CHAPTER XVI

THE EMBRYOLOGICAL AND CYTOLOGICAL EVIDENCE THAT THE CHROMOSOMES ARE THE BEARERS OF THE HEREDITARY UNITS

Long before the genetic evidence brought forward its abundant data that are explicable on the theory that the chromosomes carry the genes, embryologists had already found other evidence that led them to regard the chromosomes as the bearers of the hereditary factors. Taken as a whole, this evidence makes out a very strong case for the chromosomes, but since it did not establish the relation beyond question, the genetic evidence was all the more welcome.

The earliest evidence, sometimes cited in favor of chromosomal inheritance, was based on the statements that in some cases at least, only the head of the spermatozoön enters the egg. Since it was then thought that the head is composed almost entirely of the nucleus, and since the child inherits equally (in the older parlance) from its father and from its mother, it followed that the nucleus carries the hereditary elements. When later it became known that the head of the sperm represents almost exclusively the mass of condensed chromatin, it was supposed that the chromosomes, in particular, must be that part of the nucleus that is the bearer of hereditary characters. Such a conclusion received indirect support from the facts, then becoming known, that the chromosomes remain constant through successive generations of cells, whereas the nuclear sap becomes lost in the general cytoplasm each time that the nuclear wall is dissolved. It was also found that the spindle fibres disappear in the resting stages, while the nuclear reticulum (chromatin) remains.

This evidence failed, however, in so far as there might be present a certain amount of nuclear plasm in the sperm-head that is carried in with the head, and if so, would be later mixed with the egg cytoplasm. The discovery that at the base of the sperm-head there is present in some eggs a centrosome that becomes, through division, the dynamic centre of the next division, opened the door to suspicion that the sperm might bring in other things than the chromosomes to influence development, and hence heredity.

In conclusion then, while it may be said that the evidence that the sperm-head alone enters the egg may be claimed as favorable for the chromosome view, it cannot be accepted as critical proof, because it is uncertain whether other things also may not be brought in besides the chromatin of the sperm.

Boveri's evidence for chromosomal heredity from dispermic sea urchin eggs was open to less objection. It was known that when two sperms enter the sea urchin's egg simultaneously, the first division of the egg is into three or into four parts, because four (instead of two) division-centres appear in these dispermic eggs. It was also known that these eggs rarely produce normal embryos or larvæ. Boveri, studying the mode of division of the dispermic eggs, found that there was an irregular distribution of the chromosomes to the three or four poles that appear, and consequently to the three or four resulting cells (*Fig.* 98). The abnormal development of the whole egg that generally follows might be ascribed to the irregular distribution of chromosomes to different regions; for, quite apart from the specific nature of each chromosome or group of chromosomes, the activity of one region being quantitatively different from that of a corresponding region in another part of the egg might be responsible for the failure to develop normally. But Boveri went further in his analysis. He shook apart the three or four blastomeres coming from dispermic eggs (by using Herbst's calcium-free sea-water method), and compared the num-

ber that developed into normal plutei with the number of plutei from one-fourth normally fertilized blastomeres. From the latter a large proportion give rise to normal embryos, from the former normal embryos are rarer. Their greater rarity, Boveri thought safe to attribute to the chromosomal deficiencies present in most of such iso-

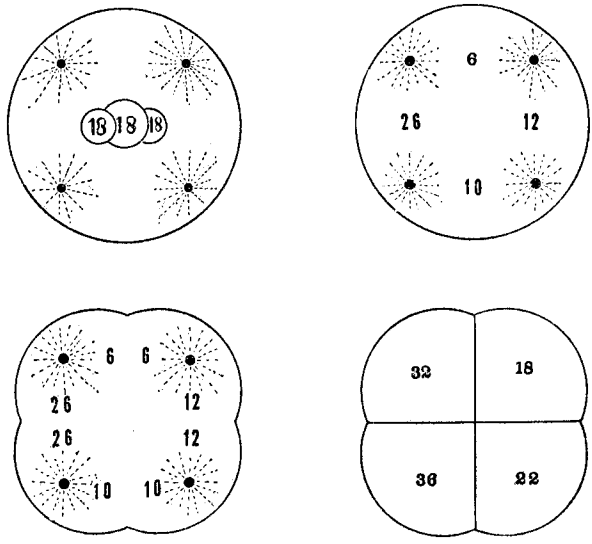

FIG. 98.—Scheme showing dispermic fertilization of the egg of the sea urchin with the subsequent irregular distribution of the chromosomes. (After Boveri.)

lated blastomeres. He suggested that the chance of a blastomere developing normally depends on its having at least one full set of chromosomes. For these triploid sea urchin eggs with three times 18 chromosomes, the chance of one full set of chromosomes getting into each blastomere is, according to Boveri's calculation, only one to 10,000. The chance of getting at least one chromosome of each kind in one cell is greater. He concluded that the few embryos he obtained came from quadrants that had at least one haploid set of chromosomes. There is, however,

to-day some uncertainty concerning the assumption that normal development is to be expected if in addition to one haploid set of chromosomes other chromosomes are also present, because while one set alone might permit normal development, it is by no means certain that if there were one, two, or more additional chromosomes, the balance might not be upset and abnormal development follow. On chance distribution alone the isolation of just one set and no more would seem a very remote possibility,

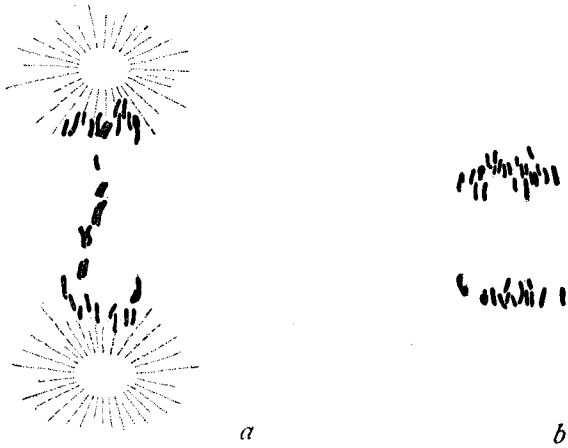

FIG. 99.—First division of a hybrid egg showing the elimination of chromosomes at the equation of the spindle, *a*. The reciprocal cross, *b*, shows no such elimination. (After Baltzer).

but if there is to some degree a tendency for a group of daughter chromosomes to move off together as a result of their method of division, there might be a better chance of such a group getting into one of the three or four blastomeres than by chance distribution alone. At present it is not possible to make any calculation based on such an assumption. While, therefore, Boveri's argument cannot be accepted as demonstrative, yet it has probability in its favor.

Baltzer has found a different kind of evidence of chromosomal influence. When the eggs of one sea urchin,

Strongylocentrotus, are fertilized by the sperm of another sea urchin, *Sphaerechinus,* the segmentation nucleus, formed by the union of the egg- and sperm-nucleus shows irregularities in the movements of the daughter chromosomes to the poles of the spindle. While some of the chromosomes after dividing pass normally to the poles, others become scattered irregularly between the two poles and fail to become incorporated in the two-daughter nuclei (Fig. 99, *a*). They appear to become lost and take no

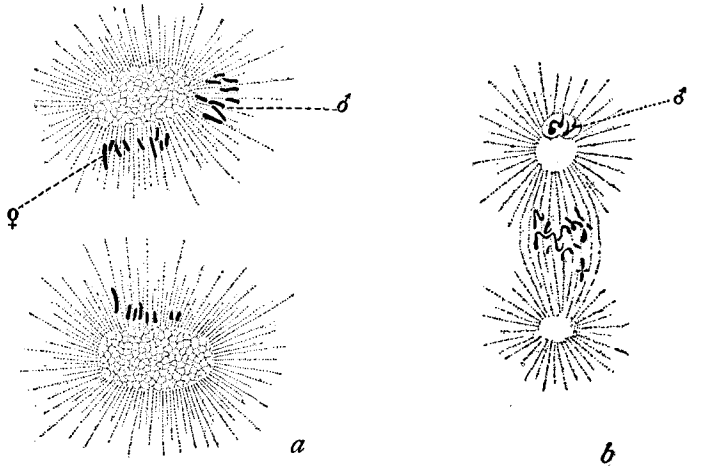

FIG. 100.—Fertilization of an egg that had started to develop parthenogenetically. The belated sperm unites with one of the daughter chromosomes groups only, *a;* an earlier condition of the same procedure. (After Herbst.)

part in the further development. Counts of the chromosome plates in the later divisions of the egg give about 21 chromosomes, whereas 36 are expected as the whole number. It appears that 15 chromosomes are lost, and presumably they belong to the foreign sperm. Many of these eggs develop abnormally, but those that reach the pluteus stage show a maternal skeleton only. This seems to mean that the sperm has done no more than start the development. It has contributed nothing, or little, to the embryo, and it seems reasonable to attribute this to the

loss of the paternal chromosomes, especially in the light of the reciprocal cross.

In this reciprocal cross, the egg of *Sphærechinus* is fertilized by the sperm of *Strongylocentrotus*. All the chromosomes of the segmentation nucleus divide and pass regularly to the two poles (Fig. 99, *b*). The hybrid embryo shows characters of both parental species.

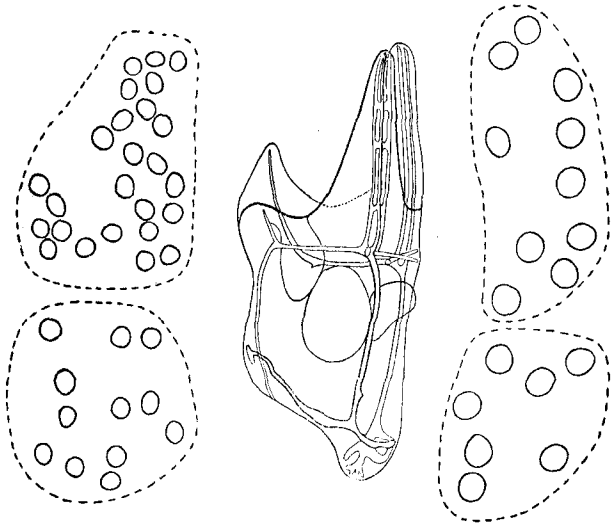

FIG. 101.—Larval sea urchin seen in side view. On one side it shows hybrid characters, on the other side it is maternal. The sizes of the nuclei on these two sides, as seen in the figure, coincide with the view that the hybrid side is diploid and the maternal side haploid. (After Herbst.)

The difference in the two cases can be safely attributed to the observed differences in the fate of the chromosomes, rather than to unrecognized differences in other elements brought in by the sperms.

Herbst's experiments contribute further evidence in favor of the chromosome interpretation. He caused the unfertilized eggs of a sea urchin to begin to develop parthenogenetically by adding a little acid to the sea water. After five minutes the eggs were removed to pure sea water, and sperm of another species, *Strongylocen-*

trotus, was added. The sperm entering the egg after its nucleus had started to divide, failed to reach the egg nucleus until the latter had divided (Fig. 100). The sperm nucleus then formed a nucleus of its own, that passed into one only of the daughter cells. This cell got two nuclei. The other cell had only one of the daughter nuclei. Such half-fertilized eggs give rise to larvæ that are maternal on one side, and hybrid on the other—or at least larvæ of this kind are sometimes found in such cultures (Fig. 101), and Herbst believes it is safe to refer them to the half-fertilized eggs. If so, there can be little doubt that the hybrid half owes its peculiarities to the presence of both sets of chromosomes in its cells, while the maternal half owes its peculiarities to its single set of maternal chromosomes. This in itself, however, shows little more than do whole hybrids and whole parthenogenetic eggs themselves, for the demonstration that it is the chromosomes and not other constituents of the sperm-nucleus that make the difference in the two sides rests on the unproven inference that if other things than the nucleus are involved they would be distributed equally throughout the cytoplasm, but produce no effects. There is no reason to suppose that they would be so distributed, and no evidence that they are. Hence the proof is not cogent, however probable it may seem that only the sperm-nucleus is responsible for those cases where there is a difference in the two sides.

On the whole, then, while I am inclined to give much weight to this evidence from experimental embryology as very favorable to the hypothesis that the chromosomes carry the hereditary characters, it is the genetic evidence that furnishes convincing evidence in favor of this view.