APPENDIX I

HISTORICAL SUMMARY OF THEORIES OF HEREDITY

In the foregoing pages, Heredity has been regarded as the relation between parents and offspring in respect of their bodily characters, and it has been shown that this relation has been brought about in some way by the germ-cells, but very little has been said about the mechanism by which this is effected. This side of the question is very largely speculative, and in order to keep speculation to some extent apart from facts, an account of theories of hereditary transmission, and of recent work on the supposed material basis of hereditary characters, has been postponed to appendices, which the reader who seeks for facts and well-founded deductions alone, may omit at will. First, a summary of the chief theories of heredity will be given, and then a short account of recent work on the subject.

In the introduction it was pointed out how closely related are our ideas of Heredity and Variation with theories of Evolution, and thus the history of the two subjects largely coincides. The first important theory was that of Lamarck, published in 1809, and although it had little influence at the time, in more recent years Lamarck's main principle has found many supporters. His theory was essentially that 'acquired' modifications are being continually produced and perfected by every organism during its life, and that they are at least partially transmitted to its offspring, so that each generation will be rather better adapted to its surroundings than its predecessor. In this way, for example, the great length of the neck of the giraffe would be explained by the continual striving through many generations to reach higher leaves on the trees; or the limbless condition of snakes and slow-worms by the gradual loss of limbs through disuse. But it has been seen that the assumption that acquired characters are inherited is open to grave doubt, and hence the followers of Lamarck are fewer at the present time than formerly.

Darwin's great theory of Evolution by Natural Selection of course depends on quite different principles, but it, like Lamarck's, is based essentially upon the laws of variation and heredity. Darwin himself made astonishing progress in the investigation of these laws, and although he would doubtless have been the first to admit the incompleteness of our knowledge, yet he collected sufficient evidence to enable him to formulate one of the first really important theories of heredity, which he called the Theory of Pangenesis [7, (1868)]. The essence of his theory was that every cell of an organism gives off minute particles or 'Gemmules' from itself, which circulate in the body and finally come to rest in the germ-cells, or in parts where buds may be developed. The gemmules were regarded as being capable of multiplication, and of transmission to a future generation in a dormant state. They were supposed to be given off from all tissues at every stage of development, so that every unit of the organism at every stage would be represented in the germ-cells. On the development of the germ-cell, the contained gemmules would give rise to cells like those from which they were derived, and so the characters of one generation would be transmitted to those which follow.

By this hypothesis Darwin accounted for the phenomena of sexual and non-sexual reproduction, regeneration of lost parts, variability, inheritance both of inborn and acquired characters, and lastly of reversion to a previous ancestor. The hypothesis was one of the first which attempted to bring all these various groups of facts into line, but it had the serious defect that there was no direct evidence whatever for the existence of gemmules, and, assuming their existence, to be accommodated in the germ-cells they must be so exceedingly minute as to be almost unimaginable. The Theory of Pangenesis never gained any very wide acceptance, but is of great importance owing to its stimulating effect on later work and thought. To a great extent it led to the formulation of other theories of heredity[1], any account of which is prevented by limitation of space. It can only be mentioned that the chief hypotheses which followed Darwin's laid successively more and more emphasis upon the idea that the germ-cells are not made up of samples taken from the body, but have a certain independence. So grew up the conception of 'germinal continuity,' that is, the idea that the germ-cell of one generation gives rise not only to the body of the next, but also directly to its germ-cells, so that the body does not produce germ-cells, but only contains them. We must now turn to the theory in which this idea finds its most celebrated expression, Weismann's *Theory of the Germ-plasm* (1885) [40, 8].

It is impossible in a short space to give an adequate account of Weismann's great theory, which he has worked out in fuller minuteness of detail than has been done with any other theory of heredity, and by which he has done more to stimulate discussion and research than perhaps any biologist since Darwin.

[1] For a summary of the more important theories of heredity, especially those of Herbert Spencer (1863, i.e. before Darwin's theory of Pangenesis), Galton (1875) and de Vries (1889), see Thomson's *Heredity* [33]. See also [8].

Weismann was led by his work on the origin of the germ-cells to a belief in germinal continuity as explained above, but the facts of regeneration of lost parts and other related phenomena caused him to give up the idea that a sharp distinction could be drawn between the cells of the body and the germ, and to substitute for it the idea of a distinction between body-substance and germ-substance, or as he calls it, body-plasm and germ-plasm. According to this hypothesis, the egg contains germ-plasm derived from that of the parent, and as the egg develops the germ-plasm increases and becomes distributed among the cells, and gradually, as the cells become specialised to form the different parts, the germ-plasm becomes converted into body-plasm and builds up the varied kinds of cells of the body. But some cells continue to possess the full complement of ancestral germ-plasm, and these will go to form the germ-cells of the next generation. When an organ remains capable of regenerating lost parts, it is assumed that germ-plasm having the power to develop such parts remains in the cells and becomes active when required. Germ-plasm can thus be converted into body-plasm, but body-plasm cannot become germ-plasm, and hence Weismann assumes that no change brought about in the body (by environment, etc.) but not affecting the germ-cells, can be inherited by subsequent generations. It is therefore impossible according to his theory, that 'acquired characters' in the technical sense should ever be inherited. The germ-plasm of one generation gives origin to the germ-plasm of the next, and no external conditions acting on the body which contains and nourishes the germ-plasm can have effects which are transmitted unless the germ-plasm itself is altered.

Weismann in a series of books and papers has built up a detailed and highly complicated and speculative scheme of the nature and composition of the germ-plasm, only a brief summary of which can be given here. Much of it will doubtless not stand the test of fuller investigation, and parts of it are already discredited; but it has had the merit of stimulating an immense amount of valuable research, and there are indications that some of his fundamental ideas will form the foundations of a true theory of the material basis of heredity.

Weismann assumes that the germ-plasm is contained in the nucleus of the cell, and, in particular, in the bodies known as chromosomes. Every nucleus contains a number of these bodies, in the ordinary condition of the nucleus distributed through its substance so as to be unrecognisable, but when the cell is about to divide they make their appearance as rod-like bodies whose number in general is constant in the nuclei of the same species of animal or plant. Before the nucleus divides the chromosomes split longitudinally so that they are accurately halved and the two halves of each go into different daughter-nuclei. Weismann supposes that the germ-plasm is contained in the chromosomes, and consists of numerous units with different properties. When the chromosome splits, each unit is supposed to divide into two similar halves, and thus each daughter-nucleus receives a similar complement of germ-plasm.

In the union of male and female cells in fertilisation, the nucleus of each cell brings its complement of chromosomes, and thus if there were no special provision, the number of chromosomes would be doubled in each generation. But it is actually found that in the cell-divisions immediately preceding the development of both male and female sex-cells, a process occurs which results in the removal of half the chromosomes from the nucleus, and thus when the male and female nuclei unite the normal number of chromosomes for the species is restored. Since Weismann regards the chromosomes as consisting of germ-plasm, and as made up of a vast number of units, each of which is the determinant for one hereditary character, he saw that, without some such process of removal of chromosomes in the formation of the sex-cells, the germ-plasm must in a few generations become infinitely complicated. He therefore predicted that some process of 'reduction' of chromosomes must occur, either by elimination of complete chromosomes or by transverse instead of longitudinal splitting, before any complete observations had been made showing that this actually happens.

Since Weismann supposes that the germ-plasm is contained in the chromosomes of the germ-cells, and since half the chromosomes are removed in the 'maturation' of these cells without preventing the transmission of any part to the offspring by inheritance, he *concluded that each chromosome contains* all the units ('determinants') necessary to a complete individual. (Later work has rendered this conclusion doubtful: see Appendix II.) When *fusion of male* and female sex-cells takes place, the resulting individual will contain a mixture of the parental germ-plasms, *the paternal in some chromosomes, the maternal in* others. In the maturation of the sex-cells half these germ-plasms will be removed and in the next generation a fresh mixture will take place. *It thus* follows that the different chromosomes contain germ-plasms descended from different ancestors, and different mixtures of these will occur in different individuals. Here then we come to Weismann's hypothesis of the origin of variation. Since different individuals contain different combinations of ancestral germ-plasms, these will lead to varying effects in the development of the body; new combinations will be continually occurring in every fertilised egg, and thus arises the variation between separate individuals. Further, although by his theory changes brought about in the body-plasm cannot be transferred to the germ-plasm, yet influences acting on the germ-plasm itself may modify it and so their effects will be transmitted. The most important of these influences is nourishment, which may favour some units of the germ-plasm rather than others. He further supposes that there may be competition for nourishment among the different units ('determinants') so that some increase at the expense of others, and if this process should be continued through a series of generations, certain characters would show a steady increase while others correspondingly decrease. Variation thus arises by changes brought about in the germ-plasm, and by the recombination of varied ancestral germ-plasms in each generation. Such variations will be inherited, and in this respect will differ entirely from changes brought about in the body during its life by the action of environment.

It has been shown that in the earlier theories of heredity it was assumed that the germ-cells were produced by the body, and that they must therefore be supposed either to contain samples of all parts of it, or at least some kind of units derived from those parts and able to cause their development in the next generation. Gradually, as the study *of heredity and of the actual origin of the germ-cells* has progressed, biologists have given up this view in favour of a belief in germinal continuity, that is, that the germ-substance is derived from previous germ-substance, the body being a kind of offshoot from it. The child is thus like its parent, not because it is produced from the parent, but because both child and parent are produced from the same stock of germ-plasm.