

A CYTOLOGICAL LIFE CYCLE.

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The figures and diagrams which are usually presented to explain the nature and significance of the reduction division to beginners, although clear enough in themselves, often fail in their purpose because they do not take account of the fact that reduction is indissolubly bound up with fertilization. To give a clear conception of the significance of reduction it is necessary to present the whole life cycle. In many respects the fern is better suited than any other type for the representation of such a cytological cycle. The alternation of generations is obvious; the haploid as well as the diploid condition is evident; the antithetic processes of fertilization and reduction occur at opposite points of the life cycle and can thus be presented far more clearly than when reduction appears to be merely the "maturation of the germ cells."

The diagrams here presented are based on a hypothetical fern with four chromosomes in the sporophyte. The cytology is that of *Ascaris** very little schematized. Each of the chromosomes of which two are represented as short and two long, is marked with a characteristic figure so that its permutations may be followed through the cycle.

The best stage with which to begin is the diploid mitosis of the sporophyte, which conforms to the familiar type of somatic karyokinesis generally described. Omitting the resting nucleus the first stage in division is the formation from the chromatin network of a long, continuous spirem which winds in and out more or less, filling the whole nuclear cavity (Fig. 1). Soon each granule of this spirem divides and it becomes double longitudinally (Fig. 2). After considerable contraction during which the chromatin granules are drawn closely together, the spirem breaks into four pieces, the chromosomes (Fig. 3). These are oriented on the spindle and divided longitudinally along the line of the early split (Fig. 4), one half going to each pole and entering into the corresponding daughter nucleus (Fig. 5), so that the progeny of every chromosome is equally divided between the daughter nuclei. As all of the cells throughout the organism are produced in this manner each is exactly like every other in chromatin content and, on the hypothesis that the chromosomes bear the hereditary characters, in heritage as well. That this is actually the case in the heritage as well as in the chromosomes may be demonstrated by the familiar facts of vegetative propagation by which

*See Griggs, R. F., A Reducing Division in *Ascaris*, OHIO NAT., 6: 519-527, 1906. Wilson, E. B., *The Cell*, 2d Ed., pp. 65-72, 183, 236-242. N. Y. 1906.

the whole plant complete in all its parts may be reproduced from any small slip which can be made to grow. In some cases e. g. the leaves of *Bryophyllum* even single cells may be made to propagate the plant which of course would be impossible unless they contained all of the hereditary characters. This type of division continues then until the reduction division occurs and the familiar nonsexual spores so frequently found on fern leaves are produced.

In the reduction division the spirem is formed and divides in the same manner (Figs 6 and 7), but breaks into only half as many pieces as in the ordinary mitosis (Fig. 9). Thus each piece really corresponds to two of the divided chromosomes seen in the metaphase of ordinary mitosis. This pairing or "synapsis" of the chromosomes is the essential difference between the two types of mitosis, for all of the subsequent difference of the reduction chromosomes is the necessary consequence of it. Before they pull apart these paired, doubled chromosomes become definitely associated together forming the variously shaped tetravalent chromosomes or "tetrads" characteristic of the reduction division. In their early stages they may be seen to be formed by the association of the two arms of the loops into which the spirem is thrown (Figs. 7, 8 and 9). As they are pulled apart they may retain the form of the original loop or may appear as crosses or rings depending on their length and the manner in which they are attached to the spindle fibres (fig 10). Curiously enough the pairs are always made up of chromosomes of exactly the same size. This is indicated in the diagrams but becomes much more striking in organisms like the hyacinth with numerous chromosomes of diverse sizes.

In the metakinesis stage of the first reduction division (Fig. 10), the pairs of chromosomes which fused or rather failed to separate in the early stages, are pulled apart so that one goes to each of the daughter nuclei (Fig. 11). Immediately after the first mitosis the spindles of the second mitosis organize at each of the poles and the doubled chromosomes separated in the first mitosis are divided along the line of the early longitudinal split (Fig. 12), giving rise to the nuclei of the four nonsexual spores. Each spore thus contains one of the four parts of each of the tetrad chromosomes of the first reduction division. It will be observed that they are not alike in the chromosomes they bear. One set of spores bears only those designated by circles and dots while the other bears only those designated by crosses. If it had so happened that one of the tetrad chromosomes of the first mitosis had been turned the other side up as is indicated in the alternative Figure 10a, it is clear that the resultant nonsexual spores would have borne a different combination of chromosomes, all of them being mixed as to crosses and dots. When the number of chro-

mosomes is larger as is the case in most organisms and each of the chromosomes is oriented by chance independently of the rest as is presumably the case it is obvious that the number of combinations i. e. the number of kinds of reduced cells increases as the square of the number of chromosomes.

Omitting the variations, however, and following one of the nonsexual spores, say that with chromosomes marked with circles and dots, we find that it produces on germination the familiar heart-shaped gametophyte (prothallus) of the fern. The mitoses occurring in the growth of this plant (Figs. 14 and 18), are exactly similar to those of the sporophyte except that they have only the reduced number of chromosomes found in the spore from which it grew, i. e. they are haploid instead of diploid. When mature the gametophyte produces archegonia bearing eggs, and antheridia bearing sperms. In the development and maturation of these gametes there is, of course, no reduction division.

Fertilization may occur between an egg and a sperm from the same plant or the sperm may come from a different gametophyte. The latter alternative is figured in the diagram and it is further assumed that the sperm came from a gametophyte derived from a spore bearing the chromosomes marked with crosses (Figs. 20 and 21). When the sperm fuses with the egg their nuclei may be in a resting condition or they may be resolved into their respective chromosomes (Figs. 19-22), and proceed at once into the first mitosis of the succeeding embryo and the cycle is complete. (Figs. 23-25).

The significance of the conventions adopted in marking the chromosomes thus becomes apparent. Those marked with dots and circles came from the egg parent and those marked with crosses from the sperm parent. In view of this, the fact commented upon above that each chromosome pairs with its appropriate mate in synapsis, takes on a new significance, for each of the tetrad or reduction chromosomes is seen to consist of a doubled chromosome of maternal origin paired with the corresponding one of paternal origin. It is also evident that while the nuclei fuse in fertilization, the chromosomes do not show any sexual affinity for each other and live together, so to speak, in the nuclei of the diploid generation as independent units, until in the first half of the reduction division the corresponding pairs of maternal and paternal chromosomes appear to develop an attraction for one another and finally unite as synaptic mates to form the reduction chromosomes, so completing the union of sexual elements begun at the time of fertilization.

It is obvious, moreover, that if by chance one of the chromosomes had been oriented differently in the reduction division, as indicated by the alternative Figure 10a, none of the spores result-

ing would have borne the same chromosome combination as their parents. The combination diagramed could never be repeated until egg and sperm containing between them the chromosomes represented by all four symbols met and in the resulting zygote the chromosomes were oriented on the spindle in exactly the proper manner and this was followed by a succeeding fertilization by pure gametes bearing respectively only dotted and crossed chromosomes. Thus in an organism with four chromosomes in the diploid generation there are no less than nine possible chromosome combinations, while in organisms with numerous chromosomes the number of combinations possible is 3^n where n is the number of chromosomes.

Without making any specific assumptions concerning differences in specific maternal and paternal chromosomes other than the common knowledge that the plasms of the two parents are in a general way different in heterozygous organisms, it is evident that there is here a mechanism varied enough to account in large measure for the large variability in inheritance which is so familiar. No two children of the same parents (except identical twins) are ever alike, be the family ever so large. When we take account of intermarriage even without considering varying racial characteristics it is not surprising that we never find two faces alike.

If however we assume that the long crossed chromosome for example bears a specific character which is absent from its mate the long dotted chromosome, it will be seen that any one of four possible combinations with respect to this one chromosome and the character it bears may be realized in fertilization: (1). An egg bearing the x chromosome may be fertilized by a sperm bearing an x chromosome or, (2), by a sperm bearing a dotted chromosome, (3), an egg bearing a dotted chromosome may be fertilized by a sperm bearing an x chromosome or (4), by a sperm bearing a dotted chromosome. In the first case all of the cells produced in the subsequent reduction would bear the x chromosome together with its character, and if inbred would continue pure ever after. In the fourth case the offspring would be pure in respect to the dotted chromosome and whatever characters it might carry, while in the second and third cases it would be mixed. This is, however, nothing more or less than a statement of Mendel's Law.

