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SYNAPSIS AND SYNIZESIS *

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The term, synapsis, has, in recent years, gained wide currency among cytologists as a designation for various real and hypothetical processes supposed to take place in the early stages of the reduction division. At the present time cytological literature abounds with contradictory accounts of various cell activities supposed to be normal, until one is not only amused but utterly confused. In order to give the word, "synapsis", a more definite meaning, McClung† has proposed the following definitions which it might be well for plant cytologists to consider. "By synapsis I mean the fusion of simple chromosomes into multiple ones, usually of a bivalent value, according to the idea of Moore, who proposed the term. I would suggest that in order to avoid the lamentable confusion that has resulted from the misuse of this designation that a new descriptive word be applied to the contraction of the nucleus in which the chromatin is found massed at one side of the vesicle, without regard to whether it is a normal phenomenon or not. To carry this idea I shall call this stage the "synizesis of the chromatin." "Synizesis'—the unilateral or central contraction of the chromatin in the nucleus during the prophase of the first spermatocyte. A term proposed to avoid the misuse of the word 'synapsis".

Evidently this is a move in the right direction but the definition of synizesis as given above must be extended to include

* Contributions from the Botanical Laboratory of the Ohio State University XXVIII.

†McCLUNG, C. E. The Chromosome Complex of Orthopteran Spermatocytes. Biol. Bull. **9**:304–340, 1905.

similar contractions in other reduction cells, as microsporocytes and megasporocytes, or any other cells, in which a similar phenomenon is observed. Accepting this terminology as conducive to lucidity of expression, synapsis will then normally mean the process by which two univalent chromosomes become united to form one bivalent chromosome; or, in case a continuous spirem is formed by the end to end conjugation of univalent chromosomes, the process by which two univalent chromosomes become so united that at the time of the transverse segmentation of the continuous spirem they do not break apart as in previous divisions but are brought into the mother star as single bivalent pieces.

This will then include the idea expressed by the term, pseudo-reduction, which refers only to the fact that half as many chromatin pieces are present as in the previous division. Synapsis must not be confounded with the fusion of chromosomes in the network during each resting period nor with the ordinary fusion by which a continuous spirem is produced.

Recently the writer has studied a considerable number of preparations in order to refresh his mind upon this subject. The few figures presented are given merely as examples of a very large number of distinct types of chromatin contraction, which may be observed.

Some confusion has been produced by the use of the terms longitudinal and transverse division. Evidently it is of no importance whether two entire univalent chromosomes conjugate to form a ring, a twisted loop, or a simple longitudinally united or folded pair, so long as they separate during metakinesis. Transverse division means a qualitative division, longitudinal division a quantitative division. In such bivalent chromosomes as occur in the megasporocytes of *Lilium philadelphicum* (fig. 1), and *Erythronium albidum* and *americanum*, and in the microsporocytes of *Lilium tigrinum* the two limbs of the chromosomes lie folded on each other and twisted together. But the real reduction division is not so much the pulling apart of the two limbs but the transverse break in the loop at the head of the chromosome which is supposed to represent the point of the synaptic fusion of the pair of univalent maternal and paternal chromosomes.

Synapsis and reduction then are simply processes by means of which entire chromosomes, presumably maternal and paternal, are segregated into the daughter nuclei; or by which at least qualitative division of the chromatin is accomplished in case there is a mixing of paternal and maternal chromatin during the "$2x$" phase of the organism. The whole process appears to be merely a mechanical contrivance for bringing about qualitative separation. We may consider chromosome reduction as a necessary

stage in the life cycle of every sexual organism containing definite chromosomes. The fusion of the chromatin in synapsis cannot have any important effect on the hereditary characters of the chromosome. At the most the effect is probably the same as that which may be experienced in the fusion of the chromatin during each resting period of the nuclei in the entire history of the "$2x$" stage. It is the association of the chromosomes in the oospore and the subsequent vegetative history that appears to be of importance whether the chromosomes are closely mingled and fused or not. And it must be apparent that hereditary tendencies are active both in the resting stage of the nucleus and in the process of karyokinesis.

The early longitudinal splitting of the spirem in the first reduction division may be looked upon as a continuation of the usual process of vegetative karyokinesis, the quantitative separation of the daughter parts being interfered with by the intercalation of the synaptic stage. Since the separation or segregation of the univalent chromosomes follows immediately, a second division spindle is organized through the influence of the double chromosomes and thus normal nuclei are again produced by the distribution of the daughter halves. The mere presence of these chromosome pairs in the daughter nuclei resulting from reduction may be the cause of the rapid formation of the second spindle, and the explanation of the quite general presence of cell tetrads following the reduction division in both plants and animals. Yet it is hardly permissible to say that the first and second divisions are not true karyokineses. Nevertheless, the second division is a karyokinesis which had its beginning in the previous stage which was interrupted by the intercalation of the synapsis and reduction processes. The first spindle formed was taken advantage of by the bivalent chromosomes and the segregation following being of paternal and maternal double chromosomes the second spindle became necessary for the separation of the daughter pieces. In the first division the number of chromatin granules is not reduced although only half the original chromatin granules are represented in the daughter nuclei because of the transverse division of the chromosome as shown by me in the reduction division of *Lilium philadelphicum*.* In such cases as in the megasporocytes of Lilium, where the process of spore formation has been abbreviated, the vegetative division following the reduction is of the same nature as the second division when the usual spore tetrads are produced. This was definitely shown to be the case in my paper on *Erythronium albi-*

*Schaffner, John H. (Contribution to the Life-history of Lilium Philadelphicum). The Division of the Macrospore nucleus. Bot. Gaz. **23** : 430–452, 1897.

*dum.** Farmer and Moore† also consider that in the second karyokinesis we have a continuation of the longitudinal splitting begun during the first. We have thus a rational explanation of the observed facts—an explanation as to why when pseudo-reduction and qualitative reduction take place these processes are so generally followed by a second karyokinesis.

Accepting McClung's term, synizesis, for the massing or contraction of the chromatin in the prophase of division, the question remains to be settled as to whether this is a normal or an artificial production. Two methods seem available for the solution of this problem. One may study the effects of plasmolizing reagents on known structures and make comparisons or else one may attempt to study the stages in question from the living material.

In 1899‡ I found that a violent distortion of the chromatin and the so-called sickle stage of the nucleolus may be produced even in resting cells of the root tips of onions by using a violent killing fluid. This fluid was made according to the following formula:

Absolute Alcohol	95 cc.
Chloroform	5 cc.
Glacial Acetic Acid	1 cc.
Chromic Acid (8% H_2O Solution)	1 cc.

The combination proved to have a very bad effect as a killing reagent and was simply one of many tried in a series of experiments. Figures 5 and 6 represent cell rows from opposite sides of a section of onion root tip (*Allium cepa*) killed in this fluid. Nearly all of the nuclei of the peripheral cells showed decided distortions. The nuclei are crowded toward the outer walls of the cells, while the nucleoli are generally pushed in the opposite direction. The chromatin and other dark-staining material is also massed to some extent on the inner side of the nucleus. In the central strands there is little displacement although the cells are shrunken. No such distortions are ever to be seen in properly killed root tips and especially is there no such symmetrical arrangement of the nuclei and nucleoli in the outer layers of cells. This appearance then is purely on artifact which may be of assistance in the interpretation of other cases. In judging of synizetic contractions, it is also important to take into account the probable expansion of the nuclear cavity. The

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* ———————. A Contribution to the Life-history and Cytology of Erythronium. Bot. Gaz. **31** : 369–387, 1901.

†FARMER, J. B., and MOORE, J. E. S. On the Maiotic Phase (Reduction Divisions) in Animals and Plants. Quar. Jour. Mic. Sci. **48** : 489–551, 1905.

‡SCHAFFNER, JOHN H. Artificial Production of the Sickle Stage of the Nucleolus. Jour. App. Micr. **2** : 321–322.

cytoplasm is often expanded to a considerable extent by the killing fluids in common use. Figure 2 represents such a case. It represents the upper nucleus of a two-celled embryosac of *Lilium philadelphicum*. The killing fluid was the stronger chrom-acetic acid solution. The nucleus is in the resting stage and is not contracted as appears from a comparison with the lower nucleus of the same sac, where the cytoplasm is in the normal condition in contact with the nucleus. When the nuclear membrane has disappeared in the prophase of the reduction division the wall of the large vesicular nuclear cavity presents a favorable object for such expansions.

Recently Cardiff* has put forward the tentative opinion that the one-sided position of the chromatin mass is due to gravity. That this is not the case can easily be discovered by a study of cells whose position is known during life and during the killing process. Figures 3 and 4 are sections of microsporocyte tissue from the microsporangia of *Marsilea quadrifolia* sectioned in the original vertical position. The synizesis has been perfectly symmetrical. The chromatin knots all being toward the periphery, up and down and to both sides in central sections. Evidently gravity had nothing to do with the phenomenon, at least from a physical point of view. The action was apparently the same as in the case of the onion roots. The hard wall of the sporocarp was probably an important factor in producing the condition.

Some have supposed that the contraction is always around or in contact with the nucleolus. This is far from being the case. In the various plants investigated by myself one might, in individual preparations, even come to the opposite conclusion. The facts are that the chromatin may be massed around the nucleolus and have a central position in the nucleus as in Figure 9, which represents a microsporocyte of *Erythronium americanum*, or it may have a lateral position, in some cases merely touching the wall of the nuclear cavity, in others crowded closely against it. The nucleolus may appear on one side of the chromatin knot either connected with it or very loosely attached and appearing as if violently squeezed out of the chromatin mass during its contraction. Figures 7 and 8 representing microsporocytes of *Sagittaria latifolia* are typical examples of this condition. But very commonly the chromatin contracts away from the nucleoli, which then lie free in the nuclear cavity, or are crowded against the wall of the cavity and represent the "sickle stage". Figures 10 and 11 are microsporocytes of *Lilium tigrinum* which show these conditions. The synizetic knot is sometimes on the side of the nucleus lying against the greater mass of cytoplasm (Fig. 7)

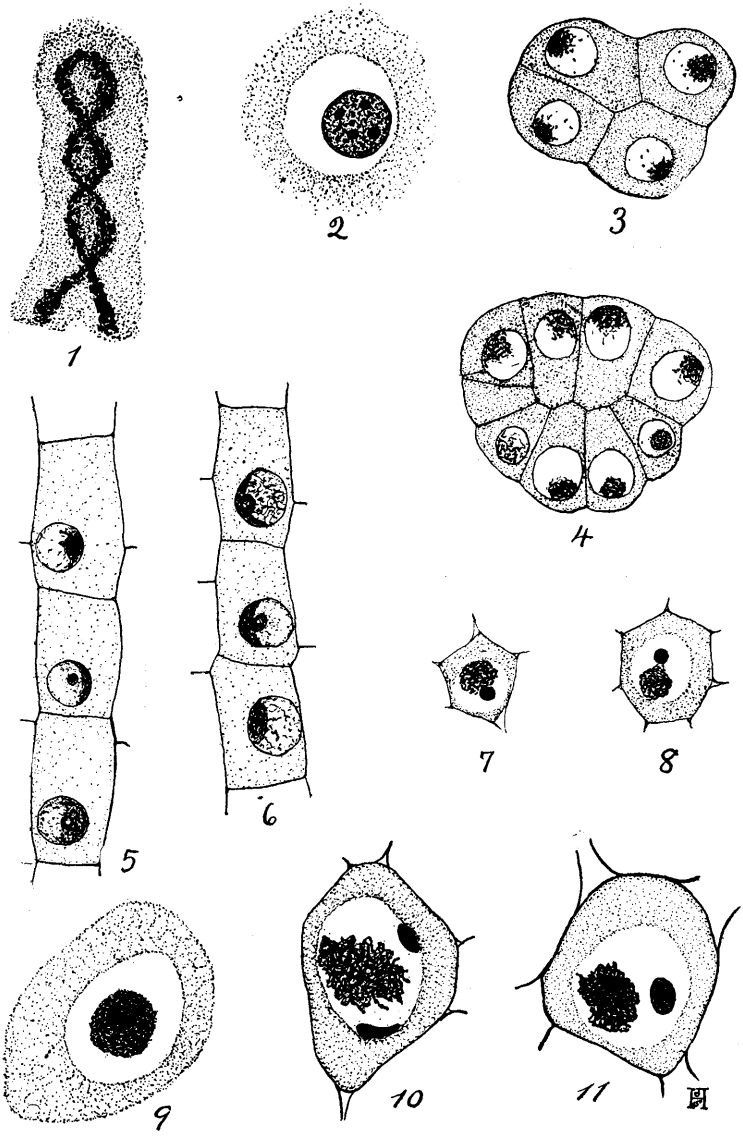
*Cardiff, Ira D. A Study of Synapsis and Reduction. Bull. Torr. Bot. Club **33** : 271–306. 1906.

at others on the side where there is the least cytoplasm (Figs. 3 and 4). There is again no uniformity in this respect.

The variety of types of synizesis might be much increased but the examples given will make it plain that there is nothing uniform in the behavior of the chromatin in synizesis either with respect to the nucleolus or the nuclear cavity. Synizesis appears to be an artifact when considered from the standpoint of plasmolysis, but the question must be settled, if possible, through the study of living material. But if staining reagents are employed, great precautions are necessary even with living material. At the present stage of the subject it seems useless to continue the investigations by merely giving conclusions from a set of preparations which may present a supposed series of uniform conditions.

The results of this investigation may be briefly summarized as follows: The synizetic knot is not always around or in contact with the nucleolus but very commonly one may find it entirely distinct from the nucleolus. The chromatin is not always unilateral but very often central. If the knot is at one side it has no evident relation to the direction of gravity. Synizesis also does not mark the stage where the chromatin threads become homogeneous. In cases like *Lilium tigrinum* the chromatin granules, if properly stained, are seen at their best after the greatest possibility for contraction is passed. It seems from an investigation of the literature of the subject that there has been much speculation and reporting on "uniform conditions" simply because synizesis or "synapsis" has not been explained. But it is at present more important to discover the actual condition of things. The time at which synizesis occurs has not shown any uniformity. When one examines figures of this condition he is surprised at the lack of uniformity present. Some have even gone so far as to describe two "synapsis" stages before the formation of the mother star. During the early stages of division the nucleus is the seat of great chemical activity and the expansion of the nuclear cavity and changes in the chromatin network give rise to conditions which are especially favorable for the production of artifacts.

After the chromatin thread becomes thicker the contractions, as one would expect, are less common though by no means entirely lacking. Later when the orientation of the bivalent chromosomes begins, distortions are again abundant in many preparations. These series of distortions and contractions included under the term "synizesis" have at present no meaning and the mechanics of the process remains unexplained from the standpoint of a natural stage of karyokinesis.



SCHAFFNER on "Synapsis and Synizesis."

Explanation of Plate IV.

The figures were drawn with the aid of an Abbe camera lucida. Figure 1 was drawn with the Zeiss 18 ocular and Leitz 1-16 objective; the others with Zeiss 18 ocular and Zeiss 8.0 objective.

Fig. 1. A single bivalent chromosome from the reduction cell in the ovule of Lilium philadelphicum.

Fig. 2. Nucleus from two-celled sac of L. philadelphicum showing expansion of the cytoplasm.

Fig. 3. Microsporocytes of Marsilea quadrifolia showing centrifugal arrangement of the chromatin in synizesis.

Fig. 4. Microsporocyte tissue of Marsilea quadrifolia showing symmetrical synizesis.

Figs. 5 and 6. Cell rows from opposite sides of sections of Allium cepa showing the nature of artificial contraction.

Figs. 7 and 8. Microsporocytes of Sagittaria latifolia with nucleoli on one side of the contracted chromatin.

Fig. 9. Microsporocyte of Erythronium americanum showing central contraction of the chromatin around the nucleolus.

Figs. 10 and 11. Microsporocytes of Lilium tigrinum showing the independent contraction of the chromatin, the nucleoli being entirely distinct in the nuclear cavity.