CHAPTER II

PARTICULATE THEORIES OF HEREDITY

THE evidence given in the last chapter led to the conclusion that there are hereditary units in the germinal material that are, to a greater or less extent, independently sorted out between successive generations of individuals. Stated more accurately, the independent reappearance in later generations of the characters of two individuals combined in a cross can be explained by the theory of independent units in the germinal material.

Between the characters, that furnish the data for the theory, and the postulated genes, to which the characters are referred, lies the whole field of embryonic development. The theory of the gene, as here formulated, states nothing with respect to the way in which the genes are connected with the end-product or character. The absence of information relating to this interval does not mean that the process of embryonic development is not of interest for genetics. A knowledge of the way in which the genes produce their effects on the developing individual would, no doubt, greatly broaden our ideas relating to heredity, and probably make clearer many phenomena that are obscure at present, but the fact remains that the sorting out of the characters in successive generations can be explained at present without reference to the way in which the gene affects the developmental process.

There is, nevertheless, a fundamental assumption implied in the statement just made, *viz.*, that the developmental process follows strictly causal laws. A change in a gene produces definite effects on the developmental processes. It affects one or more of the characters that appear at some later stage in the individual. In this sense, the theory of the gene is justified without attempting to explain the nature of the causal processes that connect the gene and the characters. Some needless criticism of the theory has arisen from failure to clearly understand this relation.

It has been said, for example, that the assumption of invisible units in the germ-materials really explains nothing, since to these are ascribed the very properties that the theory sets out to explain. In fact, however, the only properties ascribed to the gene are those given in the numerical data supplied by the individuals. This criticism, like others of its kind, arises from confusing the problems of genetics with those of development.

Again, the theory has been unfairly criticised on the grounds that the organism is a physico-chemical mechanism, while the genetic theory fails to account for the mechanism that is involved. But the only assumptions made by the theory, the relative constancy of the gene, its property of multiplying itself, the union of the genes and their separation when the germ-cells mature, involve no assumptions inconsistent with physical principles, and while it is true the physical and chemical processes involved in these events cannot be explicitly stated, they relate at least to phenomena that we are familiar with in living things.

A part of the criticism of Mendel's theory arises from a failure to appreciate the evidence on which the theory rests, and also from a failure to realize that its procedure is different from that which, in the past, has led to the formulation of other particulate theories of heredity and of development. There have been a good many of these theories, and biologists have become, through experience, somewhat incredulous in respect to any and all theories that postulate invisible units. A brief examination of a few of the earlier speculations may serve to make the difference between the old and the new procedure more apparent.[1]

Herbert Spencer's theory of physiological units, proposed in 1863, assumes that each species of animal or plant is composed of fundamental units that are all alike for each species. The elements concerned are supposed to be larger than protein molecules and more complex in structure. One of the reasons that led Spencer to this view is that any part of the organism may in certain cases reproduce the whole again. The egg and the sperm are such fragments of the whole. The diversity of structure in each individual is vaguely ascribed to a "polarity" or some sort of crystal-like arrangement of the elements in different regions of the body.

Spencer's theory is purely speculative. It rests on the evidence that a part may produce a new whole like itself, and infers from this that all parts of the organism contain material out of which a new whole may develop, but, while this is, in part, true, it does not follow that the whole must be made up of a single kind of unit. Our modern interpretation of the ability of a part to develop into a new whole must also assume that each such part contains the elements for the construction of a new whole, but these elements may be different from each other, and to this system the differentiation of the body is referred. So long as a complete set of units is present, the power to produce a new whole is potentially given.

Darwin's theory of pangenesis, proposed in 1868, appealed to a host of different invisible particles. The theory states that minute representative elements, called

[1] A full discussion of earlier theories is given by Delage in *Heredité* and by Weismann in the *Germ-Plasm.*

gemmules, are being continually thrown off from every part of the body. Those that reach the germ-cells become incorporated there with the hereditary units of the same general kind already present.

The theory was proposed primarily to explain how acquired characters are transmitted. If specific changes in the body of the parent are transmitted to the offspring, some such theory is required. If the changes in the body are not transmitted, there is no need of such a theory.

Weismann in 1883 challenged the entire transport theory, and convinced many, but not all, biologists that the evidence for the transmission of acquired characters was inadequate. This led him to develop his theory of the isolation of the germ-plasm. The egg produces not only a new individual, but other eggs like itself, carried by the new individual. The egg produces the individual, but the individual has no subsequent influence on the germ-plasm of the eggs contained in it, except to protect and to nourish them.

From this beginning Weismann developed a theory of particulate inheritance of representative elements. He appealed to evidence derived from variation, and he extended his theory to include a purely formal explanation of embryonic development.

We are concerned, in the first place, with Weismann's views as to the nature of the hereditary elements or *ids* as he calls them. The ids he identified in his later writings as small chromosomes when many small chromosomes are present, but when only a few chromosomes are present he supposed that each is made up of several or many ids. Each id contains all the elements that are essential to the development of a single individual. Each is a microcosm. The ids differ from each other in that they are the representatives of ancestral individuals or germplasms, each different from the others in one or another way.

The individual variations shown by animals are due to the different recombinations of ids. This is brought about by the union of eggs and sperms. The number of ids would become indefinitely large were it not that, at the ripening of the germ-cells, the number of ids is reduced to half.

Weismann also formulated an elaborate theory of embryonic development based on the idea that the ids are separated into their smaller elements as the egg divides, until, finally, each kind of cell in the body comes to contain one of the ultimate components of the ids, *i.e.*, determinants. In the cells destined to become germ-cells the disintegration of the ids does not take place. Hence the continuity of the germ-plasm, or of the colony of ids. The application of his theory to embryonic development lies outside the modern theory of heredity that either ignores the developmental process, or else postulates a view exactly the opposite of that of Weismann, namely, that in every cell of the body the entire heredity complex is present.

It will be seen without further elaboration that Weismann's ingenious speculation invokes, in order to explain variation, processes that are akin to those we adopt today. *Variation, he believed, is due to the recombination* of units from the parents. These are reduced to half in the process of maturation of the egg and sperm. The units are wholes and each represents an ancestral stage.

We owe to Weismann largely the idea of the isolation and continuity of the germinal material. His challenge of the Lamarckian theory was of immense service to clear thinking. The theory of the inheritance of acquired characters had obscured for a long time all problems dealing with heredity. Weismann's writings were also unquestionably important in keeping in the foreground the intimate relation between heredity and cytology. It is difficult for us to estimate to what extent his fascinating speculations have influenced our later attempts to interpret heredity in terms of chromosome constitution and behavior.

These and other earlier speculations have today mainly an historical interest. They do not represent the main path along which the modern theory of the gene has developed, which rests its claims to recognition on the method by which it is derived and on its ability to predict exact numerical results of a specific kind.

I venture to think that, however similar to the older theories the modern theory may appear, it stands apart from them, in that it has arisen step by step from experimentally determined genetic evidence that has been carefully controlled at every point. The theory need not and does not, of course, pretend to be final. It will, no doubt, undergo many changes and improvements in new directions, but most of the facts concerning heredity, known to us at present, can be accounted for by the theory as it stands.