CLASSICS OF SCIENCE: Chromosomes in Heredity

Biology

A pioneer in the study of heredity, Weismann was among the first to recognize that inheritance is carried, not by the whole reproductive cells, nor even their nuclei, but by the still more minute chromosomes within the nucleus.

Fusion of Cells

THE GERM-PLASM, A Theory of Heredity, by August Weismann (1892). Translated by W. Newton Parker, Ph. D., and Harriet Rönnfeldt B. Sc., New York, 1892.

As long as we were under the erroneous impression that the fertilisation of the ovum by the spermatozoon depended on an *aura seminalis* which incited the egg to undergo development, we could only partially explain the fact that the father as well as the mother is able to transmit characters to the children by assuming the existence of a *spiritus rector*, contained in the *aura seminalis* which was transferred to the ovum and united with that of the latter, and thus with it directed the development. The discovery that development is effected by material particles of the substance of the sperm, the sperm-cells, entering the ovum, opened the way to a more correct interpretation of this process. We now know that fertilisation is nothing more than the partial or complete fusion of two cells, the sperm-cell and the egg-cell, and that normally only *one* of the former unites with *one* of the latter. Fertilisation thus depends on the union of two protoplasmic substances. Moreover, although the male germ-cell is always very much smaller relatively than the female germ-cell, we know that the father's capacity for transmission is as great as the mother's. The important conclusion is therefore arrived at that only a small portion of the substance of the ovum can be the actual hereditary substance. . . . From his observations on the egg of the starfish, Oscar Hertwig had suspected that the essential part of the process of fertilisation consists in the union of the *nuclei* of the egg- and sperm-cells, and as it is now known that the hereditary substance is undoubtedly contained in the nucleus, this view has, in this respect at least, proved to be the right one. It is true that the nucleus of the male cell is always surrounded by a cell-body, and that Strasburger's opinion to the contrary is incorrect. We now know, through the researches of Guignard, that even in Phanerogams a small cell-body surrounds the nucleus, and that a special structure, the "centrosome",—which is absolutely essential for the commencement of development,—is contained within it. This structure will be treated of in further detail presently, but I must here lay stress upon my view, that *the "centrosome" with its "sphere of attraction" cannot in any case be the hereditary substance,* and that *it is merely an apparatus for the division of the cell and nucleus.*

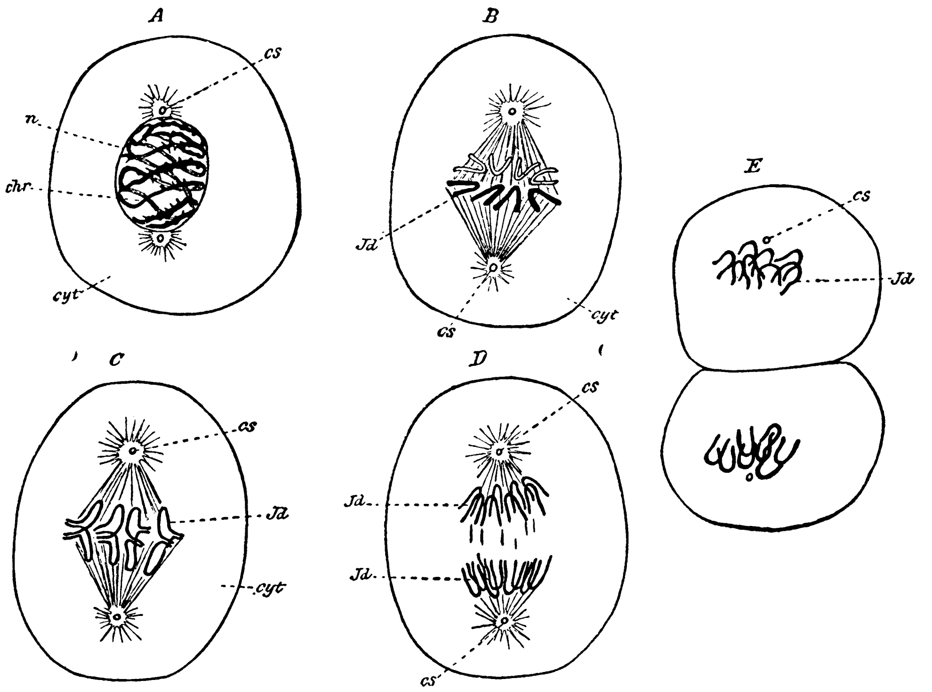

DIAGRAM OF NUCLEAR DIVISION

A.—Cell with nucleus—n, and centrosomes—cs, preparatory to division. The chromatin has become thickened so as to form a spiral thread—chr.

B.—The nuclear membrane has disappeared. Delicate threads radiate from the centrosomes, and form the "nuclear spindle," in the equator of which eight chromosomes or nuclear loops (chr) are arranged: these have been formed by the spiral thread of chromatin in A becoming broken up.

C.—The chromosomes have each become split longitudinally into two, and are about to be drawn apart by means of the spindle-threads. (For the sake of clearness only four of the eight chromosomes are indicated.)

D.—The daughter-loops pass towards the poles of the spindle.

E.—The body of the cell has undergone division; each of the resultant cells contains a centrosome and eight nuclear loops.

Both in animals and plants, however, essentially the same substance is contained in the nucleus both of the sperm-cell and egg-cell:—this is the *hereditary substance of the species.* There can now be no longer any doubt that the view which has been held for years by Strasburger and myself is the correct one, according to which *the nuclei of the male and those of the female germ-cells are essentially similar, i. e.,* in any given species *they contain the same specific hereditary substance.*

The splendid and important investigations carried out by Auerbach, Bütschli, Flemming, and many others, on the detailed processes of nuclear division in general, and those dealing more particularly with the fertilisation of the egg in *Ascaris* by van Beneden, Boveri, and others, have given us the means of ascertaining more definitely what portion of the nucleus is the substance on which heredity depends. As already remarked, this substance corresponds to the "chromosomes", those rod-like, looped, or granular bodies which are contained in the nucleus, and which become deeply stained by colouring matters.

As soon as it had been undoubtedly proved that the nucleus, and not the body of the cell, must contain the hereditary substance, the conclusion was drawn that neither the membrane of the nucleus, nor its fluid contents, nor the nucleoli—which latter had been the first to attract attention—could be regarded as such, and that the "chromatic granules" alone were important in this respect. As a matter of fact (*Turn to next page*)

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Chromosomes—*Continued*

several investigators—Strasburger, Oscar Hertwig, Köllicker, and myself—reasoning from the same data, arrived at this conclusion, independently, within a short time of one another.

It will not be considered uninteresting or superfluous to recapitulate the weighty reasons which force us to this conclusion, for it is clear that it must be of fundamental importance in a theory of heredity to know for certain what the substance is from which the phenomena which are to be explained proceed.

The Chromosomes

The certainty with which we can claim the "chromatin granules" of the nucleus as the hereditary substance depends firstly, on the process of amphimixis; and secondly, on that of nuclear division. We know that the process of fertilisation consists essentially in the association of an equal number of chromatin rods from the paternal and maternal germ-cells, and that these give rise to a new nucleus from which the formation of the offspring proceeds. We also know that in order to become capable of fertilisation each germ-cell must first get rid of half of its nuclear rods, a process which is accomplished by very peculiar divisions. Without entering into further particulars here, amphimixis may be described as a process by means of which one-half of the number of nuclear rods is removed from a cell and replaced by an equal number from another germ-cell.

The manner, however, in which the chromatin substance is divided in nuclear division strengthens the above view of its fundamental nature. This method of division leaves no doubt that it is a substance of the utmost importance. I need only briefly recapitulate the main points of the wonderfully complicated process of the so-called mitotic or karyokinetic cell-division, which follows a definite law even as regards the most minute details.

When the nucleus is going to divide, the chromatin granules, which till then were scattered, become arranged in a row, and form a long thread, which extends through the nucleus in an irregular spiral, and then divides into portions (*chromosomes*) of fairly equal length. The chromosomes have at first the form of long bands or loops, but afterwards become shortened, thus giving rise to short loops, or else to straight rods or rounded granules. With certain exceptions, to be mentioned later, the number of chromosomes which arise in this way is constant for each species of plant or animal, and also for successive series of cells. By the time the process has reached this stage a special mechanism appears, which has till now remained concealed in the cell substance. This serves to divide the chromatin elements into two equal parts, to separate the resulting halves from one another, and to arrange them in a regular manner. At the opposite poles of the longitudinal axis of the nucleus two clear bodies—the "centrosomes", each surrounded by a clear zone, the so-called "sphere of attraction"—now become visible. The importance of these was first recognised by Fol, van Beneden, and Boveri. They possess a great power of attraction over the vital particles of the cell, so that these become arranged around them like a series of rays. At a certain stage in the preparation for division, the soft protoplasmic substance of the cell-body as well as of the nucleus give rise to delicate fibres or threads: these fibres are motile, and, after the disappearance of the nuclear membrane, seize the chromosomes — whether these have the form of loops, rods, or globular bodies—with wonderful certainty and regularity, and in such a way that each element is held on either side by several threads from either pole. The chromatin elements thus immediately become arranged in a fixed and regular manner, so that they all come to lie in the equatorial plane of the nucleus, which we may consider as a spherical body. The chromatin elements then split longitudinally, and thus become doubled, as Flemming first pointed out. It must be mentioned that this splitting it not caused by a pull from the pole threads (spindle threads), which attach themselves to the chromatin rods on both sides; the division arises rather from forces acting in the rods themselves, as is proved by the fact that they are often ready to divide, or indeed have already done so, some time before their equatorial arrangement has taken place by means of these threads.

The splitting is completed by the two halves being gradually drawn further apart towards the opposite poles of the nuclear spindle, until they finally approach the center of attraction or centrosome, which has now fulfilled its object for the present, and retires into the obscurity of the cell-substance, only to become active again at the next cell-division. Each separated half of the nucleus now constitutes a daughter-nucleus, in which it immediately breaks up, and becomes scatered in the form of minute granules in the delicate nuclear network, so that finally a nucleus is formed of exactly the same structure as that with which we started. Similar stages to those which occur in the aggregation of the chromatin substance in the mother-nucleus preparatory to division are passed through during the separation of the daughter-nuclei, but in the reverse order.

It is evident, as Wilhelm Roux was the first to point out, that the whole complex but wonderfully exact apparatus for the division of the nucleus exists for the purpose of dividing the chromatin substance in a fixed and regular manner, not merely quantitatively, but also in respect of the *different qualities* which must be contained in it. So complicated an apparatus would have been unnecessary for the quantitative division only; if, however, the chromatin substance is not uniform, but is made up of several or many different qualities, each of which has to be divided as nearly as possible into halves, or according to some definite rule, a better apparatus could not be devised for the purpose. On the strength of this argument, we may therefore represent *the hereditary substance as consisting of different "qualities."* The same conclusion is arrived at on purely theoretical grounds, as will be shown later on when we follow out the consequences of the process of amphimixis.

For the present it is sufficient to show that the complex mechanism for cell-division exists practically for the sole purpose of dividing the chromatin, and that thus the latter is without doubt the most important portion of the nucleus. Since, therefore, the hereditary substance is contained within the nucleus, *the chromati must be the hereditary substance.*

August Weismann was born January 17, 1834, at Frankfort-am-Main, and died November 6, 1914, at Freiburg. After graduating in medicine from Göttingen and spending several years in travel, in the German manner, he went to Freiburg to teach zoology when he was 32 and remained there for the rest of his 80 years. Study of variability in animals led to investigation of the mechanism of heredity, and to the germ-plasm theory. Although no longer held as he fabricated it, this theory was a step toward understanding the transmission of characteristics from one generation to the next.

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