SELECTION AND CROSS-BREEDING IN RELATION TO THE INHERITANCE OF COAT-PIGMENTS AND COAT-PATTERNS IN RATS AND GUINEA-PIGS

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CONTINUOUS VERSUS DISCONTINUOUS VARIATIONS AS FACTORS IN EVOLUTION.

It is generally agreed that the course of evolution is largely influenced by two factors, variation and heredity; but opinions differ as to what sorts of variation have evolutionary significance and as to the manner of their inheritance.

It has been recognized by several investigators that variations are of two distinct sorts. Bateson has called these two sorts of variation continuous and discontinuous; more recently De Vries has called them fluctuations and mutations, respectively.

By continuous variation (or fluctuation) we understand ordinary individual variation within a species. The individuals differ among themselves in size, color, and other structural features. By examining a considerable number of them we can form an idea of what is the commonest (or *modal*) condition as regards each structural feature; and likewise what is the average (or *mean*) condition.

Usually, but not always, the modal and mean conditions are approximately the same, and any other condition is the less frequent in occurrence, the greater its deviation from them. It follows that the most extreme condition observed is connected with the most usual (or modal) condition by an unbroken series of intermediate conditions, and we may call the series as a whole "continuous." The distribution of the individuals in such a series is governed by the laws of "chance," and may be successfully analyzed by statistical methods.

We commonly think of a "chance" result as something entirely beyond the control of law, but in reality such is not the case. Nothing is beyond the control of law. If a blindfolded person puts his hand into an urn containing a mixture of black and of white balls, it is a matter of chance whether he grasps a black or a white ball; but if he repeats the operation a considerable number of times, it is perfectly certain that he will draw balls of

both sorts in approximately the same proportions in which they occur in the jar. The result is a "chance" one, but controlled by a perfectly definite mathematical law.

A "chance result" has been aptly defined as the result of a number of causes acting independently of each other. If this is a valid definition, then a continuous series of variations is due to no single cause but to several mutually independent ones. Some of the causes may be external in origin, others internal; some temporary in their action, others permanent. It should not surprise us, therefore, to find that continuous variations differ greatly in the degree of their inheritance. De Vries, indeed, has maintained that they are not inherited at all, except temporarily; that selection of abmodal variations from a continuous series is unable permanently to modify a race; that the modifications will persist only so long as selection continues, but will speedily disappear when selection is arrested. This conclusion, however, seems to us altogether too sweeping. *A priori* there is no reason to suppose that *all* the causes operative to produce continuous variation are external in origin and temporary in action, as De Vries's conclusion would seem to imply. If there are in operation, in the production of a continuous series of variations, causes internal in origin, resident in the constitution of the germinal substance, so much of the result as is due to those causes should be inherited and so should be permanent. De Vries, we believe, has overlooked this factor entering into the problem. He has assumed that all the causes of continuous variation ("fluctuations") are either external in origin or due to conditions of the germinal substance purely temporary. He holds, we believe rightly, that all inheritance is due to germinal modification; but assumes, we believe without sufficient warrant, that permanent germinal modification is not a factor in the production of fluctuations.

Another category of variations, discontinuous variations (which include the mutations of De Vries), is considered by Bateson and De Vries as the true and only expression of permanent germinal modification. But, granting the truly germinal origin of mutations, it does not follow that they are the *only* product of germinal modification.

A discontinuous variation, as the name suggests, is unconnected by intermediate conditions with the usual (*modal*) condition of the species. It represents a change, more or less abrupt, from the modal condition of the species, and is strongly inherited, a fact which indicates clearly its exclusively germinal origin.

In the category of discontinuous variations belong abrupt changes in pigmentation and hairiness among both animals and plants, changes in the number of digits or of the number of phalanges in a digit among vertebrates, in the presence or absence of horns among animals and spines among plants, and other similar conditions.

Such changes are not the result of selection; they often appear, as it seems, spontaneously, and they are permanent in the race, if isolated.

De Vries maintains that all species-forming variations are of this sort; that selection is unable to form new species, because it can neither call into existence mutations nor permanently modify a race by cumulation of abmodal fluctuations. Darwin, on the other hand, and the great majority of his followers, while admitting that races are occasionally produced by discontinuous or "sport" variation, ascribe evolutionary progress chiefly to the cumulation through long periods of time of slight individual differences, such as De Vries calls fluctuations. The issue between the two views is sharp and clear. According to De Vries, if we rightly understand him, selection is not a factor in the *production* of new species, but only in their *perpetuation*, since it determines merely what species shall survive; according to the Darwinian view, new species arise through the direct agency of selection, which leads to the cumulation of fluctuating variations of a particular sort.

De Vries and the Darwinians differ not only as to the part which selection plays in evolution, but also as to the nature of the material upon which selection acts. According to De Vries, species are not modified by selection; mutations *are* new species and selection determines only what mutations shall survive, fluctuations having no evolutionary significance. On the Darwinian view, all species, whether arising by mutation or not, are subject to modification by selection.

A great deal can be said in favor of each of these contrasted views, but discussion is at present less needed than experimental tests of the views outlined. To De Vries we owe much for showing that such tests are possible.

It was our purpose to make tests of this sort when we undertook the experiments described in this paper. The questions to which principally attention has been directed are these: (1) Can discontinuous variations be modified by selection alone? (2) Can discontinuous variations be modified by cross-breeding? A negative answer to these questions will support the view of De Vries; an affirmative answer will support the Darwinian view, because it will show that through selection new conditions of organic stability can be obtained; that is, new species may be produced.

The material used consisted of certain discontinuous variations in the color-pattern of rats. The general result obtained is this: Various color-patterns, like the several pigments found in the rodent coat, are mutually alternative in heredity. Each group of individuals referred to the same type of color-pattern forms a continuous series fluctuating in accordance with the laws of chance about a common modal condition. The different types in general do not overlap; they form a discontinuous series. Now, these types may be modified in two different ways: (a) By selection of abmodal

variates within the same continuous series, and (*b*) by cross-breeding between different types. There is no evidence that one of these methods has effects less permanent than the other. So far, then, as these experiments go, they support the Darwinian view rather than that of De Vries.

VARIATIONS OF RATS IN COAT-COLOR AND COAT-PATTERN.

Variations in the pigmented coat of rodents are of two principal sorts: (1) Variations in the character of the pigments found in the coat, and (2) variations in the distribution of those pigments. The character of the pigmentation in the wild rodent is nearly always complex. Two or three pigments are associated together in the same hair, but they differ in their regional distribution, so that a grayish or brown "ticked" coat results, inconspicuous against many backgrounds. The coat of the house-mouse (Bateson, :03) and that of the wild guinea-pig (Castle, :05) contain three optically different pigments—yellow, brown, and black. These all coexist in the same hair. In certain fancy varieties of these rodents, a single pigment is present without the others, or the distribution of the pigments is such that only one sort is conspicuous. Animals pigmented thus are known as black, chocolate, and yellow (or red) varieties. If all three pigments are absent from the coat and likewise from the retina of the eye, a condition known as total albinism obtains.

In rats, rabbits, and certain other rodents, black and yellow self-varieties are well known, but no pure chocolate animal has been observed.

Total albinism and the several "self" conditions of pigmentation are all mutually alternative in inheritance.

Variations in pigment distribution on the body result commonly either from entire absence of pigment from certain regions of the body, in which case the coat has white markings, or from the occurrence of different pigments singly in different body-regions, in which case the body bears spots of different colors. Both sorts of variation may occur simultaneously, in which case the body is spotted with pigments of different sorts and with white.

The color-varieties of rats are fewer and simpler than those of mice, rabbits, and guinea-pigs. Aside from albinos, there are only two "self" (*i. e.*, uniformly colored) varieties, namely, gray (or brown, the color of the wild *Mus decumanus*) and black. Gray is a Mendelian dominant in relation to black.

As regards coat-pattern, there occur two conditions of partial albinism, which differ from each other only in degree, but which may be obtained each probably in a pure (homozygous) condition. These two patterns may be called "Irish" and "hooded." Each occurs either with gray or with black pigmentation. The "Irish" of fanciers, as described by Doncaster (:06),