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LOST & FOUND

doi:10.17684/i1A16en
ISSN: 2393-1140
www.diacronia.ro

Are acquired variations inherited?[†]

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Are acquired characteristics inherited? We admit that individuals inherit a certain constitution, and that definite variations from this constitution are acquired during life-time, according to well-known laws. The question is: Are these definite acquired variations in any degree transmitted, or are the congenital variations in the constitution of the offspring independent of those which have been acquired by the parents?

PRESENT STATE OF QUESTION

Before opening this discussion let us draw up a balance sheet in biological philosophy for 1890, and determine exactly where we stand in point of knowledge of natural causation. Fortunately Professor Huxley balanced the Evolution account in 1871[1] in his usual accurate and candid manner, enabling us to institute a comparison:

"If I affirm that 'species have been evolved by variation[2] (a natural process, the laws of which are for the most part unknown), aided by the subordinate action of natural selection,' it seems to me that I enunciate a proposition which constitutes the very pith and marrow of the first edition of the 'Origin of Species.' And what the evolutionist stands in need of just now is not an iteration of the fundamental principles of Darwinism, but some light upon the questions, What are the limits of variation? and, If a variety has arisen, can that variety be perpetuated, or even intensified, when selective conditions are indifferent, or perhaps unfavorable, to its existence?"[3]

Thus, twenty years ago, Huxley declared Evolution well established, with the Law of Natural Selection as one of its well determined factors, while he found that we were merely upon the threshold of knowledge of the laws of Variation. Some sanguine biologists of to-day believe we have crossed this threshold in the patient researches of the two intervening decades; but others are represented by Professor Lankester, who has now taken the rank of leading English critic, and has recently summed up our knowledge in an article,[4] presumably written with the greatest care and deliberation, as follows:

"Their causes (i.e., the causes of variations) are extremely difficult to trace in detail, but it appears that they are largely due to a "shaking up" of the living matter which constitutes the fertilized germ or embryo-cell, by the process of mixture in it of the substance of two cells—the germ-cell and the sperm-cell—derived from two different individuals. Other mechanical disturbances may assist in this production of congenital variation. Whatever its causes, Darwin showed that it is all-important . . . .

Hence there is no *necessity* for an assumption of the perpetuation of direct adaptations.[5] The selection of the fortuitously (fortuitously, that is to say, so far as the conditions of survival are concerned) produced varieties is sufficient, since it is ascertained that they will tend to transmit those characters with which they themselves were born, although it is *not* ascertained that they could transmit characters *acquired* on the way through life."

The emphasis here is upon the contrast between our knowledge of the *fact* of variation (op. cit. p. 373) and our indefinite knowledge of the *causes* of variation.[6] In other words, we have been accumulating facts, and our present induction from them is

[†]Opening of a Discussion upon the Lamarckian Principle in Evolution; American Society of Naturalists, Boston, December 31st, 1891. Published in "The American Naturalist," vol. XXV, March, 1891, 291, p. 191–216.

[1]"Critiques and Addresses", p. 299. *Contemporary Review*, 1871. This passage is practically a résumé of the article entitled "Mr. Darwin's Critics," in which it occurs.

[2]Including under this head hereditary transmission.

[3]He then observes that Mr. Darwin formerly inclined to answer these questions in the negative, but latterly in the affirmative.

[4]"The History and Scope of Zoology." Enc. Brit. Vol. XXIV. Also "Advancement of Science," pp. 372-373.

[5]i.e., of acquired characters.

[6]I am very desirous to give a perfectly fair representation of the views of all authors here quoted, and am aware that a single passage is often misleading. On the present subject compare other recent essays and reviews of Prof. Lankester, principally those in *Nature*.

that the variations which have formed the main basis of evolution are fortuitous; there may be, indeed, definite causes, but the effects are largely indefinite. Now if all, or even the great majority, of naturalists were in agreement with Lankester, we might claim to have made a distinct advance since 1870, even in having reached such a negative conclusion—that is, on the principle that we progress when we recognize that no further progress is possible.

But fortunately, or otherwise, this is not the case, for in opposition to those who share Lankester's opinions are an equally large number who would balance the account differently, and claim that the distinctive feature of the past twenty years of study is that we have reached some of the fundamental principles of variation which Huxley presented as the goal of research.

But this difference in the accounts does not stop here. We biologists are obliged to frankly confess to our fellow-scientists in chemistry and physics, and to the world generally, that after studying Evolution for a century we are in a perfect chaos of opinion as to its factors. There is actually no consensus as to the powers of the natural selection principle, none as to the laws of inheritance, none as to the influences of environment! In the very heart of this disturbance is the problem we have come together to discuss. It is the medium which refracts our judgment upon every one of the factors of evolution. We may continue to accumulate facts, but no actual advance can be made in the study of natural causation until this problem is absolutely settled one way or the other. This being the case, Weismann has done a monumental service in forcing this question to an issue. It is true a very large number of naturalists consider the question no longer *sub judice*; but as half this number hold one opinion, and the other half an opinion directly opposed, we are forced to the criticism that neither side can at present offer such a clear and full demonstration of how evolution works upon their basis as to be conclusive; nor will either side admit the value of the evidence furnished by the other. Contrast two of our most vigorous writers on this point:[7]

"This is all the more necessary, in that this author (Weismann) and his followers repudiate the evidence upon which the claim is made that acquired characters, taken in the widest Lamarckian sense, can be transmitted. During a period extending over fifteen years, the present writer has devoted himself to a study of the genesis of adaptations, and with the lapse of time the conviction has grown only the clearer that these authors are laboring under a delusion. The way in which they have placed themselves upon record shows that they have not reckoned with the consequences of their reckless speculations."

A few months later Lankester, echoing Weismann,[8] writes to Nature:[9]

"Naturalists are at present interested in the attempt to decide whether Lamarck was justified in his statement that acquired characters are transmitted from the parents so changed to their offspring. Many of us hold that he was not; since, however plausible his laws above quoted may appear, it has not been possible to bring forward a single case in which the acquisition of a character as described by Lamarck and its subsequent transmission to offspring have been conclusively observed. We consider that, until such cases can be adduced, it is not legitimate to assume the truth of Lamarck's second law."

Nature of the Discussion.—Before taking up the question of evidence as to this factor in evolution, let us clearly understand what we are *not* discussing at the present time. First, the law of natural selection is well established and no longer under discussion; it furnishes by far the best, in fact the only, explanation which can be offered for many adaptations,—the question before us is only as to the extent of its action. Second, we need not discuss the inheritance of mutilations, for mutilations are not part of the regular order of nature, and while they might have strong positive, they have little negative, value; the elaborate arguments which have been recently directed against them, remind us, therefore, of Don Quixote's excursions against the windmills, as if Lamarckism mainly depended upon such evidence. Nor is it in dispute whether the effects of general atrophy or hypertrophy of the body are transmitted, for it is self-evident that an ill-fed organism will not bear as perfect offspring as a well-fed organism. As to pathological atrophy or hypertrophy, it is, I believe, admitted on both sides

[7] Ryder. "A Physiological Hypothesis of Heredity and Variation." Am. Naturalist, Jan., 1890, p. 85.

[8] "There are no observations which prove the transmission of functional atrophy or hypertrophy, and it is hardly to be expected that we shall obtain such proofs in the future." Biol. Memoirs, 1889, p. 429.

[9] March 6th, 1890, p. 415.

that in cases where it arises from certain bacilli it is possible that it may be transmitted with the bacilli. What we *are* discussing is whether the special and local variations in function and structure induced by environment and habit in the life of the parent tend in any degree to reappear in the offspring.

This is the modern or modified form of Lamarck's law. His followers admit that he overestimated the rate of inheritance of the effects of use and disuse in stating that *all* that is acquired is transmitted.[10] The element of rate or time is a secondary one, as it is with the law of Selection; the main point is whether such effects are transmitted at all. Of course there are Lamarckians of all degrees of fervor. The following statement probably reflects the average opinion:

1. In the life of the individual, adaptation is increased by local and general metatrophic changes, of necessity correlated, which take place most rapidly in the regions of least perfect adaptation, since here the reactions are greatest. 2. The main trend of variation is determined not by the transmission of the full adaptive modifications themselves, as Lamarck supposed, but of the disposition to adaptive atrophy or hypertrophy at certain points.[11]

At all events, this involves the Lamarckian principle, with all its necessary bearings upon our opinions as to Environment, Variation, Selection, and Inheritance. If we adopt it, we must accept its full consequences. Taking Spencer's definition of Life as the continuous adjustment of internal relations to external relations, we must regard the race as in part the summation of these individual adjustments, in part as the summation, by Selection, of favorable fortuitous variations. Environment must act directly in producing variations in the organism as a whole; directly also it must produce special variations wherever it induces changes of function. As these variations are in a degree transmitted, we will discover some of the laws of variation in the study of individual adaptation; variations of this kind will be found in definite lines; indefinite variations will also arise from the fortuitous combination of individual characters; the proximate causes of variation must be changing environment as well as the combination of diverse individual characters. Selection, so far as it is here involved, will be found to act mainly upon the *ensemble* of characters which have their origin in individual variation by the extinction of unadapted individuals, and races, but its action upon fortuitous variations will be concomitant. Inheritance must bear the burden not only of ancestral and race characters, but must accumulate the modifications of these characters which occur in individuals.

Let us associate the opposite principle, that special individual variations are not transmitted, with the name of Weismann, for at a time when Lamarck's principle was rising in favor[12] he boldly opposed it *in toto*. His doctrine of the continuity of the germ-plasma, and especially of the isolation of the germ-cells from influences which are exerted upon the body-cells, is a perfect and necessary complement of the doctrine that Evolution has advanced by pure Natural Selection; he carries these twin doctrines out to their legitimate conclusions. Recalling Spencer's definition and applying Weismann's principle, we must regard the race not as the summation of individual adjustments, but as the summation of the best adjusted germ-plasmata. Environment may act directly in causing the organism to vary as a whole, but none of the special individual variations which it also produces indirectly and directly can be inherited; its influences upon the germ-plasma are gradual and indefinite. The lines of variation are definite so far as they are limited by the specific nature of the organism; within these limits variations must be indefinite and numerous;[13] the proximate cause of variation is the combination of the diverse individual characters of the parents. Selection must accumulate minute existing variations in the required direc-

[10] "Quatrième loi: Tout ce qui a été acquis, tracé ou changé, dans reorganization des individus, pendent le cours de leur vie, est conservé par la génération et transmis aux nouveux individus qui proviennent de ceux qui ont éprouvé ces changements."

[11] Osborn. "The Palæontological Evidence for the Transmission of Acquired Characters." Brit. Assoc. Reports; Proc. Am. Assoc. Adv. Science; 1889.

Dr. W. H. Dall has given a very full and carefully considered statement in his paper on "Dynamic Influences in Evolution," May 8th, 1890.

[12] In 1883, when Weismann published his first essay on Heredity, the only English or American naturalist of note who was not subscribing to some form of the Lamarckian principle was Alfred Wallace.

[13] Biological Memoirs, p. 288. "It is the specific nature of an organism which causes it to respond to external influences along certain definite lines, although these may be very numerous."

tion, and thus create new characters;[14] it must act upon minute variations in single characters, as well as upon the *ensemble* of characters. Inheritance is the unbroken transmission of race and ancestral characters by subdivision of the germ-plasma; only changes which affect the body as a whole can be added to the characteristics of the germ-plasma.

This is a mere abstract of the diverse positions upon every problem to which these principles of Lamarck and Weismann lead us. No half-way ground is tenable; the result of this inquiry will be a complete rout to one side or the other. By the former we diminish the powers of Natural Selection, and increase the powers of Environment; at the same time we greatly simplify the problem of Variation, and render far more complex the problem of Inheritance. By the latter we throw the entire burden of Evolution upon Natural Selection, and eliminate the direct action of Environment; we admit definite laws or causes of general Variability, but no definite laws governing the variations of single characters; we greatly simplify the problem of Inheritance. In short, the vulnerable point with the Lamarckians is in solving the problem of Heredity, while their opponents are weakest in solving the problem of variation. From the purely theoretical standpoint both sides can offer a good working explanation of the process of Evolution, provided we grant all their premises; our duty as professed scientific men should be, therefore, to dispassionately examine how far these premises accord with *all* the phenomena which we can actually observe in Nature, and then espouse the side which is most favored by probabilities. Now I have no hesitation in saying that neither side is showing the disposition to test their premises by all the observed phenomena, and this is one of the most hopeless features of the present situation.

Variation, Repetition, Regression.—All the factors of Evolution interact. Variation and Repetition[15] in inheritance are in constant relation with every other factor. Thus we can accumulate facts as to variations *per se*, but if our observation and induction enable us to formulate certain laws, these will always involve at least two factors,—i.e., Variation as related to Environment, Variation as related to the life-history of individual organisms, Variation as related to Inheritance, Variation as related to Natural Selection.

Variability is, of course, exhibited in organisms as a whole, and in groups of characters as well as in single characters. All would be diversely affected by the two diverse principles of inheritance under discussion, but we are to examine the variable tendency as exhibited in single characters. Repetition is the conservative or static condition wherein a character in the new individual most closely resembles the average development presented by the fraternity,[16] co-fraternity, race, variety, and species to which it belongs; let us adopt Galton's term "mediocrity" for this state of average development. Variation is the unstable or fluctuating condition in which a character deviates to either side of mediocrity, either in the plus or minus direction,—i.e., to greater or less development. Regression is the tendency[17] to revert to "mediocrity"; and according to Galton's statistics we can imagine this law of regression as acting like gravitation upon the pendulum of variation: when the pendulum swings in one direction it may represent a plus-variation, in the other direction a minus-variation; mediocrity is the state of rest or balance. When we examine any species in course of evolution in time and space we find, however, that a mediocre character is a shifting quantity. An organ, for example, which is rapidly degenerating presents a certain "mediocrity" at one time and locality, and another "mediocrity" at a later time or another locality. There is, therefore, a clear distinction between the above terms and the more general terms "degeneration," "balance," and "development," which apply to characters which are either continuously static or in a downward or upward direction, not only in individuals but in whole species and larger divisions. Of course where regression ceases to exert its full gravitating force upon plus- or minus-variations, through a series of generations, development or degeneration respectively set in.

[14] Biological Memoirs, p. 275.

[15] Weismann, or his translators, uses the terms Variability and Heredity, as tendencies equivalent to these. But it seems to me clearer to use Heredity in the larger sense, so as to include Variation = the act of Varying, and Repetition = the act of repeating, ancestral characters. Variability = the tendency to vary.

[16] Galton. "Natural Inheritance," p. 94. All the offspring of the same mid-parent (= male and female) form a fraternity. All the off-spring of a fraternity of mid-parents form a co-fraternity.

[17] Op. cit., p. 95.

Another source of confusion, which is inevitable in observation but not in theory, is the difficulty of distinguishing between "congenital" and "individual variations." Weismann has marked the distinction by the useful terms "blastogenic" and "somatogenic."[18] Theoretically these congenital and acquired variations are quite distinct; but as some blastogenic variations do not manifest themselves until advanced life, it is extremely difficult in many cases to decide how far certain variations are really blastogenic and how far somatogenic in origin; in other words, how far they are due to inherited predispositions and how far due to life habits.[19]

A war of words has recently been waging as to the meaning to be attached to such adjectives as "fortuitous," "chance," "kaleidoscopic," or "indefinite." My understanding of these terms is that when we see characters fluctuating from mediocrity, in either the plus or minus direction, according to the ordinary laws of chance, we may describe them as in a state of indefinite variability; whereas, when they exhibit a tendency to fluctuate principally in one direction, we describe them as in a state of definite variability. This is the only sense in which the terms "definite variations" and "indefinite variations" can be fairly used in this discussion.

In two of his most recent essays Weismann says:[20]

"My theory might be disproved in two ways,—either by actually proving that acquired characters are transmitted, or by showing that certain classes of phenomena admit of absolutely no explanation unless such characters can be transmitted. Only if it could be shown that we cannot now or ever dispense with the Lamarckian principle would we be justified in accepting it."[21]

We may gather evidence from the data of Embryogeny, or of Ontogeny and Phylogeny. It is neither possible nor desirable to separate these data; but as previous writers have dealt extensively upon the evidence of embryogeny, I will emphasize the ontological and palæontological evidence, with which I am, in fact, much more familiar. I shall endeavor principally to concentrate attention upon the phenomena to which future observation must be especially directed. We already have a number of valuable essays and criticisms in this line,[22] but none, so far as I have seen, examine the question in view of all the difficulties which the adoption of either principle involves us.

I believe we are far from understanding all the phenomena of variation, and put the question, therefore, in the following form: Does our present knowledge of variation in living and fossil forms lend greater support to Lamarck's or to Weismann's principle?

1. *What is the Origin of Variability?*—According to Weismann, the *ultimate* or primordial origin of variability is somatogenic,[23]—that is, we must trace variability back to the unicellular organisms in which the environment acts directly upon the whole organism; in the multicellular organisms the source of variability becomes restricted to the germ-cells, and the proximate or secondary origin of variations is in the union of the diverse characteristics contained in the germ-plasms of the two sexes. This view as to the primordial origin of variations does not seem to me to enter directly into the problem we are discussing, although it is one of the legitimate conclusions from his premises. But I would like to call attention to one important point, viz., that it involves the operation of Lamarck's principle of the transmission of adaptive reactions to environment[24] in the unicellular, and therefore to some degree in the lower multicellular, organisms. I think it can be shown that Lamarck's principle would be highly advantageous to every organism by transmitting direct adapt-

[18] i.e., as arising from the germ-plasma and body respectively.

[19] In his review of Wallace's "Darwinism" Lankester has pointed out this defect in some of Wallace's observations. *Nature*, 1889, p. 567.

[20] Biol. Mem., p. 388.

[21] *Nature*, Feb. 6th, 1890, p. 322.

[22] Especially those of Ryder, Cope, Eimer, and Cunningham. A very valuable review of the whole subject is found in C. V. Riley's paper, "On the Causes of Variation in Organic Forms." Proc. Am. Assoc. Adv. Sci., 1888.

[23] Biol. Memoirs, p. 277. "The origin of hereditary individual variability cannot be found in the higher organisms, but it must be sought for in the lowest,—the unicellular organisms . . . . As such organisms reproduce by division, individual acquired characters will be transmitted to the offspring."

[24] This is, of course, no new idea. It was most fully elaborated in Spencer's "Principles of Biology." The mode of transmission in the former is by simple cell division; the principle of the continuity of original and acquired characters is the same.

ations (see Query 4); if this be the case, every step in the gradual loss of this principle by the isolation of the germ-plasma would have been disadvantageous. Therefore, if Selection was constantly acting, as Weismann supposes, it would have preserved this very principle. This is, of course, in the nature of pure speculation; but turning this supposed enormous power of Selection to the service of Lamarckism, we can conceive how the extremely complex correlation between functional changes in the somatic and germ-cells, which is an essential part of the Lamarckian theory, may have had its beginnings in these transitional organisms.

The question of the *present* or proximate origin of variations does, however, bear directly upon these diverse principles:

(*a*) All observers must agree that sexual reproduction is one of the endless sources of indefinite variations.[25] Weismann's theory offers a beautiful idea of the *modus operandi*, and accords thoroughly with Galton's researches. Such variations originate in the germ-cells; there is no reason why we should trace them to the somatic cells.

(*b*) Some plus- or minus-variations must also originate from the union of germ-cells. If the same character is strongly developed in both parents, it may appear still more strongly developed in the offspring; the same rule applies conversely to weakly developed characters. But this simply puts the question one stage back, for variations which are indifferently plus, minus, or mediocre are certainly not definite, although the union of two similar variations produces a definite result.

Before considering the possible origin of definite variations we must consider whether there are such variations.

2. *What Variations are Definite and What Indefinite?*[26]—This is really the most important and central question. Its solution has a vital bearing upon Weismann's principle as well as Lamarck's. Following Huxley,[27] Geddes[28] has most clearly stated these bearings:

"In the absence of any theory of definite and progressive change,[29] and in the presence of multitudinous variations under domestication and in nature which we can neither analyze, rationalize, nor hardly even classify, we are not only justified but logically compelled to regard variation as spontaneous or indefinite,—i.e., practically indeterminate in direction, and 'therefore unimportant, except as the groundwork for Selection to act on.' Conversely, variation must be indefinite, else the paramount importance of natural selection must be proportionally impaired as this becomes definite . . . . It would exchange its former supremacy as the supposed determinant among the indefinite possibilities of structure and function for that of simply accelerating, retarding, or terminating the process of otherwise determined change."

We cannot emphasize too strongly these cardinal factors of indefinite Variation (so far as adaptation is concerned) and paramount Selection as two of the foundation stones of Weismann's theory of Evolution. This must be kept in mind in analyzing every argument advanced by his school. (The idea is that variations are definite only so far as they are limited by the specific nature of the organism, by special phenomena of nutrition, or in some cases by environment acting directly upon the germ-cells.[30] See Query 3. They are indefinite so far as they arise from the fortuitous union of diverse germ-plasmata.)[31]

I have made it clear in the introduction that this is no longer a matter of ignorance, as it was professedly with Darwin:

"I have hitherto sometimes spoken as if the variations, so common and multiform with organic beings under domestication, and in a lesser degree with those under nature, were due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of

[25] Weismann's latest view is that sexual reproduction is the most important, but not the *only* factor which maintains Metaphyta and Metazoa in a state of variability. *Nature*, Feb. 6th, 1890, p. 322. (In answer to Prof. Vines.)

[26] "Natural Selection trusts to the chapter of accidents in the matter of variation." Lankester.

[27] Article "Evolution," Enc. Brit., Vol. VIII.

[28] Article "Variation," Enc. Brit, Vol. XXIV.

[29] Such as has been postulated by Gray, Nägeli, and Mivart, or based upon the Lamarckian principle by Spencer, Cope, and others.

[30] See Biol. Mem., p. 410.

[31] See Biol. Mem., p. 275. "Natural Selection must be able to do infinitely more than this: it must be able to accumulate minute existing differences (arising by these fortuitous combinations) in the required direction."

[32] "Origin of Species," 6th edition, p. 106.

each particular variation."[32]

I have already quoted Lankester upon this principle, and refer below to a passage in which he reiterates it and carefully defines the sense in which "indefinite" is employed by him.[33] Prof. Thiselton Dyer, a leading English botanist, has supported this position:[34]

"If with Prof. Lankester we say that the combinations are kaleidoscopic, I do not see that we go beyond the facts . . . . The area of fortuity is narrowed down to the variable constitution of the ovum . . . . And this is quite in accord with the remark of Weismann that variation is not something independent of, and in some way added to, the organism, but is a mere expression for the fluctuations in its type."

One reason why I have endeavered to emphasize the unanimity of opinion upon this point among those who deny Lamarck's principle is this: If there are definite lines in blastogenic variation which cannot be explained by Selection, or by Environment acting upon germ-cells, we must find some other causes or laws governing them. Therefore the Lamarckians must first establish their claim that there are definite lines of variation; second, that these lines have not been directed by Selection (see Query 6). The opinions of Lamarckians on this point is that "there are variations which follow from their incipient stages a certain definite direction towards adaptation, independent of Selection in their origin."[34] This, it will be observed, does not exclude the existence of variations of the class accounted for by Weismann, but it constitutes substantially a distinct class of variations which Weismann, Lankester, and others do not account for, because, upon their hypothesis, we have no evidence that there is such a class.[35]

This opinion has frequently been asserted without adequate support from observation, otherwise we should not find such candid writers as those quoted above dismissing it so summarily. The fact is, it is very difficult, if not impossible, to prove that there are definite lines of variation (which cannot be explained by Selection) from the examination of zoological and botanical collections, for we are, from the nature of the material, principally examining variations by divergence in space. In such complete fossil series as are now available palæontologists enjoy the distinct advantage of following divergence both in space and time. They are thus in a better position to study lines of variation than ever before, because they are in at the birth, so to speak, of many useful and adaptive characters, and can follow the gradual rise from the minute infinitesimal stages to the advanced condition in which are constituted what we call specific and generic characters. Not only so, but it is possible to observe pedigrees, since the condition of surrounding parts prior to their appearance is known.

The history of the teeth of the Mammalia affords the most direct evidence, since these structures furnish not only the most interesting correlations and readjustments (quantitative variation), but also the successive addition of new elements (qualitative variation). I believe the unanimous opinion of all those who have examined such series is that such variations follow definite lines from their incipient stages. This is a positive form of evidence, unless the observers are at fault, but cannot be considered as proof if it can be shown that these infinitesimal stages arise indefinitely, for if the advanced condition is useful the incipient condition must possess some degree of utility, and would *ex hypothesi* be selected. This objection is met, however, by the additional fact that the first appearance of such structures is also not indefinite,—i.e., at definite adaptive points. In other words, the birth is as definite as the growth.[36]

To sum up, the opinions of the two sides as to the nature of blastogenic variations are as follows:

Both will admit:

I. That there are general fortuitous variations, which may be best explained as due to the spontaneous variability of the germ-cells, especially seen in their union.

II. That there is also a class of variations, also springing from the germ-cells, which are in one sense

[33] The latest is in *Nature*, March 6th, 1890. "This disturbance of the parental body (I compared it to the shaking up of a kaleidoscope), and with it of the germs which it carries, resulting in "sporting" or "variation" in the offspring, is, it should hardly be needful to state, a totally different thing to the definite acquirement of a structural character by a parent, . . . and the transmission to offspring of that particular acquired structural character."

[34] See Osborn. "Palæontol. Evidence," etc.

[35] That is, no class of variations which conform to direct individual adaptations.

[36] Some idea of the enormous mass of material available may be gained from the recent generalization that the teeth of all the Mammalia have sprung from a similar type and passed through similar stages. See the papers of Cope, Wortman, and the writer.

definite,—i.e., in certain directions,—but not necessarily adaptive.

One side denies, the other affirms:

III. That there is also a large class of blastogenic variations which follow definite lines of adaptation.

What are the relations of these three classes of variations to environment?

3. *What are the Direct and Indirect Relations between Environment and Variability?*—How far does environment affect the germ-cells directly, and how far through changes in the somatic cells? It is well known that a change of environment, especially to more favorable conditions, as in domestication, increases Variability,[37] —i. e., variations of Class I. In the analysis of such effects effects we should carefully examine:

(*a*) Whether this variability in all the characters of the organism is an effect of the action of Environment directly upon the germ-cells, through the general channels of increased or diminished nutrition; or, whether the environment produces a general disturbance of the functions of the organism, and this acquired disposition to altered functions is transmitted to the germ-cells.[38]

(*b*) Whether changed environment produces variability in any special characters or in all characters alike? Here again the question as to the mediate action of the somatic cells comes up, and is not only much more pertinent than in (*a*), but probably more capable of solution.

On these points Weismann holds that luxuriance of growth results from the better nutrition of the germ-cells during development,[39] while poverty of growth, or general degeneration, conversely results from deficient nutrition of the germ-cells, as in the case of Falkland ponies.[40] The effects of these influences he thinks may be more specialized; they may act only upon certain parts of the germ-plasma.[41] Weismann discusses such cases as follows (p. 433). Observe that the modifications referred to are not necessarily adaptive:

"The wild pansy does not change at once when planted in garden soil; at first it remains apparently unchanged, but sooner or later in the course of generations, variations, chiefly in the color and size of the flowers, begin to appear; these are propagated by seed, and are therefore the consequences of variations in the germ. The fact that such variations *never* occur in the first generation proves that they must be prepared for by a gradual transformation of the germ-plasm . . . . It is therefore possible that the modifying effects of external influences upon the germ-plasm may be gradual, and may increase in the course of generations so that visible changes in the body (*soma*) are not reached until the effects have reached a certain intensity."

The best-attested instances of the action of Environment in producing special characters are those seen in its action upon the reproductive organs. A slight change of conditions sometimes produces sterility, as seen in the cases of "isolation" and "divergence" advanced by Gulick and Romanes. Here the best explanation seems to be that the environment has acted directly upon the germ-cells. This could only be proved, however, by experiments in artificial impregnation, for it is possible that the cause of sterility might lie in some of the somatic functions accessory to impregnation or intercourse. A second instance of this kind is the effect of nutrition in the determination of sex, as proved by the experiments of Yung and Giron,[42] and employed as one of the main principles in the two theories of Heredity advanced respectively by Ryder and Geddes.

It is not necessary to enumerate the many well-known cases of rapid response to new environment by modifications, which we must analyze somewhat

[37] This we can attribute to the greater molecular activity of the cells. Darwin believed (*a*) that exposure to new conditions must be long continued to set up any new variation. (*b*) Excess of food increases variability. (*c*) Changed conditions may affect the whole organism, or certain parts alone, or merely the reproductive system. (*d*) Indefinite variability is the commonest result of changed conditions.

[38] The point raised by Mivart (*Nature*, Nov. 14th, 1889, p. 41) is not fairly taken. Of course nutrition must pass through some *somatic* cells of the digestive system on its way to the germ-cells; this is a different matter from its first passing to the peripheral somatic cells in certain organs and then conveying their modifications to the germ-cells.

[39] Biol. Mem., p. 98.

[40] Op. cit., p. 99.

[41] Op. cit., p. 104. Or as discussed upon p. 408, in the criticism of Hoffman's experiments upon flowers.

[42] Yung raised the percentage of females among tadpoles by high nutrition from 56 per cent. to 92 per cent. Giron found that sheep, when well fed, bred 60 per cent. males; when poorly fed, only 40 per cent. See Geddes and Thompson, "Evolution of Sex," Chap. IV.

differently. Among the best recorded are those of Saturnia (imported to Switzerland from Texas),[43] and Artemia.[44] Now it is a very important fact that the modifications observed in such cases are in the main adaptive,—that is, in course of a very few generations not only are the organisms thoroughly acclimated, but they develop substantially new adaptive characters.

We can readily understand how the germ-plasm might respond directly to new environment by general variability, and even by such special variations as above cited by Weismann; but, keeping in mind the fortuitous principle, why do we also discover variations, not merely in size and efflorescence,[45] but in the nature of direct adaptations? This point has recently been raised by Mivart, with his usual acuteness in destructive criticism.

I do not consider that it has been demonstrated that Environment does act directly upon the germ-cells. In the case of animals we certainly cannot determine how far the nervous and other somatic cells are mediate, besides the somatic cells of the nutritive system. Yet in the acceleration of variability, and in the direct production of variations of Class II., we have examples of such rapid response to changed environment that the presumption is somewhat in favor of Weismann's view. In either case, such mediate action of certain somatic cells cannot be advanced in support of Lamarck's principle that the effects of environment on special groups of somatic cells make themselves felt in, or transmitted to the germ-cells in such a manner as to reappear in some degree in the same special groups of somatic cells in the new individual. Let us therefore concentrate our attention upon the evidence as to the possible modes of origin and transmission of variations in definite adaptive lines (Class III.). Three explanations are open to us: 1. That these adaptations have been selected from a number of variations of the fortuitous class; 2. That the germ-cells respond to environment by adaptive variations; 3. That the variations originate in adaptive reactions of the somatic cells, under environment, which have been transmitted to the germ-cells. Let us first consider the question of individual variations.

4. *Are Individual Variations Adaptive?*—I should hardly have thought it necessary to consider this question but for the fact that a recent writer, who claims the sanction of Mr. Romanes and Mr. Poulton, has advanced the proposition that the inheritance of individual variations would be an actual evil.[46] This is tantamount to saying that adults are less adapted to their environment than young individuals, and that the most perfect individual adaptation will be secured by inertia. This would, as Mr. Ball maintains, be a severe blow to the Lamarckian principle, but it would be a still more severe blow to the Natural Selection principle, for, to give a single instance, it can be shown conclusively that the skeleton of the limbs of all the Mammalia has mainly been evolved upon the broad lines of use and disuse, and Selection would thus be eliminated entirely. To express this idea of the utility of the greater part of individual variation, Semper applies the term "adaptations," and his work[47] abundantly illustrates and demonstrates this law. It is based, of course, upon the general physiological principle that the tissues react and their structure diversifies proportionally with their functions.[48] Life is the continuous adjustment of internal relations to external relations, in which the general adaptation of the organism to its surroundings is, upon the whole, steadily increasing up to the period of general decline.

This principle of individual adaptation is strikingly illustrated in recent studies upon the feet of the Mammalia, in connection with instantaneous photographs of animal motion.[49] These studies show, for example, in the extremely complex readjustments of the carpal bones, necessitated by the simultaneous

[43] Recorded by Wagner. See "Die Entstehung der Arten durch Räumliche Sonderung." Basel, 1889.

[44] Schmankewitsch.

[45] Huxley has thus analyzed Environment on the pure Selection hypothesis: "Environment does not cause a variation in any particular direction, but favors and permits a tendency in that direction which already exists .... Conditions are not actively productive, but passively permissive." "Critiques and Addresses," p. 309.

[46] W. P. Ball. "Are the Effects of Use and Disuse Inherited?" Nature Series, 1890, p. 128.

[47] "Animal Life," 1877.

[48] Lamarck is still ridiculed for his idea that the wants or desires of animals produce new parts, but the only ridiculous points are in some of his illustrations of this idea. Every vertebrate is literally made up of "wish-bones" in one sense, since all parts are developed by the voluntary efforts of the animal to obtain its food, etc.

[49] See the papers of Cope and Ryder, and the writer's "Evolution of the Ungulate Foot." Memoir upon the Uinta Mammalia.

reduction of one of the bones of the fore-arm and of the lateral toes, that the very redistribution of the lines of pressure is constantly tending to perfect the adaptation by the natural reactions of growth in the bone tissue. Some of these adaptations are in the nature of plus- or minus-variations from the original constitution of the limb; other elements remain *in statu quo*,[50] or in a state of balance where their adjustments are perfect.

There is also a large class of adaptive, characters, both in animals and plants, upon which the law of individual adaptive variation operates very obscurely if at all,—e.g., protective coloration.

5. *How Far Does Race Variation Follow Individual Variation?*—The study of individual variations led Spencer to the conclusion that all higher forms (of vertebrates) have arisen by the superposing of adaptations upon adaptations.[51] The students of vertebrate palæontology observe that race adaptations conform so closely to the laws of progressive individual variation that they are impelled to seek the explanation of the origin of various structures in the reactions occurring in individuals. Here are the definite lines of variations spoken of above.

But if they jump to the conclusion that individual variations are the *cause* of these race variations, may they not fall into the old fallacy of *post hoc ergo propter hoc?* For every genetic line will be found to exhibit variations in definite lines of adaptation and many of these lines of variation occur in characters in which no individual adaptation can be observed.[52] Now there is no theoretical difficulty in supposing that the three classes of variations have different modes of origin, but in order to demonstrate the probability of a causal relation between individual and race variations of Class III. it is further necessary to show: 1. That in this special class of characters, in which obvious mechanical or dynamical principles are operative, race variations invariably conform to individual variations; for if some of these characters do not conform, other principles must be in operation. That is, if we once invoke the Lamarckian principle, we must apply it consistently to every case. 2. That no definite lines of variation arise in characters of this class without the antecedent operation of these individual reactions. These first tests of invariable antecedence and consequence would lend a high degree of probability to the existence of causal relationship; this probability would be increased if it could be shown that no other explanation of this class of variations will stand the same test.

First, as to sequence. The overwhelming majority of variations as observed in the fossil series[53] occur along the lines of use and disuse. Weismann has urged that all variations in this class are substantially quantitative, that where an organ becomes stronger by exercise it must possess a certain degree of importance, and when this is the case it becomes subject to improvement by natural selection.[54] It follows from embryological development and the laws of growth by cell division that all new characters are in one sense quantitative, but in tooth evolution we have examples of the rise of structures which are qualitative,—i.e., essentially new, and not simple modifications of preexisting forms. I refer to the successive, addition of new cusps. As already observed, there is absolutely no evidence for indefinite variation in these characters. The new cusps do not rise spontaneously at random points and then disappear, to be replaced by the gradual development of those which happen to rise at adaptive points.[55] One of the most surprising recent discoveries is that one after another these successive cusps are added to the simple conical crown at the point of maximum wear; that is, the most-worn points in an earlier series of generations are those at which the new cusps appear in the later series.

Palæontologists cannot, however, claim that this sequence is universal. Among the rare exceptions there are, first, some secondary cusps[56] which arise from the base of the crown,—i.e., entirely out of the region of use and disuse and pursue the same steady

[50] A beautiful example of the effects of use in producing joints in the tail fins of fishes has been given by Ryder. Proc. Am. Phil. Soc, Nov. 21, 1889.

[51] As quoted by Ryder from British and Foreign Medico-Chirurgical Review, Oct. 1858.

[52] Such as are seen in the adaptations of mimicry and protective coloration.

[53] See the exact studies of Kowalevsky, Cope, and Ryder among the vertebrates, and of Hyatt, Dall, and others among the invertebrates.

[54] Biol. Memoirs, p. 84.

[55] See "The Evolution of Mammalian Molars to and from the Tritubercular Type," American Naturalist, December, 1888.

[56] Such as appear in some molars of the later Tertiary ungulates.

development until they reach a stage in which they are obviously useful and subserve attrition. Second, upon the principle that the action and reaction of two opposing surfaces must be equal, it is difficult to explain some cases in which we observe a cusp in one jaw developing, while the cusp in the other jaw, opposing it and presumably stimulating its development, is degenerating.[57] The force of these exceptions will weigh seriously against the Lamarckian principle, unless they also can be proved by subsequent research to conform to the laws of individual adaptation. I consider that the strongest line of attack which can in future be taken against Lamarckism will be in showing that certain characters (such as the above), in which it is supposed to operate, could not be produced on principles of direct adaptation.

But if we reject the Lamarckian principles we must assign Selection as the cause of these definite lines in variation, for no one would urge the third alternative.

6. *What is the Relation between Variation and Selection?*—The question of Utility is the first which arises when we attempt to explain the origin of such variations as we are here considering by the selection principle. In the recent animated discussion which has taken place between Romanes,[58] Mivart, and others on the one side, and Wallace[59] and Dyer on the other, great difference of opinion has been shown as to Utility. So far as the question bears upon the substitution of pure natural selection for Lamarck's principle, we may, in this argument, avoid the broader question by admitting that all characters possess, or have once possessed,' some degree of utility, or the reverse. This is as necessary for Lamarck's as for Weismann's principle. The essential question here is whether the plus- or minus-variations in advanced stages, or the variations in initial stages, or still more the variations which constitute the initial stages themselves, are of such importance as to weigh sufficiently in the scale of survival, to accumulate definite lines of adaptive variations.[60] Let us assume that they can be, what further assumptions are necessary?

We start with the proposition that all these variations have their origin under the laws which we have seen govern variations of Classes I. and II., for upon Weismann's principle we cannot admit any other modes of origin. They must start, therefore, indefinitely, but secure a definite direction by the selection of those in favorable, and elimination of those in unfavorable, directions. This direction must be continuously plus where the characters are developed by direct Selection,[61] or neutralized where the characters are under the sustaining power of Selection, or minus where the characters are degenerating under the influence of Panmixia (free intercrossing), or even of reversed Selection.[62] Every union of new individuals, according to Galton's law of regression, however, will tend to draw back all the plus- and minus- variations to mediocrity, even where both parents show a tendency in the same direction. This regressive tendency to mediocrity, seen in the union of a single pair, will be further hastened by Panmixia.[63] We have assumed the continuous operation of Selection and abundant favorable variations to draw from, but we have seen, under Query 3, that variability is generally greatest when external conditions are most favorable; at the same time Selection must be least active, for the struggle for existence is least severe,—that is, Selection is least rapid when its materials are most abundant. So much for the probabilities of the production of definite lines of variation in single characters of this class. Evolution is not, however, a "log-rolling" process, in which some parts lag behind while others are improved by selection; in the fossil series, as all parts of the skeletal organism are observed in course of evolution at the same time, we must assume indefinite variability in every part, and admit the probability that, especially in uncorrected parts, the sum of favorable variations, will be equal to the sum of unfavorable variations, and thus neutralize each other, so far as Selection is concerned. We must, therefore, add the assumption

[57] I refer to the paraconid and hypocone.

[58] "The majority of specific differences are inutile (non-adaptive)." *Nature*, 1989, p. 8.

[59] "There is no proof that specific characters are frequently useless."

[60] Darwin distinctly abandoned the utility principle in the case of Saturnia. See letter to Moritz Wagner, "Life and Letters," Vol. III.

[61] See Biol. Memoirs, pp. 264, 85, 101, 275.

[62] Romanes has endeavored to show that where a character becomes detrimental Selection will tend actively to eliminate it.

[63] Galton has shown that in the union of two individuals showing exceptional characteristics only a few of the offspring would be likely to differ from mediocrity so widely as the mid-parent. "Natural Inheritance," p. 106.

that these definite lines will be selected in correlation with those observed to occur in all the surrounding parts, and granting that groups of correlated parts may vary simultaneously[64] (e.g., fore and hind limbs, or a series of vertebrae), we have still further to assume that these variations are selected with coordinate variations in parts which are not in the remotest degree correlated, viz., the teeth.[65] We must still further assume that Selection acts at the same rate to produce simultaneously exactly parallel lines of adaptive variations in related species over widely distributed areas, as in the American and European species leading to the horse series. If it is maintained that this parallelism has been sustained by interbreeding, then the arguments based upon Divergence and Isolation lose their force. If it be said that combinations of favorable variations occur in nature, not only in correlated but in uncorrelated parts, and Selection acts upon these combinations, then those who support Weismann's principle must further assume that there are definite lines of blastogenic variation. This *argumentum in circulo* would bring us back to the original question, What is the cause of definite lines of variation?

Can Acquired Variations be Inherited?—It must be admitted by every one that, as the germ-cells are usually differentiated and set apart from the somatic cells at an early age, it is very difficult to conceive how definite changes in certain peripheral somatic cells occurring in the higher adult Metazoa can produce such changes in the germ-cells as to be reproduced in the offspring, even if we allow a very long time for the process. If, however, such a process does take place, it rests with the embryologists to work out a theory for it, so we are not concerned with the process, but the evidence. All the evidence above considered belongs properly to Evolution; we must now consider the bearings of some of the classes of evidence from Inheritance.

The evidence from mutilations is somewhat conflicting. It has been fully discussed recently by Weismann, Eimer, and others. It involves two elements which are not observed in the ordinary course of evolution: 1. Immediate transmission of the full characters. 2. Transmission of characters impressed upon the organism, and not self-acquired. I believe that no indisputable evidence for the inheritance of acquired characters has been produced under this head.

Another class of evidence consists in what are believed to be cases of the inheritance of maternal influences upon offspring *in utero*. It is an axiom among breeders that an ill-bred sire may affect all future strains. One of the most striking cases is that of Lord Morton's Arabian mare, which was sired by a Quagga, and later by a pure Arab, the foal of the latter showing zebra-like markings. Professor Turner says of this case: "I believe that the mother had acquired during her long gestation with the hybrid the power of transmitting quagga-like markings. The ova must have been modified while still in the ovary."[66]

I refer to papers of Vines[67] and Turner[68] as bearing especially upon the supposed isolation of the germ-cells, and showing that in the lower Metazoa and some of the higher Metaphyta the germ-plasm is diffused through the organism, and thus related to the *soma*.

We should find in these transitional organisms, as I have suggested under Query 1, that the relation between the somatic and germ-cells was established, if it exists. It is a necessary deduction from Weismann's theory that if this relation was advantageous it must have been preserved by Selection. If Selection can bear the burden of Evolution, it certainly can account for the origin of the Lamarckian principle in inheritance.

Conclusions.—The conclusions we reach in this discussion must finally turn upon the existence of definite lines of blastogenic variation. If there are no such lines, the Lamarckian principle falls *ipso facto*; if there are, we have still to estimate the probabilities between Weismann's and Lamarck's principles as affording the most adequate explanation for them, keeping in mind the problem of Inheritance as affecting these probabilities.

The Weismann principle depends upon Selection as the source of definite lines of Variation. What evidence has been advanced for the initial but all es-

[64] The fact that they do so may be used as an indirect argument for the Lamarckian principle.

[65] Or adaptive characters for protection, mimicry, sexual ornamentation, etc.

[66] See *Nature*, 1889, p. 532.

[67] "An Examination of Some Points in Prof. Weismann's Theory of Heredity" *Nature*, October 24th, 1889, p. 62.

[68] "The Cell Theory, Past and Present." *Nature*. November 6th and 13th, 1890.

sential assumption that, for example, a tiny adaptive cusp is a factor in survival, while its tiny inadaptive fellow is a factor in extinction? not to mention the succeeding assumptions which overwhelm us when we seek to derive definite adaptation from indefinite variations.

The Lamarckian principle furnishes us with an explanation of the observed phenomena of simultaneous progressive adaptation in most of those parts which it affects, including Correlation and Parallelism. It cannot be said at present to explain *all* the phenomena within its sphere; we must explain these phenomena, or abandon the principle.

It follows as an unprejudiced conclusion from our present evidence that upon Weismann's principle we can explain Inheritance, but not Evolution, while with Lamarck's principle and Darwin's Selection principle we can explain Evolution, but not, at present, Inheritance. Disprove Lamarck's principle, and we must assume that there is some third factor in Evolution of which we are now ignorant.