

The Role of Selection in Evolution—II*

An Agency for the Elimination of Variations

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In the case of certain characters in guinea-pigs I have repeatedly attempted modification of a racial character by selection within an inbred race, without success. Thus a very dark form of Himalayan albino, after a certain amount of improvement by selection, could not be further darkened to any appreciable extent. A race selected simultaneously for large size and for small size showed so little change that the experiment was abandoned after a few generations. No indication was forthcoming that we could thus ever approach in size either the small wild *Cavia Cutleri* of Peru, or the large races of guinea-pig kept in captivity by the natives of the same region. Yet evolution had in some way evidently produced these divergent conditions from a single original source. The changes were probably too slow to be observable in the life time of one observer.

On the other hand, certain characters of guinea-pigs, rabbits, and rats have been found to respond readily to selection in a particular direction. This is notably true of color patterns which involve white spotting. A selection experiment with hooded rats selected simultaneously in plus and minus directions has produced one race which is black all over except a white patch of variable size underneath, and another race which is white all over except for the top of the head and the back of the neck, which are black. The races do not overlap at all and have not done so for many generations, though they still continue to diverge from each other as a result of continued selection.

In similar experiments with Dutch marked rabbits it has been found possible by selection to increase or decrease the amount of white at will. In a series of such rabbits ranging from nearly all black to nearly all white, stages far enough apart to be certainly identifiable behave as Mendelian allelomorphs in crosses, but regularly emerge from such crosses in a slightly modified form, the whiter stages having been darkened and conversely the darker stages whitened. The principle of the pure line manifestly does not apply to these cases. White spotting is apparently a character which from its nature fluctuates constantly, such fluctuations having, to some extent at least, a genetic basis, since continuous selection invariably produces a modified race. Even in wild species, such as the skunks, white-spotting is manifestly a variable character, which no doubt will respond to the selective efforts of our skunk farmers, who desire an all-black race. Why white spotting should be a less stable character genetically than some others, it is impossible to say, but the fact is beyond question. Morgan has suggested that in general the genetic basis of a Mendelian character may be a single molecule, and gives this as a reason for believing in its constancy. But white spotting can hardly fall in with this conception. It seems to me more probably due to a quantitative deficiency in the germ of some substance which normally finds its way into all epidermal cells of the body and which is responsible for the development in them of melanin pigment. Greater and greater deficiencies of this substance cause more and more extensive white areas.

Complete or total albinism behaves very differently. It results from a complete change in some color factor which may well be a simple molecule since it appears to be incapable either of contamination in crosses or of modification under selection. Nevertheless the color factor (molecule or whatever it may be) evidently is not so simple but that it can assume at least four mutually allelomorphic forms as shown for the guinea-pig by Wright, a like number of allelomorphs, though not their exact equivalents, being known also in the rabbit.

As regards the agouti factor in mice, rabbits, and guinea-pigs, this too may assume several different allelomorphic conditions, though it is not certain that any one of these fluctuates or can be modified other than by associating with it unrelated genetic factors.

The divergent conclusions which students of genetics have reached concerning the stability of Mendelian genes and the consequent effects of selection for their modification are probably due in part to the particular choices which they have made of test cases. A study of albinism alone would lead one to believe in the fixity and constancy of Mendelian genes and the impossibility of modifying them by selection. A study of white spotting leaves one with the unshakable conviction

that this form of gene is plastic and yields readily to selection. Where only genes of the former sort are involved, the principle of the pure line is applicable; where genes of the latter sort are involved, it is not applicable. The divergent results obtained by Jennings when dealing with *Paramecium* and when dealing with *Dillugia* indicate that among asexually reproducing organisms, also, genes are involved, some of which are stable, some of which are not. Accordingly, what conclusion we reach as to the applicability of the pure line theory in the breeding of animals and plants will depend upon how common we find stable and plastic genes respectively to be, and in what sorts of variations they are involved.

My own opinion, based upon a study through many years of a variety of inherited characters in the smaller mammals, inclines to the view that in such animals very few characters can safely be referred to the agency of perfectly stable genes. Even in color characters, probably the simplest as well as the most studied of inherited characters, there is much fluctuation which yields substantial results to selection by the discriminating breeder. The yellows are not all of one shade, nor the blacks of equal depth. The golden yellow of the Guernsey cow is very different from the fawn of the Jersey or the dark red of the Devon. Yet all are yellows, allelomorphs of black, but each is selected for a different standard to which the breeder must adhere very carefully in his selections, if he wishes to win prizes or sell breeding stock.

When it comes to size and shape and that consistent inter-relation of parts which the breeder calls "conformation," stable genes cannot be detected. Crosses produce blends as regards size and shape, and conformation is completely dissipated by a cross. That is why the breeder is so reluctant to resort to an outcross unless he is engaged merely in meat or wool production and is not attempting to breed to a type. *Aside from color there are very few valued economic characters in our domestic animals which are not inherited after the manner of blends.*

Weight of carcass, quality of wool, milk production in cattle, egg production in fowls—all these are blending characters which in later generations show either no segregation or imperfect segregation (fowls, Pearl¹). I do not say that in these cases no Mendelian inheritance is involved, but merely that no stable genes are in evidence, nothing that would preclude the probable effective use of selection in maintaining or raising breed standards.

If we turn from the breeding of animals, in which manifestly the pure line principle has little applicability, to the breeding of plants other than those which are self-fertilized, we again find that this principle has a very limited applicability. Probably the most valuable open pollinated field crop in cultivation is maize. But a pure line of maize is not known to exist. An experiment which should have led to the production of pure lines, if such a thing were attainable in maize, has been in progress at the University of Illinois for the past twenty years. Selection has been made for increased and for decreased protein content of the grain, and also for both increased and decreased oil content, with the result that steady progress in the direction of selection has in every case been made. The high protein strain now contains twice as much protein as the low protein strain; and the high oil strain contains four times as much oil as the low oil strain. The divergence of the selected lines from each other is not now as rapid as at first but it still continues steadily, with no indication that it is soon to cease, as must be the case if only stable genes were involved.

Those characters in maize which directly affect the yield, such as size of plant, or of the grain which it bears, are blending in inheritance and show imperfect segregation subsequently. They are probably all of them quite as amenable to selection as the oil content

¹It is true that Pearl (1912) has described fecundity in fowls as "typically Mendelian" in heredity but his figures show that in crosses between Barred Rocks and Cornish Indian Games, the average fecundity of the F_1 birds is in both the reciprocal crosses intermediate between that of the respective parent races though nearer the racial average of the sire, which supports his contention that a sex-linked gene is involved, but shows also that this is not the only factor involved. Back-crosses of F_1 of both sexes with the pure races give evidence of further blending (or imperfect segregation) on the part of the non-sex-linked factor or factors.

and protein content of the seed, experimented upon in Illinois.

Finally, as evidence that even in self-fertilized plants the pure line principle may be inapplicable because of the existence of genes which are plastic, let me cite a very extensive and carefully executed piece of work on garden peas done by Hoshino. He studied the behavior of flowering time, and showed that its inheritance involves a Mendelian gene coupled with flower color (white or red). The inheritance of flowering time is intermediate, but F_1 is closer to the late than to the early parent in this character. Segregation is imperfect in F_2 with a range practically all the way from the early to the late parent, but not transgressing this range. F_3 and F_4 families from self-fertilized parents are in many cases quite variable but others are no more variable than the pure parental varieties and so may be treated as practically "constant." A study of the average flowering time of each of the 230 "constant" F_4 families shows that these fall into three main groups, some falling into a *modified early* group, not quite so early as the early parent, others falling into a *modified late* group, not quite so late as the original late parent, but most of all falling into an intermediate group occupying the region midway between the parent varieties in flowering time. Considered all together, the F_4 families "constant" for flowering time form an almost uninterrupted series of conditions connecting the respective parental conditions seen in the early flowering and in the late flowering race.

These observations show the existence of a gene for flowering time in peas which is decidedly plastic. That a gene actually exists is shown by its coupling with flower color. That it is plastic is shown by the fact that it emerges from the cross nearly always in a modified form. When the possibility of modification has been continued as long as the F_4 generation, the majority of the "constant" families are found in the intermediate or middle group. The plasticity is here shown in a tendency of the contrasted genes to blend into one of intermediate character. It is also shown in data given by Hoshino as to flowering time in parent individuals and their offspring in the late flowering variety. Although this variety is treated by Hoshino as a "pure line," it is evident that within this line itself the later flowering individuals have later flowering offspring and *vice versa*. In other words selection within this supposed "pure line" is evidently effective. Accordingly either the gene here involved is plastic or the supposed pure line is not pure.

From the various lines of evidence which have been cited (and I might have cited many more) it is clear that the pure line principle, valid as a working hypothesis for seed size in beans and for certain morphological characters in self-fertilized cereals, does not fit in with the observed facts as regards the effects of selection in the majority of the domesticated animals and cultivated plants, nor even with the behavior of certain characters in self-fertilized plants and asexually propagated animals. In the case of such characters as white spotting in mammals, it is evident that a change in the mean of the character in a particular direction in consequence of selection actually displaces in the direction of selection the center of gravity of variation, so that in a very true sense selection makes possible further variation in that same direction. The same is probably true as regards protein content and oil content in the Illinois corn experiment. It is doubtful whether, outside of that particular experiment, maize with as high a protein content as 15 per cent. has ever been observed, or maize with as high an oil content as 8.5 per cent. It is not then a misuse of terms to say that the selection has in this case been the cause of further variation in the direction of selection and so an agency in the progressive evolution of a new type.

If this is true concerning a single character under experimental study for a period of twenty generations, may it not also be true of entire organisms and groups of organisms subjected to keen competition with all other organisms in a struggle for existence which has continued for millions of generations? If there are characters which are plastic under artificial selection, why need we be skeptical about the plasticity of organisms subjected to natural selection? If artificial selection can, in the brief span of a man's life time, mould a character steadily in a particular direction,

*A lecture delivered before the Washington Academy of Sciences. From the Proceedings of the Academy.

why may not natural selection in unlimited time also cause progressive evolution in directions useful to the organism? I am not ready to say that natural selection is proved as the method *par excellence* of evolution, but I am not ready to abandon it as the most reasonable explanation of evolution until something better supported than the mutation theory is offered as a substitute for it. At the same time the fact should be emphasized that biology has benefited greatly from the investigation and the discussion initiated by the mutation theory. Even though the mutation theory cannot be accepted as a general theory of evolution it has done us great good in dispelling or clarifying the hazy notions which formerly existed as to what natural or artificial, is, as the mutation theory rightly holds, primarily an agency for the elimination of variations, not for their production. It can only act on variations actually existing, and while it can, I believe, continue and extend variation already initiated by shifting in the direction of selection the center of gravity of variation, it cannot initiate new lines of variation. It cannot change a vertebrate into something else nor something else into a vertebrate. It is limited to the modification of existing types of organisms, and to their modification in directions in which they show a tendency spontaneously to vary.

Discoloration of White Paint

By D. F. Twiss, D.Sc., F.I.C.

IN the use of a white "enamel" of good quality trouble was experienced in the tendency of the dried films to undergo discoloration, especially when articles painted with it were stored in a fairly warm situation; under these conditions the whiteness was soon replaced by a yellow or yellowish brown color, the result being much the same whether painted surface was exposed to the light of an ordinary room or was kept in the dark. The enamel or paint normally consisted of an oil varnish mixed with zinc oxide as pigment, and at first the almost natural tendency was to attribute the discoloration to the presence of some impurity in the pigment; as zinc oxide pigment at the present time is also often adulterated with lithopone, consisting mainly of zinc sulphide and barium sulphate, the zinc sulphide in this, by slowly reacting with lead compounds simultaneously present in the pigment or in the oil, might give rise to a gradual discoloration. Although these impurities were found in some samples of the paint, not only did exposure of dried films in an atmosphere of hydrogen sulphide fail to induce a greatly accelerated color change, but samples of similar paint were discovered to be free from lithopone and lead and yet to undergo discoloration in a similar manner. A peculiarity of the discoloration was that it appeared to be confined mainly to the outer surface of the films, the under side against the painted article being affected to a relatively slight extent.

It is an interesting fact that some zinc pigments are not above suspicion as to their fastness; lithopone on exposure to light undergoes a reversible color change, which, however, is hindered by admixture with linseed oil, an extreme and probably exaggerated statement of such behavior having been made many years ago in a description of the behavior of a lithopone paint on certain gate posts, which were "black all day and white all night" (Chemical News, 1881, 43, 282). Zinc oxide, however, is relatively insensitive to light, and the fact that light was not essential to the discoloration now in question disposed of the possibility that the trouble was due to the effect of light either on zinc oxide or on any accompanying lithopone.

Another common cause of the discoloration of white paints, which is often not fully realised, is the ease with which the surface becomes stained with dirt from the external atmosphere, and, among others, H. E. Armstrong and C. A. Klein (Jour. Soc. Chem. Ind., 1913, 329) have drawn attention to the fact that the blackening of white lead paints is frequently due to this cause rather than to the action of atmospheric hydrogen sulphide. In any case the conditions under which the present discoloration occurred rendered this explanation inapplicable.

As the evidence indicated that the source of the discoloration was not in the pigment, attention was turned to the medium, and the seat of the trouble was then located. When a little of the medium was separated from the mixture and was absorbed into paper free from mineral impurities, the dried film, on being kept in a warm place, was found to develop gradually a marked yellowish brown color, a very marked change occurring in a few hours at 60° C. Linseed oil free from "gum," either alone or mixed with pigments, was found to suffer a similar alteration to the oil varnish, but in a still more marked degree.

In order to investigate the change further, strips of paper coated with the white paint, and also with lin-

seed oil only, were hermetically enclosed in glass tubes from which the air had been expelled by a current of carbon dioxide; this gas was generated from marble and recently boiled dilute hydrochloric acid, and was then washed with water and dried with sulphuric acid before use. It was expected that under these conditions the discoloration would be prevented, but the unforeseen result was that the development of the yellow or brown color occurred even more readily. As this color change was effected in the dried paint film in a few hours at 60° C., in an atmosphere of carbon dioxide, the alteration in the oil would appear to be independent, not only of the oxidation to linoxyn, but also of the polymerisation process for which a temperature in the neighborhood of 260°—280° C. is necessary (e. g., see Morrell, Jour. Soc. Chem. Ind., 1915, 105).

Tests were made as to the conditions under which the yellow or brown discoloration could be removed and the original whiteness restored. It is a matter of common knowledge that such bleaching may generally be effected by exposure to sunlight, but for convenience a Cooper-Hewitt mercury vapor lamp was used as a more readily available source of chemically active radiation. In accordance with the natural expectation, it was found that, unlike the discoloration process, the bleaching process required the presence of air or oxygen. When the discolored film, sealed in a glass tube containing carbon dioxide, was exposed to the actinic rays of the mercury lamp the discoloration persisted, although it changed somewhat in tint, becoming a shade browner. Bleached films could again be discolored by keeping in a warm place, and the discoloration and bleaching processes could be repeated many times in succession, the tendency to discoloration then appearing to undergo gradual but only slight diminution. It was not possible to prevent the subsequent occurrence of discoloration in a dried white film by a preliminary prolonged exposure to ultra-violet light with access of air.

During the course of this work the following brief reference to white paints was noted in Lewkowitsch's treatise on "Oils, Fats, and Waxes" (Vol. 3, p. 61): "The paint oil *par excellence* is linseed oil. In the manufacture of high-class white paints for the use of artists cold pressed walnut oil and poppy seed oil are employed in considerable quantities" (see also *ibid.*, Vol. 2, pp. 100 and 125). Although this statement is not definite with respect to any discoloration, it is suggestive of the possibility that white paints made with linseed oil have a less permanent color than similar paints made with the other oils named. Tests showed that poppy seed oil, apart from being paler in color when fresh, certainly has less tendency than linseed oil to discolor in this way, but a distinct, although slower, discoloration was perceptible under comparable conditions, the change in color being still less obvious, although yet distinct, in the presence of a pigment. The especial tendency of linseed oil to discoloration is masked more effectively by white lead than by zinc oxide, doubtless because of the greater covering power of the former pigment, but even with a mixture of white lead and linseed oil the gradual development of the yellow coloration is observable, the possibility of the color change being due to external causes being again excluded by the occurrence of the change in an atmosphere of carbon dioxide in a sealed glass tube. The more feeble covering power of zinc oxide naturally causes the alteration of the color of the medium to be more perceptible.

As to the nature of the chemical change underlying the alteration in color, the experiments now described give no explanation other than that it is apparently independent of the well-known phenomena of oxidation and polymerisation of the oil. Probably some minor ingredient of the oil other than the glyceride mixture which forms the main constituent is to be regarded as the cause of the trouble, but further investigation is necessary before any definite conclusion can be drawn in this direction.—A Paper read before the Birmingham Section of the Soc. of Chem. Ind.

Cold Work on Copper

At a meeting of the British Institute of Metals a paper was read by Mr. W. E. Atkins describing some experiments on the effect of progressive cold work upon the tensile properties of pure copper.

He remarked that while it has long been known that most metals when submitted to cold work, by hammering, forging, drawing through dies, and so on, have their physical and mechanical properties altered, but few if any attempts have hitherto been made to discover whether any quantitative relationship exists between the amount of cold work done on any metal and the magnitude of the change in its properties. In this experiments a billet of copper was cast and hot-rolled to $\frac{3}{8}$ -inch diameter in the ordinary way. After rolling

the bolt was annealed for four hours at about 600° C. to ensure removal of the stresses inside the metal, and was allowed to cool slowly. It was then pickled in sulphuric acid to remove external scale, and was cold-drawn by light drafts down to 0.04 inch without further annealing. From the bolt after pickling and from the wire after each draft a few feet were scrapped from the end, and three 2-foot lengths cut for testing. The successive drafts corresponded to the successive sizes of the Imperial Wire Gauge from No. 000000 down to No. 19, or 25 drafts in all. The tensile strength of the wires was determined in the Whitworth laboratories of Manchester University on a 5-ton Buckton machine reading to pounds. Five determinations were made, and these were in every case concordant within 1 per cent; the mean of the five was taken as the actual breaking load, and was converted into tons per square inch.

While the results give a smooth curve for the tensile strength against diameter or sectional area, they at the same time show that the effect of a certain amount of cold work at any stage is intimately connected with the previous history of the metal. Thus there is one stage in the drawing at which a reduction of area of almost 10 per cent (from 0.372 inches to 0.348 inch diameter) is accompanied by no change in tensile strength. The phenomena that present themselves in the drawing of copper are not of the simple nature that might be expected on the amorphous theory. That theory regards the process as continuous, in that further cold work always produces more amorphous material, and therefore gives increased hardness; but the theory, as at present interpreted, offers no explanation of the fact that over a limited range reduction in area by cold working is accompanied by no change in tensile strength. In the absence of quantitative data it appears legitimate to assume that the amount of cold work actually performed on a metal during drawing is measured by the decrease in cross-sectional area; this assumption granted, the necessary conclusion is that two distinct changes, not simultaneous, occur during the cold drawing of copper.

Density, elongation—both general and at fracture—scleroscope hardness, and so on, were all found to change in a similar way to tensile strength. Thus the density becomes constant over a limited range at 8.889, which corresponds to the specific volume 0.11251, the values for the annealed bolt being 8.9165 and 0.11214 respectively. As a tentative explanation the author suggested that the first change is allotropic in nature. After this change is complete, *i. e.*, presumably when the whole of the metal has undergone transformation, a second change sets in, which may be regarded either as allotropic or as explicable on the lines of the amorphous theory; of the two possibilities, the latter appears the more probable.—London Times Engineering Supplement.

Reduction of the Oxides of Nitrogen to Ammonia Stability of Nitric Oxide

IN Switzerland the conditions are such that oxides of nitrogen can be manufactured more conveniently than ammonia, so that a knowledge of the conditions under which the former are reduced to the latter becomes necessary. The authors have carried out such an investigation, using a special apparatus in which known mixtures of hydrogen with the respective oxides of nitrogen were passed over heated reduced nickel as catalyst. In order to decompose nitric oxide under atmospheric pressure, it is necessary to keep the temperature at or above 575° C. for several hours, even in the presence of spongy platinum as catalyst. Under these conditions, and contrary to what takes place under pressure, there is no formation of nitrous oxide. The primary products of decomposition are nitrogen and oxygen; on cooling, the oxygen reacts with undecomposed nitric oxide to give nitrogen peroxide. Nitrous oxide decomposes into nitrogen and oxygen. In the reduction of nitric and nitrous oxides and nitrogen peroxide by hydrogen, with nickel as catalyst, two reactions take place simultaneously, the one giving ammonia and the other nitrogen. Both in the reduction of nitric oxide and of nitrogen peroxide, the formation of intermediate products (nitrous oxide and nitric oxide respectively), does not occur. Temperatures of 250°–300° C. appear to be the best for the formation of ammonia. Below these temperatures the reduction takes place slowly, while above these temperatures the nickel gradually loses its activity and the ammonia is appreciably decomposed into its elements. Nitric oxide gives the best yields, 70 per cent of the gas on an average being transformed into ammonia; 25–39 per cent of nitrogen peroxide and only 3–7 per cent of nitrous oxide is reduced to ammonia. The reduction of the oxides of nitrogen to ammonia does not, therefore, appear to be of advantage except, perhaps, in the case of nitric oxide, where a more systematic study of the conditions may give better results.—Note in Jour. Soc. Chem. Ind. on a paper by P. A. Guye and F. Schneider, in Helvetica Chimica Acta.