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The palæontological evidence for the transmission of acquired characters[†]

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As a contribution to the present discussion upon the inheritance of acquired characters I offer an outline of the opinions prevailing among American naturalists of the so-called Neo-Lamarckian school, and especially desire to direct attention to the character of the evidence for these opinions. This evidence is of a different order from that discussed in Weissmann's Essays upon Heredity, and while it cannot be said to conclusively demonstrate the truth of the Lamarckian principle, it certainly admits of no other interpretion at present, and lends the support of direct observation to some of the weightiest theoretical difficulties in the pure selection principle.

1. I regard natural selection as a universal principle, explaining the "survival of the fittest" individuals and natural groups, and as the only explanation that can be offered of the origin of one class of useful and adaptive characters. I supplement this by the Lamarckian principle as explaining the "origin of the fittest" in so far as fitness includes those race variations which correspond to the modifications in the individual springing from internal reactions to the influences of environment. There is naturally a diversity of opinion as to how far each of these principles is operative; not that they conflict.

2. If both principles operate upon the origin of the fittest we should find in every individual two classes of variation, both in respect to new characters and to modifications of the old:—First, chance variations, or those which, with Darwin and Weissmann, I attribute to the mixture of two diverse hereditary strains. These may or may not be useful; if useful they depend entirely upon selection for their preservation. Second, variations which follow from their incipient stages a certain definite direction towards adaptation. These are not useful at the start; thus while, as they accumulate, they favor the individual, they are not directly dependent upon selection for their preservation. These I attribute to the Lamarckian principle.

My present purpose is to show that variations of the second class are of an extent and importance not suspected previous to our recent palæontological discoveries, and that the Lamarckian principle offers the only adequate explanation for them.

3. The general theory as to the introduction and transmission of variations of the second class may be stated as based upon the data of palæontology—the evolution of the skeleton and teeth.

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. 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. The variations thus arising are accumulated by the selection of the individuals in which they are most marked, and by the extinction of inadaptive natural groups. Selection, in so far as it affects these variations, is not of single characters, but of the *ensemble* of characters.

The evidence is of a direct and indirect character. The direct evidence is that by actual observation in complete palæontological series, the origin of adaptive structures is found to conform strictly to the lines of use and disuse. The indirect proof is that the natural selection of chance variations is unsupported by observation and is inadequate to explain the variation phenomena of the second class.

4. I will first briefly consider the former. The distinctive feature of palæontological evidence is that it covers the entire pedigree of variations, the rise of useful structures not only from their minute, apparently useful condition, but from the period before

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they appear. The teeth of the mammalia render us the most direct service, as compared with the feet, since they furnish not only the most interesting correlations and readjustments, but the successive addition of new elements. With a few exceptions which need not be noted here, all the mammalia started with teeth of the simple conical type—like the simple cusps of reptiles. Practically every stage between this single cusp and the elaborate multicusped recent molars is now known. Every one of the six main cusps of the molar of *Hyracotherium*, for example, a type of an important central stage in the ungulate dentition, is first indicated at the first point of contact or extreme wear between the upper and lower molars; this point of wear is replaced by a minute tubercle, which grows into a prominent cusp. These are the laws of cusp development, as observed in every known phylum of mammalia:

I.—The primary cusps first appear as cuspules, or minute cones, at the first points of contact between the upper and lower molars in the vertical motions of the jaws.

II.—The modeling of cusps into new forms, and the acquisition of secondary position, is a concomitant of interference in the horizontal motions of the jaws.

5. The evidence, of which this is only a single illustration, has accumulated very slowly. The line of reasoning from this particular series of observations is as follows: 1. The new main variations, in the teeth and skeleton of every complete series, are observed to follow certain definite purposive lines. 2. By careful analysis of the reactions to environment which would occur in the individuals by the laws of growth, we observe that the race variations strictly conform to the line of these reactions. 3. We further observe that no variations of this class occur without the antecedent operation of these reactions; the working hypothesis thus stands the test of prediction. 4. We accept this invariable sequence of race adaptation upon individual adaptation as proof of a causal relationship.

6. I admit that this proof may be invalidated in several ways: 1. By showing in more extended research that these observations of sequence are inaccurate or offset by others in which there is no such sequence. 2. By showing that the Lamarckian principle, while explaining some of the variations of this dass, is directly contradictory to others. 3. By showing that all these phenomena may be explained equally well or better by natural selection. 4. By proving, independently, that the transmission of acquired characters never occurs.

I will now consider each of these cases:

First.—As regards these observations. They may be examined in detail in the studies of Cope, Wortman, or Ryder, and in a paper I presented to this Association last year. As the question of transmission has been generally assumed in the foregoing studies, I think it is now important to review the whole field, searching for facts which look against the Lamarckian principle, for as we have been hitherto studying with a *bias* in favor of it, some such adverse points may have been overlooked. At present, however, I can recall only a single adverse observation, that is, in the development of one of the upper cusps, the lower cusp which opposes it, and which is therefore supposed to stimulate this development, is found to recede. I have no doubt others will be found presenting similar difficulties.

Second.—As regards the Lamarckian principle. Several objections to the special application of this principle to the evolution of the teeth have been raised by Mr. E. B. Poulton:

A.—To the objection that the teeth are entirely formed before piercing the gum, and that use produces an actual loss of tissue as contrasted with the growth of bone, it may be said that by our theory it is not the growth itself, but the reactions which produce this growth in the living tissue, which we suppose to be transmitted.

B.—To the objection that this proves too much,—that the cusps thus formed would keep on growing, it may be said (*a*), that in the organism itself these reactions occur least in the best adapted structures. This proposition is difficult to demonstrate in the case of the teeth, but may be readily demonstrated in what are known as the phenomena of displacement in the carpals and tarsals where growth has a direct ratio to impact and strain. (*b*), In the organism itself growth does not take place beyond the limits of adaptation; there is, therefore, no ground for the supposition that overgrowth will take place by transmission. (*c*), Either by the selection or Lamarckian theory development is held in check by competition between the parts; there is a limit to the nutritive supply; in the teeth, as elsewhere, the hypertrophy of one part necessitates atrophy of another.

C.—A general objection of considerable force is that we find other adaptations, equally perfect, in which the Lamarckian principle does not apply; why then invoke it here? To this it may be said that there is no theoretical difficulty in supposing that while natural selection is operating directly upon variations of the first class, the Lamarckian principle is producing variations of the second class, and while selection does explain the former, it falls far short of explaining the latter.

D.—Finally, if Weissmann succeeds in invalidating the supposed proofs of the Lamarckian principle derived from pathology and mutilations, this will not affect the argument from palæontology and comparative anatomy, for these proofs involve two elements which are not in our theorem: (*a*), immediate transmission of characters; (*b*), transmission of characters impressed upon the organism and not self-acquired.

Third.—As regards the adequacy of the selection principle to explain these variation phenomena. It is not necessary to repeat here the well-known current theoretical objections to this principle, but simply to point out the bearing of this palæontological evidence. In Weissmann's variation theory the preponderating influence must be conservative; however it may explain progressive modification, or even correlation of old characters, it does not admit that the genesis of new characters should follow definite lines of adaptations which are not preexistent in the germ plasma. We find that new characters of the second class do follow such purposive or directive lines, arising simultaneously in all parts of the organism, and first appearing in such minute form that we have no reason to suppose that they can be acted upon by selection. The old view of nature's choice between two single characters, one adaptive, the other not adaptive, must be abandoned, since the latter do not exist in the second class.

Fourth.—The most serious obstacle to the Lamarckian principle is the problem of transmission. How can peripheral influences be transmitted in the way we have outlined—now that we have such strong evidence for the continuity of the germ plasma? If acquired characters are not transmitted it is clear that the whole Lamarckian principle is undermined, and all these instances of sequence express no causal relationship. We are then, however, left without any adequate explanation of the laws of variations of the second class, and are thus driven to postulate some third, as yet unknown, factor in evolution to replace the Lamarckian principle.