APPENDIX II

THE MATERIAL BASIS OF INHERITANCE

In Appendix I, it has been mentioned that Weismann regarded the chromosomes of the nucleus as the bearers of hereditary characters, and more recent work has added to the probability of this view, while not as yet providing anything which can be called proof. That some, if not all, the hereditary characters are determined by the *nucleus* of the germ-cell is indicated by several facts. In the first place, the spermatozoon consists of little else but a nucleus with a vibrating tail, and the tail may be shed as the spermatozoon enters the ovum. Secondly, experiments in fertilising non-nucleated fragments of sea-urchin eggs by sperm of a different species, give evidence that the hereditary characters of the resulting larvae are exclusively those of the paternal species. This conclusion however has been disputed, and can only be regarded as probable rather than certain. Again, experiments in fertilising one egg simultaneously by more than one spermatozoon, lead

Boveri [3] to believe that the subsequent development of the cells of the embryo depends on the distribution of the chromosomes in the abnormal divisions consequent on double fertilisation. And Herbst [16] has obtained sea-urchin larvae made by crossing distinct species, which on one side of the body resemble one parent, and on the other side the other parent. He shows that these differences are connected with differences in the size of the nuclei of the two sides, and that probably the part with maternal characters contains only maternal nuclear substance, while the part showing the *paternal character* has nuclei derived from both parents.

But probably the best evidence for regarding the chromosomes as bearing the essential determinants for hereditary characters is provided by the behaviour of the chromosomes themselves in the maturation divisions of the germ-cells. It has been pointed out that at these nuclear divisions the chromosome number is halved, and restored to the full number again in the next generation by the union of two germ-cells each bearing the half-number. Now it has been found in certain cases that the chromosomes are *not all alike, but differ among themselves* in size and shape, and when this is so it can be seen that the nucleus just before maturation contains *two* of each kind. If the different kinds of chromosomes

are represented by letters, *A*, *B*, *C*, *D*..., there will then be two *A*'s, two *B*'s, etc. in the nucleus. The actual processes in the reduction division are somewhat complex, but briefly they consist in a pairing together of the chromosomes, followed by a division of the nucleus in which the two members of each pair are separated into different daughter-nuclei, so that the daughter-nuclei each contain half the full number. When the chromosomes differ among themselves, it is seen that two similar ones always pair together, i.e. *A* with *A*, *B* with *B*, etc. *Thus the daughter-nuclei each contain the whole series A, B, C..., but have only one of each, instead of two.*

If then it is imagined that each chromosome is the bearer of the determinant (or 'factor') for a Mendelian character, we may regard one individual as having a double series of chromosomes *A*, *B*, *C*..., etc., and another as bearing the allelomorphic characters *a*, *b*, *c*..., etc. When these individuals are mated, the heterozygote will bear both series, *A* and *a*, *B* and *b*, etc. In the formation of the germ-cells, *A* will segregate from *a*, *B* from *b* in exactly the way required by Mendelian theory. But there is no reason to suppose the series *A*, *B*, *C*... should all go into one germ-cell, and *a*, *b*, *c*... into the other; *A* may go into the first daughter-nucleus and *a* into the second, but *b* may go with *A* into the first, and *B* into the second. So in crossing races differing

in more than one allelomorphic pair, all possible combinations can be produced, except that no germ-cell can contain both the members of one pair.

The suggestion that this segregation of chromosomes, which can be seen to take place, is the mechanism by which the members of an allelomorphic pair of characters are segregated, is quite speculative; but it seems exceedingly unlikely that machinery so exactly adapted to bring it about should be found in every developing germ-cell, if it had no connexion with the segregation of characters that is observed in experimental breeding. There is also the further fact in support of the suggestion, that it is known in many insects that one pair of chromosomes is closely connected with sex, for in the males of these species one chromosome of the pair is absent or much reduced, but in the female both are similar. These sex-chromosomes separate from one another like the others (when both are present), and it has been seen that there is experimental evidence for the view that the sex-determiners behave like Mendelian allelomorphs. One serious difficulty however suggests itself at once; the chromosomes are limited in number, and it is undoubted that more allelomorphic pairs of characters may exist in a species than there are pairs of chromosomes, although in such cases there is no evidence that members of different pairs are always associated together. Several suggestions have been

made to meet this difficulty, of which perhaps the most adequate is that the chromosomes are not indivisible entities, but are composed of smaller units, each of which corresponds with one Mendelian factor. The chromosomes are not permanently present in the distinct form which is seen during cell-division, but during the resting condition of the nucleus their substance becomes diffused over a network of threads, only to be collected again into definite chromosomes, having the same number and form as before, preparatory to the next division. If each chromosome consists of a series of units having a definite arrangement, and these units become scattered in the 'resting phase,' but are re-collected in the same order when the chromosomes are re-formed, it does not seem unlikely that a unit *N* may take the place of the corresponding unit *n* from the other chromosome of the pair, so that if the chromosome *A* consisted at one division of units *M, N, O*..., and the corresponding chromosome *a* consisted of *m, n, o*..., after the resting stage *N* and *n* might have exchanged places, and chromosome *A* would consist of *M, n, O*. . and *a* of *m, N, o*.... By some process of this kind it seems probable that the observed phenomena of chromosome reduction would account for all the facts of Mendelian segregation.

It must be stated quite clearly, however, that the study of the possible relation between chromo-

somes and body-characters is as yet in its infancy; and this brief note can only sketch the lines on which modern work seems to support Weismann's hypothesis that the chromosomes are the physical basis of inheritance. It will be seen that his suggestion that all the chromosomes are on the whole similar is not confirmed, but the evidence that chromosomes do bear factors for inherited characters is considerably stronger than when the idea was first put forward[1].

[1] The suggestion referred to in the note on p. 97 must also be borne in mind, that it is not the '*factor*' alone which determines the development of a character, but a physiological relation between the factor contained in a chromosome and the surrounding protoplasm. If the latter is altered from any cause, the relation may be changed and the character modified, just as the plants raised from one sample of seed may be modified by growing them in different soils. If, as is quite possible, the relation is a reciprocal one, the factor may in some cases be permanently modified, and there would thus be a mechanism for the transmission of acquired modifications. At present, however, it must be admitted that experiment hardly provides sufficient basis for speculations such as these.