SCIENCE

FRIDAY, JANUARY 23, 1920

CONTENTS

MSS. intended for publication and books, etc., intended for review should be sent to The Editor of Science, Garrison-on-Hudson, N. Y.

WHITMAN'S WORK ON THE EVOLUTION OF THE GROUP OF PIGEONS

THE three volumes containing the work of Professor Charles Otis Whitman on pigeons published by the Carnegie Institution of Washington is a fine memorial to one of the leaders of zoological research in America. In the course of the sixteen years devoted to this work Whitman brought together birds from all parts of the world, bred them, studied their juvenile and adult plumages, and their habits, and made many crosses between different species. When he died in 1910, his extensive and valuable collection of living birds was saved through the devotion and sacrifices, both personal and financial, of Dr. Oscar Riddle, the editor of these posthumous volumes. After that first year of precarious existence, the Carnegie Institution met during the five years following the expenses of maintenance, and during this time the birds, under Dr. Riddle's care, were transferred to the laboratory at Cold Spring Harbor where Whitman's work is being carried forward. Without this support only a fragment of Whitman's results could have been preserved or the birds kept to complete many of the important problems that were at the time of Whitman's death still unfinished. The editing of the work has been admirably done by Dr. Riddle. It is a fortunate circumstance that what was left fell into the hands of one familiar with Whitman's ways of thinking, and thoroughly conversant with the many problems that had grown out of Whitman's studies; for "not more than one fifth of the matter" was in shape for publication when Whitman died.

Volume I. gives Whitman's views and his evidence for orthogenetic evolution. The editor says in the preface, Whitman "has accumulated the most weighty evidence for

[1] Posthumous words of Charles Otis Whitman. The Carnegie Institution of Washington, 1919.

continuity as against discontinuity in the phenomena of variation, inheritance and evolution." And with this verdict his reviewer is not inclined to disagree, because as a careful study of Whitman's evidence and meaning shows, there is not much difference between what he understood by continuity and what is to-day called more often discontinuity.

In the introductory chapter from a manuscript written in 1909 that formed part of a lecture given at Clark University, the keynote to Whitman's antagonism to the mutation theory of de Vries is struck—a note that recurs throughout the first two volumes. Weismann, he says, taught us to look to germinal variation as the source of all variation that is hereditary. Then follows a paragraph that takes us to the heart of the matter: "Do we not have, then, in germinal variation, a better criterion of what is specific than we get in sudden appearance? Indeed, is it not here that the seeming suddenness of first appearance finds its explanation, and likewise the fact that so-called mutations involve the whole organism? If we are to accept the physiological conception of development, as is inevitable in my opinion, it is easy to see that a change, however slight, in the primordial constitution of the germ would tend to correlate itself with every part of the whole germ-system, so that the end stage of development would present a new facies and appear as a total modification, answering to what deVries would call a mutation. That some thing of this order does sometimes occur I have indubitable evidence, and in such form as to dispel the idea of discontinuity and sudden gaps in transformation."

With a slight shift of wording and emphasis the essential part of this statement is not very different from what we think to-day, for who will dispute now that a change (mutation) in the germ-plasm may affect many parts of the organism that develops out of such a changed germ-plasm? Such a view has not been found to dispel the idea of "discontinuity" of characters; on the contrary it is in full accord with it.

But the unit character is Whitman's *bête noir*. "The idea of unit-characters, however, as distinct elements that can be removed or introduced bodily into the germ does not appeal to me as removing difficulties, but rather as hiding them; in short, as a return to the old pangenesis view of preformed characters. In this theory, as is well known, we have two miracles involved. The first consisted in a centripetal migration of preformed gemmules, and the second in the centrifugal distribution of the same elements. DeVries dismisses the first of these, but accepts the second, and on it rears the superstructure of his theory of mutable-immutable unit-characters. With all due respect to the distinguished author of this theory, and with abounding admiration for his great work and model methods, which have aroused universal interest and stimulated enormously experimental bionomics, I am strongly persuaded that his hypothesis of unit-character fails as a guide to the interpretation of the species and its characters."

"It is true a great amount of work on Mendelian heredity seems strongly to support the unit-character hypothesis, and that cytology offers some further support. Nevertheless, I have to confess a wholesale scepticism. The germ, as I believe and have long maintained, stands for an organized whole. It is a unit-organism, not an organism of units; all the features that arise in the course of development are within the sphere of the individual unity and integral parts of it, and whatever specificity they possess is completely determined and not of independent origin."

"The strongest suggestion of unit-characters is found in the phenomenon known as segregation. I do not understand the importance of this striking behavior of so-called alternative unit-characters. I am familiar with it and deeply interested; but I am unable to see in them the sum total of all we know about heredity. What I have said in regard to unit-character applies to the Mendelian doctrine. Mendelism, like mutation, neglects the natural history of the characters, it experiments with and is not primarily concerned to know how characters have originated and multiplied."

It may be that the emphasis laid on unit-character by some of the earlier enthusiastic followers of Mendel and the frequent confusion in their writings between the unit-character, so-called, and the change in the germ-plasm that gave rise to it, may justify Whitman's scepticism; but this charge can hardly be brought against de Vries, who stated over and over again that a single change in the germ-plasm may be the cause of manifold although slight changes in the characters throughout the whole organism.

In contrast to change by mutation Whitman opposes orthogenesis. Evidence for the latter he finds in his study of the group of pigeons. The evidence is the familiar argument from comparative anatomy and from the hypothesis of "recapitulation."[2] Before taking up the evidence I can not refrain from quoting a fine and characteristic statement of Whitman's in the same lecture:

"I take exception here only to the implication that a definite variation-tendency must be considered teleological because it is not 'orderless.' I venture to assert that variation is sometimes orderly and at other times rather disorderly, and that the one is just as free from teleology as the other. In our aversion to the old teleology, so effectually banished from science by Darwin, we should not forget that the world is full of order, the organic no less than the inorganic. Indeed what is the whole development of an organism if not strictly and marvelously orderly? Is not every stage, from the primordial germ onward, and the whole sequence of stages, rigidly orthogenetic? If variations are deviations in the directions of the developmental processes what wonder is there if in some directions there is less resistance to variation than in others? What wonder if the organism is so balanced as to permit both unifarious and multifarious variations? If a developmental process may run on throughout life (*e. g.*, the lifelong multiplication of the surface-pores of the lateral-line system in *Amia*) what wonder if we find a whole species gravitating slowly in one or a few directions? And if we find large groups of species all affected by a like variation, moving in the same direction, are we compelled to regard such 'a definite variation-tendency' as teleological, and hence out of the pale of science? If a designer sets limits to variation in order to reach a definite end, the direction of events is teleological; but if organization and the laws of development exclude some lines of variation and favor others there is certainly nothing supernatural in this, and nothing which is incompatible with natural selection. Natural selection may enter at any stage of orthogenetic variation, preserve and modify in various directions the results over which it may have had no previous control."

How far one is justified in extending the orderly sequence of embryonic development to the sequence shown in evolutionary advance is a large question and will no doubt be settled some day by fuller knowledge. At present our speculations must rest on the evidence at hand, and this evidence, Whitman finds, as stated, in his comparative studies of pigeon coloration, and in a most ingenious experiment of feather plucking.

His studies of domesticated breeds and their wild relatives led him to conclude that the blue wing with two black bars is not the original pattern as Darwin supposes, but rather the checkered wing covered with black spots. Both patterns are found to-day in wild birds, hence these birds can not be appealed to for a decision. But an examination of other species of pigeons shows that the checkered type is widespread and occurs in many varieties; and the young in many groups show a more checkered pattern than do the adults themselves. The Japanese turtle dove comes nearest, in Whitman's opinion, to the original type of wing pattern. The elaborate consideration that Whitman devotes to the subject indicates how important the question appeared to him;

[2] Whitman uses the word "recapitulation" in the sense for which the reviewer argued in 1903 ("Evolution and Adaptation," Chap. III.). As so used it means something essentially different from the word "recapitulation" in the original sense of Darwin and Haeckel, unless the changes in the germ-plasm add stages only to the end of ontogeny as Whitman seems to think is the way in which the process takes place. (See a later footnote.)

for, from it he derives the support of his orthogenesis. Since the same kinds of advances are observed over and over again in different groups, and since no plausible reason can be given why such changes are of benefit to the species, it follows, on Whitman's view, that some internal agency has brought about these parallel advances.

The change at molting that transforms the young plumage into that of the adult is often abrupt, almost like a mutation, yet a simple experiment shows that in the interval the constitution of the bird has been progressively advancing. If feathers are plucked in the intervening stages, the new feathers show an advance over the young feathers still present, an advance in the direction of the feathers that are to come at the next molt. And the nearer to molting time the operation is performed the nearer the approach to the newer feathers. Here then what appears to be a sudden change has in reality been led up to by a continuous series of preparatory stages; so, in Whitman's view, what appear at times to be sudden and great changes in evolution (mutations) are in reality only end stages of continuous advance. The development of the bird repeating the history of the race shows continuous change but the exegesis of molting gives us only the earlier and the later picture. To discuss this theme would take us too far afield, but it is a matter not unfamiliar to the morphologist. It should be pointed out that a change (mutation) in the germ-plasm affecting principally the end stages would be expected to give results that are in no sense incompatible with this picture.

Whitman obtained a few "mutations," *i. e.*, new types of pattern that were transmitted. The mutant change, he points out, is only an extension of a character already faintly present in the birds and present in certain wild species. What is produced is not new but a "continuous" extension of a character already present. Hence such mutations are not, he contends, new unit-characters but extension or diminution of characters already in existence. Such, in fact, are the majority of mutations known to us to-day.

Whitman thinks a very old idea reincarnated in Darwin's theory of pangenesis (that the body characters impress their influence on the germ cells) while nominally rejected survives in more subtle guise in some more modern theories such as de Vries's theory of pangenesis. In this theory the nucleus is looked upon as the seat of the hereditary complex. Its "vital" units are self-perpetuating by division, so that the nucleus in every cell remains the store house of all of the hereditary materials. In the course of embryonic development these vital elements, pangenes or genes, are set free in the surrounding cytoplasm of the cell, where they multiply and determine the fate of the cell. "The myth of transmission was not eliminated; it was only reduced in its field." "Transmission thus became more direct, but its mysteries remained as unfathomable as before. The unit-characters are assumed to preexist in the chromosomes and to stand in need of transportation from the nucleus to the body of the cell in order to develop." But "if an innumerable host of specifically distinct unit-characters are let loose in the cell-plasm, how are they to reach precisely predetermined points in the organism, and at just the time when needed? It is here that the theory breaks down, for the difficulty is not one that further investigation may hope to solve, but one that lands us in hopeless speculation. So long as the primary assumption is that of ready-made unit-characters, specifically distinct and independently variable, whether located in the nucleus or in the cytoplasm, or in both, the problem of development will remain inscrutable."

A perusal of de Vries's pangenesis theory will show that Whitman has put his finger on a weak spot in the speculation, in so far as this view pretends to explain how the specific pangens of the nucleus are supposed to migrate out of the nucleus of each cell at the right time in particular regions of the embryo, but de Vries laid no emphasis on this and was familiar with the absence of evidence for such an interpretation. The same difficulty confronts us to-day, but if I understand

the situation rightly no one would be bold enough to claim any such time relations of pangen migration nor does the theory of nuclear influence call for such a hypothesis in any sense. It is ony necessary that nuclear influence should in some way affect the chemical changes that go on in the surrounding cell to cover completely the situation. No time relation is expected or called for, and who to-day will deny, in the face of extensive evidence, that the nucleus does have an important influence on the cell? With this understanding one can agree cordially with Whitman's concluding thrust: "The doctrine of germs laden with independent unit-characters, or pangens, each predestined, so to speak, to flower in its own place and time strikes me as teleological mythology, fine spun, to the verge of absurdity. We have not yet fathomed primordial organization, but it is safe to assume that the germ sets out with a biophysical constitution of a given specific type, within which metabolic, generative and differentiating processes under normal conditions run on in a self-regulating way."

The title of Volume II. epitomizes its contents, "Inheritance, Fertility and the Dominance of Sex and Color in Hybrids of Wild Species of Pigeons." Seven manuscripts of less than one hundred pages, nearly 2,000 pages of breeding records, and two hundred illustrations comprised the original material of this volume of two hundred twenty-three pages. Only a few chapters, viz., I. (1904–05), XII. (1897), XVI. (1898), and XVII. (1906) were left complete. The remaining chapters (containing fragments and sections by Whitman, and his breeding records) consist in large part of analyses and discussions by the editor based on Whitman's data to which have been added many of the later observations and views of the editor. This work of elucidation and summarization has been well done, making the text readable, and guiding the reader through a maze of not completed and intricate data.

One of the outstanding results of the hybridization work, which constitutes the bulk of this volume, is that offspring produced by crossing species of generic or family rank are males. This fact is in conformity with results obtained in other species of birds (see Guyer). The result is however complicated, according to the editor, by a second result, viz., "that, in many crosses of very distinct genera and species, fertility (developmental power) is shown to be highest in the spring and lowest in the autumn, and that male offspring predominate in the season of highest fertility, while females largely predominate in the season of lowest fertility." Several pages attempting to explain the apparent contradiction follow this statement, but since "it may be emphasized that Professor Whitman was by no means inclined to dogmatize as to the interpretation of this sex series," the subject need not be further discussed here.

In certain crosses between checkered and barred domesticated races the results show that checkered birds may throw some barred offspring. That the two may differ by a single factor difference may seem probable, especially in the light of other evidence (Bonhote and Smally, Staples-Browne) not referred to in the text. The relation is mentioned here because it elucidates a point not fully understood by opponents of Mendelian interpretation, viz., that such a relation is not claimed by most Mendelians as showing necessarily that the barred character must have arisen by a single mutation, although it may have done so. There may have been, as Whitman thinks, a long line of more graded intermediate steps between the two; still the barred and the checkered types might be differentiated to-day by a single factor difference provided both contained all other genes in common. In other words the modern checkered and barred birds, as compared with the old checkered type, would be supposed to carry an entire series of gradually acquired factors, and the checkered birds one further factor. Thus one change in the complex that gave the barred type is supposed to have sufficed to suppress all of the new stages. The two checkered birds would differ then in the entire series of gradually acquired factors, and also in the single final factor that caused the apparent back-throw. There are also records, some of them too fragmentary to be

significant, bearing on the question of the greater likelihood of the first egg being a male in "pure" species—a question that goes back to Aristotle and has as often been denied as affirmed. A table on page 171 (Table 170) appears to indicate that this is the case in the Streptopelia senegalensis where twelve males came from the first egg, and only two females came from the first egg, while only two males came from the second egg and nine females from the second egg. The evidence that has been advanced in refutation of this relation is due, the editor suggests, to the use of "mongrels, collectively known as domesticated pigeons." More data must be obtained and statistical treatment applied to settle this question. The genetic evidence shows that the female is heterozygous for the sex-chromosome, and if the method of disjunction of the sex-chromosome in the egg is affected by the conditions that prevail when the first egg is set free from the ovary, we may possibly find in this relation an *excuse* for such a result. If this should turn out to be true, the cause of the maleness of the generic hybrids must be sought in some other direction.

The chapter (XIV.) on Heredity contains mainly the more general points of view reached by Whitman in 1907. Coming at a time when Mendel's discoveries had received general notice and had been, even then, confirmed from many sources, the chapter contains results of exceptional interest. The grounds for Whitman's objection to any theory resting on the assumption of unit-characters is contained in the following striking paragraph:

"Every theory founded upon the postulate of unit-characters, or specific determinants stored in the nucleus is necessarily committed to some form of centrifugal distribution during the course of development; and for each element to be distributed it is necessary to assume either that it is passively transported to its destination or that it finds its own way automatically. In either case it would be nothing less than a miracle for a specific pangen to reach a prescribed point in such a complex mosaic field as the organism represents; and, for this to be fulfilled, not only at the predetermined point, but also just at the moment for harmonious development with its immediate neighbors, with symmetrical and correlated groups, with inter- and intra-locking systems constituting a microcosmic whole, incomparably more difficult to grasp than the stellar universe—for all this to be fulfilled is utterly beyond the bounds of scientific credibility. To try to conceive of normal development as thus prepunctuated in all its time and space relations—as proceeding from ready-made elemental characters, automatically distributing themselves or guided by entelechies—is to indulge in ultra-scientific teleology."

The statement imputes apparently, to Mendelism in so far as it deals with unit-factors and unit-characters an implication from de Vries's hypothesis of pangenesis; viz., the migration from the nucleus of "organic bodies" which multiply in the cytoplasm and determine the fate of the cell. There is the further implication that the migration is so timed that it takes place at each critical place in development. With Whitman's criticism most students of heredity will agree, but it should be noted, as I have pointed out above, first that Mendelism makes no such appeal, second that the relation of specific materials in the nucleus need not be supposed to have any such time relations as here stated, and third a careful reading of de Vries's "pangenesis" shows that he does little more than make a passing reference to such an interpretation and to-day, at any rate, it is not an essential part of the doctrine of nuclear action. Whitman's own view makes it evident that he is not inclined to disregard the nucleus as one of the elements in the "organization" that supposedly has some action on "the cell as a unit." Granting that differences may exist in the nucleus of different species, different end products are expected. The evidence that such differences may be related to specific substances in the nucleus is no longer a speculation but rests on the analytical evidence from Mendelian heredity. In what way and at what times the nuclear materials take part in the determination of characters we do not know. The essential point is that we are in

no way committed to any interpretation. Stated negatively we might add that there is nothing known at present to preclude the possibility that the influence is a purely chemical process. We find ourselves, therefore, practically in agreement with Whitman's attitude when he says:

"Now while ontogeny is so wonderfully exact that we never cease to be amazed at its performances, we must not forget that germ-cells are subject to slow variation. In fact, it is only germ-variation that has to be considered in phylogeny as in ontogeny. Consequently, when the germ-cell takes a step forward, ontogeny begins with an initial difference that sets the whole series of ontogenetic stages on a diverging line that digresses so little as to be undiscoverable until nearly at the end of development."[3]

Whitman's failure to find "dominance and recessiveness" of character in his pigeon crosses led him to attack the supposed importance of these relations. To-day we know more cases where the hybrid shows in some degree an intermediate development of the contrasted characters than where dominance is complete Obviously the distinction has no importance since the law of segregation is found to hold as well when blending occurs as in cases where the somatic differences are clearly evident. The hybrid pigeons fall, therefore, in this respect into line with familiar phenomena. The failure of "splitting" in subsequent generations is a point that calls to-day for special consideration, but will not be dwelt on here.

In this chapter, and in several that precede it, Whitman and the editor speak rather frequently of what is called "weak" and "strong" germs as having an importance in determining the "strength" to which a character develops, even causing a "reversal of dominance." Curiously enough their effects are supposed to be transmitted so that fertility in the offspring is also affected. Even the occasional mutations found by Whitman are ascribed to this source. Pigeons unquestionably furnish unusual material for the study of this appearance. It is perhaps too soon to attempt to state how much or how little in variation to ascribe to such an influence, aside from the obvious effect in the immediate offspring. No doubt further work along these lines will help us to define more sharply what is to be understood by the somewhat vague attributes "weakness" and "strength."

There are important discoveries recorded in this volume that can only be referred to briefly; the "divisibility" of characters (meaning intermediate conditions) as seen in hybrids, the study of a "dominant" mutant character; the discovery as early as 1896 of sex-linked inheritance (of which a number of cases in other birds are well understood to-day), the cross between the last surviving members of our wild passenger pigeon and the ring dove, the relative influence of egg and sperm on the time of hatching of the hybrid young. Each of these results marks an advance in our understanding of heredity.

The third volume containing Whitman's observations on the "Behavior of Pigeons" is edited by Professor Harvey A. Carr. Thirty-two short manuscripts were left. It appears that Whitman's first period of study in this field was from 1895–98. In a few lectures at Woods Hole in 1897–98 some of his conclusions are given. After a period of five years a renewed interest in these directions recurred and many notes were made. The Woods Hole lecture in 1906 gave an opportunity for further consideration. Despite the very fragmentary remains of this work—fragmentary only in comparison with the extensive observations that Whitman had made, this volume contains many observations of great interest and gives an insight into the character of Whitman's methods, where the most careful and minute observations are interpreted with a breadth of intelligence that is truly remarkable. There are few if any groups of animals

[3] The reviewer would add an important reservation, viz., that a "forward step" in the germplasm might affect any stage in the course of development, or in the extreme case every stage in the development. This view is obviously consistent with what Whitman states, but, if emphasized, would to a large extent undermine the value of the evidence from ontogeny in interpreting ancestral stages.

so well suited to studies of this kind as are the pigeons. The elaborate courtship, the fidelity of the individuals to each other, the mating and nesting habits, the part taken by the female and the male in incubation, the feeding instinct of old and young, the weaning and the rythmic sequence of broods offer a fascinating opportunity to the student of animal behavior. Whitman obviously had in view a large program toward the accomplishment of which he had progressed much further that these notes indicate. Some of the lines of work opened up by him have been pursued successfully by his students Professor Craig and Dr. Riddle, but according to their statement his knowledge far outstripped that of any other observer in this field. The many observations here recorded are clearly only the material out of which, in time, he had expected to link up the evolution of instincts with the study of the evolution of structure and color. "If Professor Whitman had completed his work, he would have produced an extensive treatise on the phylogney of the pigeon group. . . . The voices and the behavior of the various species would have been used, like the color patterns, to throw light on the relationships, derivation and method of origin of pigeon species" (Craig and Riddle). According to Carr, Whitman developed "what one may term an orthogenetic conception of instinctive development. Instincts are not novel and unique constructions which spring, without ancestry, into being; rather each new instinct is but a slight modification or organization of tendencies already in existence." When one sees how vital the instincts are for the existence of the species it is probable that however the changes originated the advances would most probably be those involving only slight modifications of intincts already in action.

The Carnegie Institution and equally Dr. Riddle are to be sincerely congratulated on having preserved for American zoologists the last great work of Whitman. The wonderful colored pictures, almost entirely the work of the Japanese artist Hyashi, are marvels of beauty and accuracy, and stand for the minute attention that Whitman demanded at every stage of his work. The same attention to detail is shown in Whitman's early work on cell-lineage, on the leeches of Japan, and on the embryology of fishes, and explains in part his far reaching influence on American zoologists. It is rare to find combined such delicacy in treatment of detail with the sweep of philosophical interpretation of which Whitman was equally master.

Whitman stood at the parting of the ways. We may regret that he did not enter into the new era that even at that time was opening up its far reaching vistas, but this need not blind us to the fine example he set—an example of unworldly devotion and absorption in his work, of self-criticism made possible by simplicity and honesty of character, of fairness that led him to appreciate and to state accurately and kindly the opinions of others with whom he disagreed heartily.

T. H. Morgan

Columbia University

A PALEONTOLOGIC REVIVAL AT YALE UNIVERSITY

Othniel Charles Marsh was appointed professor of paleontology at Yale in 1866, this being the first time such a chair was established at any university He was unquestionably one of America's leading men of science, and in vertebrate paleontology "he stood without a peer." He had collected fossils long before his graduation from Yale in 1860, and after taking the doctorate at Heidelberg, he became deeply interested in the wonderful array of extinct vertebrates that the U. S. Geological and Geographical Survey of the Territories was finding in the "bad lands" of Nebraska. In the meantime, his uncle, George Peabody, had founded at Yale the Peabody Museum of Natural History, though the building was not erected until 1875. Marsh saw the great western wilderness for the first time in 1868, going over the Union Pacific into Nebraska and Wyoming. In 1870 he fitted out the first Yale College Scientific Expedition, and took west with him twelve enthusiastic students. From this time the flood of boxes shipped to the university grew annually greater and greater. In 1899 Pro-