The Ohio Naturalist,

PUBLISHED BY

The Biological Club of the Ohio State University.

Volume V. MAY, 1905. No. 7.

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THE NATURE OF THE REDUCTION DIVISION AND RELATED PHENOMENA.

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It is generally conceded that the primitive plants and animals were nonsexual. In the primordial life of the earth no conjugation of any kind took place. Some organisms have come through all the geological ages in this primitive condition but the great majority even of the lowest forms have acquired some type of sexuality and retained it while a considerable number have no doubt fallen back from a sexual to a nonsexual condition. If the process of sexual conjugation of cells is then not a primitive property or function of protoplasm various questions naturally suggest themselves.

1. What caused the original nonsexual forms to develop the sexual process?
2. What disturbances were introduced in the life cycle of the organism and in the cell activity?
3. In what ways were the new life cycles established?
4. How do the life cycles of plants compare with those of animals?
5. What significance does the reduction division have in the higher forms?

In most plants conjugation takes place between two naked gametes, and it is probable that such specialized types of sexuality as are present in the Conjugatae and Phycomycetes originated from the more typical gamete conjugations. We can readily believe that all the Archeophyta were naked cells and that the cell-wall was developed as a protective covering. When these primitive cells were in process of division there could be an interchange of food from the one to the other so long as the protoplasmic connection was not completely cut. After complete separation the two daughter cells, still lying in contact, could exchange food by osmosis, the one having a less amount of food taking from the one having a greater supply. After the two cells had separated they might exchange food in the same way on coming in contact for any length of time by accident. In this way sexual evolution may have had its beginning as well as parasitism in all of its forms. After the process of temporary or permanent conjugation was once established it would be of advantage to the species under many adverse conditions. A set of starved or weak organisms meeting with a well nourished lot could conjugate either temporarily or permanently, greatly to their advantage, without doing the stronger individuals any special harm. Such is apparently the behavior of various lower organisms at the present time. Furthermore a swarm of unicellular organisms or zoospores in a given area is, by conjugation, reduced to just half the previous number. The mere reduction in the number of units might be a very important factor in the immediate welfare of the species especially when the further delay of reproduction incident to the process of conjugation is taken into account. In many of the lower plants the arrival of adverse conditions is the stimulus to the formation of resting zygospores or oospores by means of which the organism is preserved until a more favorable environment is again at hand. Rejuvenescence, using the term in its broadest sense, seems at least a very plausible cause of the origin of sexuality if it is once admitted that conjugation is not one of the fundamental properties of the protoplasm of primordial organisms. Other means of rejuvenescence should serve the same purpose as the stimulus and reaction which one mass of protoplasm must exert on another during conjugation, leaving out of consideration the fact of the reduced space occupied by the two united organisms and consequently the less surface in contact with the surrounding medium. A tree may be rejuvenated by placing a fertilizer about its roots. So organisms which naturally rejuvenate only through conjugation may be rejuvenated through a favorable change of food or other factors of environment, thus actually delaying the necessity of a conjugation for a long period of time.

Whether conjugation was long or short in its evolution is of no special importance in the discussion of the remaining questions formulated above. The first time that nucleated cells conjugated so completely as to act in cell division as a single cell a disturbance was present not operative in the race previously. The two nuclei having fused contained twice the amount of chromatin as before and from two sources, therefore with somewhat different hereditary tendencies. Evidently a fusion or mixing and doubling of nuclei generation after generation is impossible, especially if the chromatin is organized into definite chromosomes. A reduction division of some kind is the inevitable accompanyment of a conjugation process in the life cycle. This fact being recognized we may proceed to find out in what ways the life cycle may be established. Theoretically a number of possible modes may be developed and the reduction division established at three points in the life cycle.

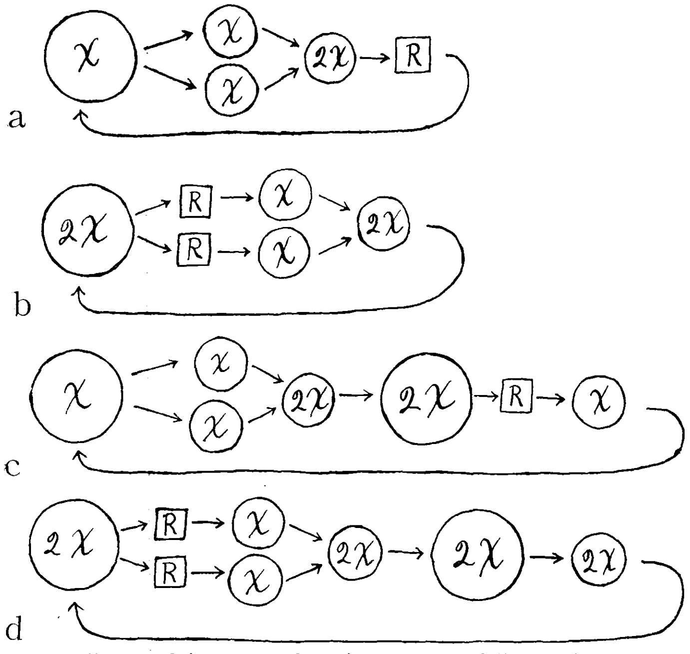

Fig. 1. Diagrams of various types of life cycles

1. Suppose an organism with x chromosomes to give rise to zoospores which conjugate completely; the resulting zygote would have $2x$ chromosomes. If, however, reduction takes place at the first division or germination of the zygote, the new organism would have the reduced or x number of chromosomes. The double number of chromosomes exists only in the resting stage of the zygote and the result is a simple sexual cycle, the gametes being produced without a reduction division (Fig. 1a).

2. If an organism with x chromosomes gives rise to conjugating zoospores, the zygote will contain $2x$ chromosomes.

Suppose that this spore, on germination, fails to reduce the chromosomes. The resulting individual will have the double number in each cell. Now if, when reduction takes place, the cells reduce the chromosomes and the resulting cells are gametes, a new condition arises in which a "$2x$" sexual generation originated from an "x" nonsexual type gives rise to gametes as the result of a reduction division. A simple sexual cycle is established with a "$2x$" sexual generation producting gametes as the result of reduction (Fig. 1 b). Such plants as Fucus must have established their life cycle in this way. The Fucus plant is a $2x$ sexual generation which develops ovaries and spermaries. A cell in the ovary undergoes the reduction division and by further divisions usually produces eight eggs with x chromosomes each. In the spermaries a cell also undergoes reduction and by subsequent divisions a number of spermatozoids are produced having the x number of chromosomes.

3. The third point at which the reduction division may be established is after the sporophyte stage in connection with an alternation of generations. Suppose a nonsexual organism develops zoospores which conjugate and the zygote fails to reduce the chormosomes at the first division. An individual is produced with $2x$ chromosomes. When zoospores are produced as the result of a reduction division they come out not as gametes but as nonsexual spores which give rise to an x generation. This generation being similar to the original generation produces gametes without reduction which have the x number of chromosomes. This is the process in the plants with a true, antithetic alternation of generations. A gametophyte generation is followed by a sporophyte generation which reduces the chormosomes before the development of nonsexual spores (Fig. 1 c).

Other life cycles might be and perhaps are developed. A sporophyte coming from the zygote might develop spores without reduction and these might develop into gametophytes with the $2x$ chromosomes, and the gametes would then be produced as the result of a reduction division (Fig. 1 d). It will be seen, therefore, that there are two types of sexual or gamete-producing generations, one with the $2x$ chromosomes giving rise to gametes through reduction, the other with x chromosomes giving rise to gametes directly without reduction.

Now in the higher plants the life cycle is invariably established, unless in abnormal cases, with an alternation of generations, a gametophyte generation with x chromosomes is followed by a sporophyte generation with $2x$ chromosomes. The reduction division takes place in special cells, sporocytes, and usually by two successive divisions. The resulting spores have the reduced number of chromosomes and represent the first cell of the gametophyte generation (Fig. 2). There is no more reason for saying, as some do, that the gametophyte generation begins with the sporocyte than it would be to insist that the first stage of the sporophyte consists of the egg and sperm before conjugation. The gametophyte is, of course, the sexual generation and the sporophyte the nonsexual generation, both from the morphological and physiological points of view. In the higher plants the gametophytes are very much reduced and some have insisted in retaining the old misapplied sex terms for the sporophyte. But this leads merely to a confuison of terms and ideas. To compare pollination, the growth of the pollentube, and the other processes connected with the development of the gametophytes of higher plants with fertilization, as it exists in the sexual generations of plants and animals, is only comparing things that are not even analogous and giving such diverse meanings to sex terms that they lose their real significance entirely.

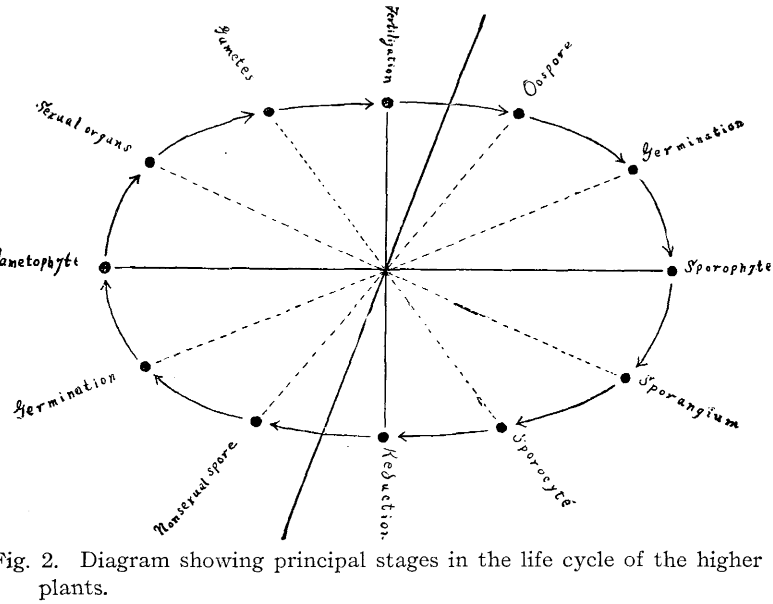

Fig. 2. Diagram showing principal stages in the life cycle of the higher plants.

In the higher animals we appear to have a condition similar to that in Fucus, a "$2x$" gamete-producing organism in which reduction takes place before the formation of gametes. The egg with its polar bodies represents four original eggs comparable to the four spermatozoids developed from the spermatocyte. It is interesting to note that in some of the Brown Algae part of the eight eggs which are produced after reduction also degenerate. Furthermore, the eggs of the Fucaceae are discharged while in all

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ADIANTUM	Homosporous Sporophyte	Sporocyte	Reduction	Spore	Hermaphrodite Gametophyte			Spermatozoid Oosphere	Fertilization	Oospore in Ovary	Parasitic Embryo	
ANGIOSPERM	Heterosporous Sporophyte	Microsporocyte Megasporocyte	Reduction	Microspore Megaspore	Pollengrain (Male) Embryo-sac (Female)			Sperm cell Oosphere	Fertilization	Oospore in Female Gametophyte in Ovule	Intraseminal Embryo	Sprouting
MAMMAL					Male Female	Spermatocyte Oocyte	Reduction	Spermatozoon Ovum	Fertilization	Fertilized Egg in Uterus	Intrauterine Embryo	Birth
FUCUS					Hermaphrodite or Male and Female Individuals	Reduction cell in Antheridium Reduction cell in Oogonium	Reduction	Spermatozoid Oosphere	Fertilization	Oospore in Water		

Comparison of the life cycles of plants and animals.

gametophytes with a true alternation of generations they are retained in the ovary. The plant life cycles together with a typical animal are compared in Plate XXI.

Among the interesting things which have recently come to light and which appear to have their basis in the phenomena of the reduction division is Mendel's law of heredity in hybrids. The operation of this law can be explained on the hypothesis of pure sex cells. In 1897 the writer worked out in detail the reduction division which takes place in the ovule of Lilium philadelphicum. Although the development and subsequent division of the chromosome was followed out in considerable detail in this work, the facts presented were not accepted by a number of botanists, as admitted by Strasburger, because of supposed authority in the opposite direction. So soon, however, as Mendel's law was rediscovered it became self-evident that belief in a qualitative or true reduction division of some kind was necessary if the whole chromatin hypothesis was not to fall to the ground. Accordingly a re-investigation by some of the foremost cytologists, among them Strasburger and Farmer, resulted in a confirmation and acceptance of the propositions presented in my papers on Lilium and Erythronium, as also of similar work done previously by a number of zoologists.

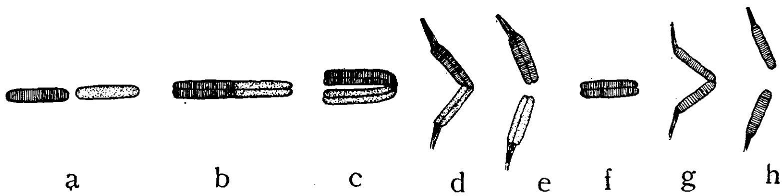


Fig. 3. Diagramatic representation of the transverse division of a chromosome.

If then a transverse division of the chromosomes occurs during the reduction karyokinesis each of the chromosomes resulting from the process of pseudo-reduction may be regarded theoretically to be made up of a pair of chromosomes, one being a male chromosome and the other a female chromosome, joined end to end. There are also some obrsevations which appear to indicate that this actually takes place. In such cases then as in Lilium and Erythronium the formation and nature of the twisted loop can be diagramatically represented as in Fig. 3, a-e. In the following division in which a longitudinal splitting occurs the daughter halves of the chromosomes formed early in the previous division become separated (Fig. 3, f-h).

Mendel's law of heredity, so far as it has a direct bearing on the nature of the reduction division, may be briefly stated as follows: When two organisms differing in some character are crossed it frequently occurs that the resulting hybrids exhibit the character from one parent only. The character which appears is said to be *dominant* while the corresponding character from the other parent not in evidence is called *recessive*. But if these hybrids are bred among themselves they give rise to offspring of two types, some showing the dominant character and some the recessive, and these usually appear in the proportion of 3:1. By further trial it is found that about one-third of the dominant individuals are pure and two-thirds of mixed nature.

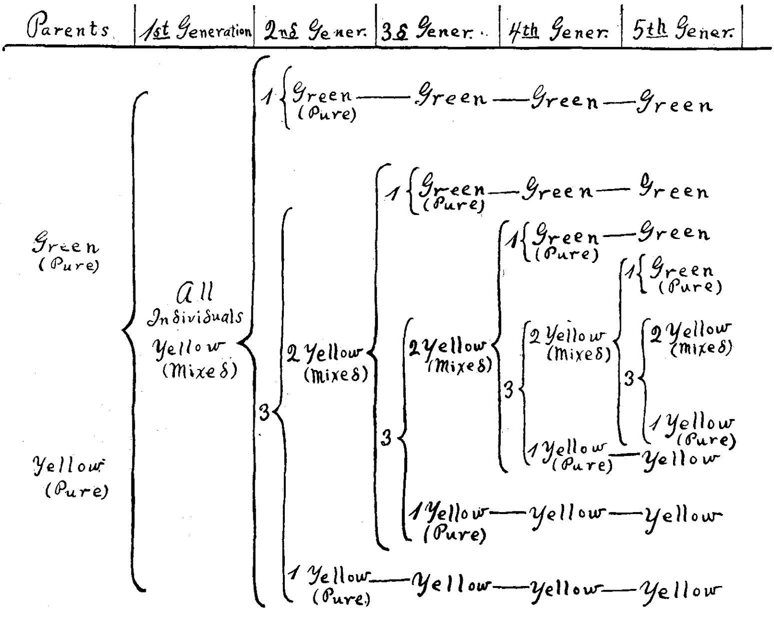
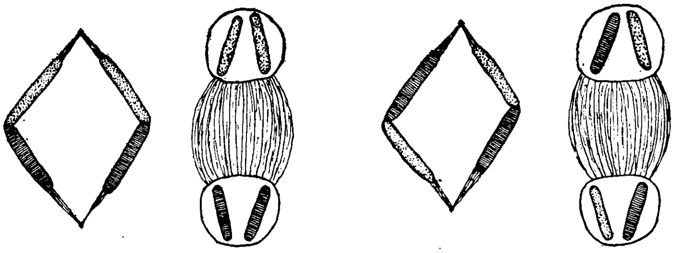


Fig. 4. Diagram showing the operation of Mendel's law with peas having yellow and green cotyledons.

These latter will again produce offspring of both types the same as the original hybrids, and so on for many generations. The first instance discovered by Mendel related to the color of the cotyledons in peas. The yellow color of cotyledons was found to be dominant over green. The operation of Mendel's law as regards the yellow and green colors of cotyledons is shown in Fig. 4. Albinism among animals also furnishes a familiar example of the operation of Mendel's law. If albino mice are mated with gray mice the offspring are gray, but in the following generation one-fourth will again be albinoes. The gray is the dominant and the albino the recessive character.

As stated above, Mendel's law can be explained on the theory of pure sex cells. In working out the peculiar activities of the chromatin during cell division, cytologists have come to look upon the chromosomes as special bearers of hereditary tendencies although other parts of the protoplasm may also have something to do with the transmission of heredity. Now if a transverse division occurs and the chromosomes are pure the daughter nuclei could then be organized as pure having only chromosomes derived from the egg or sperm (Fig. 5, a-b). No difference how many subsequent, longitudinal splittings take place before the formation of gametes, the gametes would always be pure cells.



a b c d

Fig. 5. Diagram of transverse division showing possible production of pure and mixed cells.

In conjugation there is twice the chance for a mixed oospore to be formed as a pure one and hence the splitting of the hybrid race in the proportions given by Mendel's law. But suppose that the chromosomes were joined in pairs and arranged in the mother star in such a way that half of the male chromosomes were on one side and half on the other and the same for the female chromosomes then the transverse splitting would always result in mixed cells and no splitting of the race could occur (Fig. 5, c-d). The daughter nuclei would be mixed even if the chromosomes making up the pair were pure. Other arrangements are possible, and in case the chromosomes are not reorganized as pure bodies the cells resulting from reduction could of course not be pure. But whatever the facts may be it appears that all cases of hybrids that follow Mendel's law as well as those which do not can be accounted for on the theory of pure chromosomes and a qualitative reduction division. This would not prove however that the chromosomes are organized as pure bodies or that there is a transverse splitting of chromosomes. These facts must be worked out from a study of nuclear division, and this is the important and difficult problem to be solved. Anyone can compare the results of cytology and plant and animal breeding after the facts have been ascertained. But to work out these problems is a slow and difficult process as the writer has discovered from experience.

Finally a word may be added as to the significance of reduction and conjugation in the origin of species. The mixing of protoplasms with diverse hereditary characters must cause a great disturbance in the hereditary apparatus. We may think of a struggle of two characters one against the other, the one becoming dominant and the other unable to reassert itself. We may picture to ourselves the powerful stimulus of the one on the other and the reaction and rearrangement of the material mosaic which may result in the evolution of a monstrosity or a new species. But crossing must after all tend to uniformity. It is the origin of sexual barriers and the barriers induced by the activity of one hereditary tendency over another which has led to diversity in plant and animal life so far as this has any relation to the sexual process. Variation and diversity of type is just as prominent a characteristic of nonsexual as of sexual organisms. The new forms resulting from near or distant crosses must be regarded as merely incidental in the great process of the evolution of the diverse life of the earth, the real and fundamental cause lying in the nature of protoplasm itself whether of sexual or nonsexual organisms. Variation is a property of protoplasm and reproduction is primarily a matter of assimilation and growth. If sexuality were the primary cause of variation we would logically have to suppose a multitude of sexual races in the beginning rather than a simple nonsexual and uniform group of organisms which has evolved and segregated into new types without any special reference as to whether the units in the process have acquired sexuality or having acquired it once have lost it again in ages past.
