

WHAT ARE “FACTORS” IN MENDELIAN EXPLANATIONS?¹

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IN THE MODERN INTERPRETATION OF MENDELISM, facts are being transformed into factors at a rapid rate. If one factor will not explain the facts, then two are invoked; if two prove insufficient, three will sometimes work out. The superior jugglery sometimes necessary to account for the result, may blind us, if taken too naïvely, to the common-place that the results are often so excellently “explained” because the explanation was invented to explain them. We work backwards from the facts to the factors, and then, presto! explain the facts by the very factors that we invented to account for them. I am not unappreciative of the distinct advantages that this method has in handling the facts. I realize how valuable it has been to us to be able to marshal our results under a few simple assumptions, yet I cannot but fear that we are rapidly developing a sort of Mendelian ritual by which to explain the extraordinary facts of alternative inheritance. So long as we do not lose sight of the purely arbitrary and formal nature of our formulae, little harm will be done; and it is only fair to state that those who are doing the actual work of progress along Mendelian lines are aware of the hypothetical nature of the factor-assumption. But those who know the results at second hand and hear the explanations given, almost invariably in terms of factors, are likely to exaggerate the importance of the interpretations and to minimize the importance of the facts.

By way of illustrating empirically what I have in mind, I should like to point out certain implications in the current assumption that the factors (sometimes referred to as the actual characters themselves — unit-characters, not infrequently) are dissociated in the germ-cells of the hybrids into their allelomorphs. For instance a tall pea crossed with a dwarf pea produced in the first generation a tall hybrid. Such tall peas inbred produce three tall peas to one dwarf. Such are the surprising facts. Mendel pointed out that the numerical results could be explained if we assume that the hybrid peas produce germ-cells of two kinds, tall-producing and dwarf-producing. The simplicity of the explanation, its wide applicability and what I may call its intrinsic probability will recommend his interpretation to all who have worked with such problems of heredity. Out of this assumption the

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modern factor-hypothesis has emerged. The tallness of the tall all pea is said to be due to a tall-factor; the dwarfness of the dwarf-pea, to be a dwarf factor. When they meet in the hybrid, the tall-factor gets the upper hand. So far we do little more than restate Mendel's view. But when we turn to the germ-cells of the hybrid we go a step further. We assume that the tall-factor and the dwarf-factor retire into separate cells after having lived together through countless generations of cells without having produced any influence on each other. We have come to look upon them as entities that show a curious antagonism, so that when the occasion presents itself, they turn their backs on each other and go their several ways. Here it seems to me is the point where we are in danger of over-looking other possibilities that may equally well give us the two kinds of germ-cells that the Mendelian explanation calls for.

In the first place the assumption of separation of the factors in the gametes is a purely preformation idea. The factors have become entities that may be shuffled like cards in a pack, but cannot become mixed. The whole mechanism turns on the old preformation conception of the way the characters of the adult are contained in the egg. The success of the method as a ready means of explanation does not, in my opinion, justify the procedure; for the preformation idea has always led to immediate, if temporary, successes; while the epigenetic conception, although laborious, and uncertain, has, I believe, one great advantage, it keeps open the door for further examination and re-examination. Scientific advance has most often taken place in this way.

Can we offer one or more alternative points of view that will accord with the assumption of two kinds of germ cells in the first generation of hybrids? Until all the possibilities are exhausted it will be at least judicious to hold the segregation hypothesis, as currently interpreted — a purely formal procedure.

I think that the condition of two alternative characters may equally well be imagined as the outcome of alternative states of stability (or of conditions) that stand for the characters that make up the individual. We can conceive of tallness and dwarfness as two protoplasmic stages or states without intermediates, just as chemical compounds are alternative and separate, each with its own properties. If we mix, in the hybrid materials that have, the power to produce one, or the other condition, it is conceivable that they remain at first independent; the stronger the result in most cases, although the weaker not infrequently shows its presence also. In one and the same individual both the dominant and the recessive characters may appear. For example, chocolate and black mice Mendelian results; but I have obtained individuals that were black in front and chocolate behind. Again black-eye and pink eye are Mendelian alternatives, yet I have three mice with one pink-eye and one black one. Local conditions, I infer, determine, in these heterozygotes, that at one time the dominant and at another the recessive characters come to the front, and I could bring forward evidence to show that the results are not due to segregations of unit-characters. The continuous series of types not infrequently shown in the second hybrid generation, shows also, I think,

that segregation of characters in the germ-cells is by no means an established Mendelian rule.

There is a consideration here of capital importance. The egg need not contain the *characters* of the adult, nor need the sperm. Each contains a particular material which in *the course of the development produces* in some unknown way the character of the adult. Tallness, for instance, need not be thought of as represented by that character in the egg, but the material of the egg is such that placed in a favorable medium it continues to develop until a tall plant results. Similarly for shortness. The fertilized egg of the hybrid between these types likewise contains both possibilities. In the soma or body of these produce their characters — one kind at least. If the germ cell of the hybrid can be traced directly to the undifferentiated germ plasma of that individual, it too contains as yet not the characters but the undeveloped materials from which the characters develop. It follows that we are not justified in speaking of the materials in the germ-cells as the same thing as the adult characters until they develop. As already stated, it seems possible that at some time in the history of the germ-cells, the new materials reach in some cells one condition of equilibrium; in others the alternating condition. On the average it is possible that equal numbers of each are formed, if they are equally potent — but only on an average; for it is well known that Mendelian results are only average results, and it by no means follows that in all individuals equal numbers of the two states are present. In fact the well-recognized principle of pre-potency clearly indicates that equal numbers of the alternative conditions are not always present in each individual. In some such way, I think, it is possible to conceive of the admitted presence of two kinds of germ-cells that produce the average Mendelian proportions. The point of view lacks the sharpness of the preformed-factor assumption — which is not altogether a disadvantage when all the facts are considered! The view has two advantages of its own, one is that it shows at least the possibility of another interpretation, and the more such we have the less likely are we to become blind followers of one idea. The other advantage, to my mind, is that the assumption is more epigenetic in character than the conventional one. This, however, may not be conceded by everyone.

The crucial point for the view here presented is found in the critical stage in the germ-cells of the hybrid. It is an equally difficult point for the segregation theory. According to the latter, the characters separate at this time; according to my view, they now enter into an intimate relation with each other — for which view there is good cytological evidence — and emerge in such a condition, that, in some cells, the state that will produce one character has established itself; in other cells, the opposite state.² We have fairly good evidence to suppose that in the

² This statement has a superficial resemblance to another view I proposed two years ago, namely of alternate dominance. In the present view alternate dominance is different in so far as the recessive need not contain the dominant latent, etc. Also in other respects.

critical stage the maternal and paternal elements are brought into a new relation to each other — one that has not existed in the somatic cells. It is at this time that the changes take place that lead to the postulated differences.

In conclusion I wish to point out a parallel that we cannot afford to ignore. In the development of the egg the organs of the individual become just as sharply separated from each other as are the characters of Mendelism. Experimental embryology has made it more than probable, that the alternative nature of the characters of the different organs is not the result of disjunction of unit-characters present in the egg, although the preformationists have attempted to explain development in this way. The process is far more subtle and in a sense more complicated. It may be claimed that we have here only an analogy, not a similar series of events, but I incline to think that the comparison worthy of serious consideration.