. sativa*) in the summer of 1847, and sowed under changed conditions of life in the spring of 1848. The plants grown from these wild seeds were for the most part like wild plants; but some of them had "already (i.e. in the autumn of 1848) the light green and smooth aspect devoid of hairs which is peculiar to the cultivated plant; and among the latter there were a few with longer leaves and broader divisions of leaf-lobes than the rest—the leaves, too, all growing systematically round one central bud. The roots of the plant when taken up were observed to be for the most part more fleshy than those of wild examples^[75]." [Pg 125]

Professor Buckman then proceeds to describe how he selected the best samples for cultivation in succeeding generations, till eventually the variety which he called "The Student" was produced, and which Messrs. Sutton still regard as the best variety in their catalogue. That is to say, it has come true to seed for the last forty years; and although such great excellence and stability are doubtless in chief part due to the subsequent process of selection by Professor Buckman in the years 1848-1850, this does not affect the point with which we are here concerned—namely, that the somatogenetic changes of the plants in the first generation were transmitted by seed to the second generation, and thus furnished Professor Buckman with the material for his subsequent process of selection. And the changes in question were not merely of a very definite character, but also of what may be termed a very *local* character—affecting only particular tissues of the soma, and therefore expressive of a high degree of *representation* on the part of the subsequently developed seed, by which they were faithfully reproduced in the next generation. [Pg 126]

Here is another case. M. Lesage examined the tissues of a large number of plants growing both near to, and remote from, the sea. He suspected that the characteristic fleshiness, &c. of seaside plants was due to the influence of sea-salt; and proved that such was the case by causing the characters to occur in inland plants as a result of watering them with salt-water. Then he adds:—

"J'ai réussi surtout pour le *Lepidium sativum* cultivé en 1888; j'ai obtenu pour la même plante des résultats plus nets encore dans la culture de 1889, entreprise en semant les graines récoltées avec soin des pots de l'année précédente et traitées exactement de la même façon^[76]."

Here, it will be observed, there was no selection; and therefore the increased hereditary effect in the second generation must apparently be ascribed to a continuance of influence exercised by somatic tissues on germinal elements; for at the time when the changes were produced no seed had been formed. In other words, the accumulated change, like the initial change, would seem to have been exclusively of somatogenetic origin; and yet it so influenced the qualities of the seed (as this was afterwards formed), that the augmented changes were transmitted to the next generation, part for part, as the lesser changes had occurred in the preceding generation. "This experiment, therefore, like Professor Buckman's, shows that the alteration of the tissues was carried on in the second generation from the point gained in the first. In both cases no germ-plasm (in the germ-cells) existed at the time during which the alterations arose, as they were confined to the vegetative system; and in the case of the parsnips and carrots, being biennials no germ-cells are produced till the second year has arrived^[77]."

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Once more, Professor Bailey remarks:—

"Squashes often show remarkable differences when grown upon different soils; and these differences can sometimes be perpetuated for a time by seeds. The writer has produced, from the same parent, squashes so dissimilar, through the simple agency of a change of soil in one season, that they might readily be taken for distinct varieties. Peas are known to vary in the same manner. The seeds of a row of peas of the same kind, last year gave the writer marked variations due to differences of soil.... Pea-growers characterize soils as 'good' and 'viney.' Upon the latter sort the plants run to vine at the expense of the fruit, and their offspring for two or three generations have the same tendency^[78]."

I think these several cases are enough to show that, while the Weismannian assumption as to the seeming transmission of somatogenetic characters being restricted to the lowest kinds of plants is purely gratuitous, there is no small amount of evidence to the contrary—or evidence which seems to prove that a similar transmission occurs likewise in the higher plants. And no doubt many additional cases might be advanced by any one who is well read in the literature of economic botany.

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It appears to me that the only answer to such cases would be furnished by supposing that the hereditary changes are due to an alteration of the residual "germ-plasm" in the wild seed, when this is first exposed to the changed conditions of life, due to its growth in a strange kind of soil—e.g. while germinating in an unusual kind of earth for producing the first generation. But this would be going a long way to save an hypothesis. In case, however, it should now be suggested, I may remark that it would be negatived by the following facts.
^[79]

In the first place, an endless number of cases might be quoted where somatogenetic changes thus produced by changed conditions of life are not hereditary. Therefore, in all these cases it is certainly not the "germ-plasm" that is affected. In other words, there can be no question that somatogenetic changes of the kinds above mentioned do very readily admit of being produced in the first generation by changes of soil, altitude, &c. And that somatogenetic changes thus produced should not always—or even generally—prove themselves to be hereditary from the first moment of their occurrence, is no more than any theory of heredity would expect. Indeed, looking to the known potency of reversion, the wonder is that in any case such changes should become hereditary in a single generation. On the other hand, there

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is no reason to imagine that the hypothetical germ-plasm—howsoever *unstable* we may suppose it to be—can admit of being directly affected by a change of soil in a single generation. For, on this view, it must presumably be chiefly affected during the short time that the seed is germinating; and during that time the changed conditions can scarcely be conceived as having any points of attack, so to speak, upon the residual germ-plasm. There are no roots on which the change of *soil* can make itself perceptible, nor any stem and leaves on which the change of *atmosphere* can operate. Yet the changed condition's may produce hereditary modifications in any parts of the plant, which are not only precisely analogous to non-hereditary changes similarly produced in the somatic tissues of innumerable other plants, but are always of precisely the same kind in the same lot of plants that are affected. When all the radishes grown from wild seed in Paris, for instance, varied in the direction of rotundity and dark colour, while those grown in the country presented the opposite characters, we can well understand the facts as due to an entire season's action upon the whole of the growing plant, with the result that all the changes produced in each set of plants were similar—just as in the cases where similarly "climatic" modifications are not hereditary, and therefore unquestionably due to changed conditions acting on roots, stems, leaves, or flowers, as the case may be. On the other hand, it is not thus intelligible that during the short time of germination the changed conditions should effect a re-shuffling (or any other modification) of the "germ-plasm" in the seeds—and this in such a manner that the effect on the residual germ-plasm reserved for future generations is precisely similar to that produced on the somatic tissues of the developing embryo.

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In the second place, as we have seen, in some of the foregoing cases the changes were produced months—and even years—before the seeds of the first germination were formed. Therefore the hereditary effect, if subsequent to the period of embryonic germination, must have been produced on germ-plasm as this occurs diffused through the somatic tissues. But, if so, we shall have to suppose that such germ-plasm is afterwards gathered in the seeds when these are subsequently formed. This supposition, however, would be radically opposed to Weismann's theory of heredity: nor do I know of any other theory with which it would be reconcilable, save such as entertain the possibility of the Lamarckian factors.

Lastly, in the third place, I deem the following considerations of the highest importance:—

"As other instances in which peculiar structures are now hereditary may be mentioned aquatic plants and those producing subterraneous stems. Whether they be dicotyledons or monocotyledons, there is a fundamental agreement in the anatomy of the roots and stem of aquatic plants, and, in many cases, of the leaves as well. Such has hitherto been attributed to the aquatic habit. The inference or deduction was, of course, based upon innumerable coincidences; the water being supposed to be the direct cause of the degenerate structures, which are hereditary and characteristic of such plants in the wild state. M. Costantin has, however, verified this deduction, by making terrestrial and aerial stems to grow underground and in water: the structures *at once* began to assume the subterranean or aquatic type, as the case might be; and, conversely, aquatic plants made to grow upon land *at once* began to assume the terrestrial type of structure, while analogous results followed changes from a subterranean to an aerial position, and *vice versa*."

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This is also quoted from the Rev. Prof. Henslow's letters to me, and the important point in it is, that the great changes in question are proved to be of a purely "somatogenetic" kind; for they occurred "at once" *in the ready-grown plant*, when the organs concerned were exposed to the change from aquatic to terrestrial life, or *vice versa*—and also from a subterranean to an aerial position, or *vice versa*. Consequently, even the abstract possibility of the changed conditions of life having operated on the *seed* is here excluded. Yet the changes are of precisely the same kind as are now *hereditary* in the wild species. It thus appears undeniable

that all these remarkable and uniform changes must originally have been somatogenetic changes; yet they have now become blastogenetic. This much, I say, seems undeniable; and therefore it goes a long way to prove that the non-blastogenetic character of the changes has been due to their originally somatogenetic character. For, if not, how did natural selection ever get an opportunity of making any of them blastogenetic, when every individual plant has always presented them as already given somatogenetically? This last consideration appears in no small measure to justify the opinion of Mr. Henslow, who concludes—"These experiments prove, not only that the influence of the environment is *at once* felt by the organ; but that it is indubitably the *cause* of the now specific and hereditary traits peculiar to normally aquatic, subterranean, and aerial stems, or roots^[80]." [Pg 132]

He continues to furnish other instances in the same line of proof—such as the distinctive "habits" of insectivorous, parasitic, and climbing plants; the difference in structure between the upper and under sides of horizontal leaves, &c. "For here, as in all organs, we discover by experiment how easily the anatomy of plants can be affected by their environment; and that, as long as the latter is constant, so are the characters of the plants constant and hereditary."

[The following letter, contributed by Dr. Hill to *Nature*, vol. I. p. 617, may here be quoted. C. Ll. M.]

"It may be of interest to your readers to know that two guinea-pigs were born at Oxford a day or two before the death Dr. Romanes, both of which exhibited a well-marked droop of the left upper eyelid. These guinea-pigs were the offspring of a male and a female guinea-pig in both of which I had produced for Dr. Romanes, some months earlier, a droop of the left upper eyelid by division of the left cervical sympathetic nerve. This result is a corroboration of the series of Brown-Séquard's experiments on the inheritance of acquired characteristics. A very large series of such experiments are of course needed to eliminate all sources of error, but this I unfortunately cannot carry out at present, owing to the need of a special farm in the country, for the proper care and breeding of the animals.—LEONARD HILL.

"Physiological Laboratory, Univ. Coll. London, Oct. 18, 1894."]

CHAPTER V. CHARACTERS AS HEREDITARY AND ACQUIRED (*continued*).

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(A. and B.)

Direct and Indirect Evidence in favour of the Non-inheritance of Acquired Characters^[81].

The strongest argument in favour of "continuity" is that based upon the immense difference between congenital and acquired characters in respect of heritability. For that there is a great difference in this respect is a matter of undeniable fact. And it is obvious that this difference, the importance of which must be allowed its full weight, is just what we should expect on the theory of the continuity of the germ-plasm, as opposed to that of pangenesis. Indeed it may be said that the difference in question, while it constitutes important *evidence*

in favour of the former theory, is a *difficulty* in the way of the latter. But here two or three considerations must be borne in mind.

In the first place, this fact has long been one which has met with wide recognition and now constitutes the main ground on which the theory of continuity stands. That is to say, it was the previous knowledge of this contrast between congenital and acquired characters which led to the formulation of a theory of continuity by Mr. Galton, and to its subsequent development by Prof Weismann.

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But, in the second place, there is a wide difference between the certainty of this fact and that of the theory based upon it. The certain fact is, that a great distinction in respect of heritability is observable between congenital and acquired characters. The theory, as formulated by Weismann, is that the distinction is not only great but absolute, or, in other words, that in no case and in no degree can any acquired character be ever inherited. This hypothesis, it will be observed, goes far beyond the observed fact, for it is obviously possible that, notwithstanding this great difference in regard to heritability between congenital and acquired characters, the latter may nevertheless, sometimes and in some degree, be inherited, however much difficulty we may experience in observing these lesser phenomena in presence of the greater. The Weismannian hypothesis of *absolute* continuity is one thing, while the observed fact of at least a *high relative degree* of continuity is quite another thing. And it is necessary to be emphatic on this point, since some of the reviewers of my *Examination of Weismannism* confound these two things. Being apparently under the impression that it was reserved for Weismann to perceive the fact of there being a great difference between the heritability of congenital and acquired characters, they deem it inconsistent in me to acknowledge this fact while at the same time questioning the hypothetical basis of his fundamental postulate touching the absolute continuity of germ-plasm. It is one merit of Galton's theory, as against Weismann's, that it does not dogmatically exclude the possible interruption of continuity on some occasions and in some degree. Herein, indeed, would seem to lie the central core of the whole question in dispute. For it is certain and has long been known that individually acquired characters are at all events much less heritable than are long-inherited or congenital ones. But Lamarckian theory supposes that congenital characters were in some cases originally acquired, and that what are now blastogenetic characters were in some cases at first somatogenetic and have become blastogenetic only in virtue of sufficiently long inheritance. Since Darwin's time, however, evolutionists (even of the so-called Lamarckian type) have supposed that natural selection greatly assists this process of determining which somatogenetic characters shall become congenital or blastogenetic. Hence all schools of evolutionists are, and have long been, agreed in regarding the continuity principle as true in the main. No evolutionist would at any time have propounded the view that one generation depends for *all* its characters on those acquired by its *immediate* ancestors, for this would merely be to unsay the theory of Evolution itself, as well as to deny the patent facts of heredity as shown, for example, in atavism. At most only some fraction of a *per cent.* could be supposed to do so. But Weismann's contention is that this principle is not only true in the main, but *absolutely* true; so that natural selection becomes all in all or not at all. Unless Weismannism be regarded as this doctrine of absolutism it permits no basis for his attempted theory of evolution.

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And, whatever may be said to the contrary by the more enthusiastic followers of Prof. Weismann, I must insist that there is the widest possible difference between the truly scientific question of fact which is assumed by Weismann as answered (the base-line of the diagram on p. 43), and the elaborate structure of deductive reasoning which he has reared on this assumption (the Y-like structure). Even if the assumption should ever admit of inductive proof, the almost bewildering edifice of deductive reasoning which he has built upon it would still appear to me to present extremely little value of a scientific kind. Interesting though it may be as a monument of ingenious speculation hitherto unique in the history of science, the mere flimsiness of its material must always prevent its far-reaching

conclusions from being worthy of serious attention from a biological point of view. But having already attempted to show fully in my *Examination* this great distinction between the scientific importance of the question which lies at the base of "Weismannism," and that of the system which he has constructed on his assumed answer thereto, I need not now say anything further with regard to it.