SYNAPSIS CONSIDERED AS A SEXUAL PHENOMENON.*

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The first decade of the 20th century witnessed the establishment of the theory of the individuality of the chromosome, through numerous cytological investigations, on a firm basis of fact. The acceptance of this deduction had and still has a most profound influence on biological theory. The discovery by Montgomery (8) and others that the bivalent chromosome is actually made up of a pair of univalents, one from the maternal and one from the paternal side, laid the cytological basis on which genetics can be substantially built. But in recent years it has been found that many irregularities in conjugation and segregation occur, which shows that the properties of the chromosomes that cause them to unite and separate are properties that may appear and disappear regularly or irregularly in the life cycle. This property of specific attraction at a single special point in the life cycle is appropriately considered as a second development of primary sexual states, the first being in the gametes themselves. The specificity of the chromosomes in relation to synaptic attraction is far more remarkable then the fact of individuality of material and form.

Most cytologists have been impressed by the peculiarities of the reduction division. But the reduction division shows no special deviation from ordinary vegetative karyokinesis except as it is modified by the synaptic properties of the chromosomes during the prophase and metaphase stages. The writer worked out the details of the reduction division long before he knew what relation these chromosome shiftings had to heredity or what the actual probable cause was for the peculiar deviations from the vegetative divisions. (10). Several re-examinations of the original materials have reassured him that his first interpretation of the figures was essentially correct, and gave the proper basis also for the later developed facts of Mendelian heredity.

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A comparison of the sexual conjugations of gametes with the conjugations of synaptic pairs of chromosomes shows that the phenomena are alike in many respects and tends decidedly to the conclusion that the synapsis of specific pairs of chromosomes is due to the presence in them of primary sexual states of the same nature as the primary sexual states of the entire protoplasts, including their nuclei, i. e., of gametes, and which cause them to be attracted to each other and thus associated during the diploid stage of the organism. Just as there is more or less specific compatibility or indifference in the conjugation of gametes so also is there a specific compatibility or aversion of chromosomes of the same set to conjugate or of different sets in the case of extreme hybrids. The characteristics and peculiarities of isogamous gametes and the various degrees of heterogamous gametes are also paralleled to a certain extent although not entirely by the evolution of allosomes in some organisms. From this point of view a sexual organism has two stages in its life cycle in which primary sexual states arise. In one stage (gamete stage) the entire protoplast, but more especially the entire nucleus, which is normally haploid, becomes + or − in relation to another protoplast; in the other stage (reduction or synapsis stage) the chromosomes become + or − in relation to each other individually, without any special reference as to whether the sporocytes are for the time being in the secondary male or female state, namely are microsporocytes or megasporocytes, or are in a neutral condition as for example in homosporous plants. This sexual union of synaptic mates was suggested in a general way in 1908 but up to the present has not been developed further by the writer. (Schaffner 13).

In case of polyplody the normal sequence of events may, of course, be considerably changed. Belling found that in triploid Cannas (1) the three chromosomes of each kind or set come together. Multiple conjugation of chromosomes is possible just as triple fusion or other multiple fusions of nuclei in the gametophytes of Angiosperms.

In many species synapsis first becomes manifest by the development of the protochromosomes. In this early stage evidently the individual chromosomes must be attracted into their appropriate synaptic pairs and in the ordinary types of karyokinesis this is the only time when such proper association

is possible; and we know that the chromosomes are properly
paired off both from the consequent Mendelian behavior and
from direct cytological evidence as first definitely shown by
Montgomery (8). Were there no cytological evidence for the
individuality of the chromosome and for definite synaptic mates
we would be compelled by the genetic evidence to hypothecate
such a condition in spite of the so-called crossing over of hered-
itary factors. But the evidence for individuality and specific,
synaptic mating in normal reductions is convincing. The genetic
evidence properly interpreted and the cytological evidence are
in accord. The peculiar notion of a parasynapsis by which two
complete threads each made up of a chain of chromosomes, are
supposed to come to lie side by side for the entire length of the
chain during synizesis requires a mechanism and activity of the
chromatin entirely outside the method of behavior of the
nucleus in the vegetative karyokinesis.

    The first division of meiosis or the true reducing division
proceeds then along the same lines as an ordinary nuclear
division except that the pairs of chromosomes become sexual-
ized in relation to each other and are associated first as proto-
chromosomes. From this stage on they elongate, join end to
end in a continuous chain as in any vegetative division, and
produce a thread with a single row of chromatin granules which
later divide and form the double spirem. It is this enlarged state
of the nucleus with its extended and delicate, continuous thread
that shows synizesis in ordinary microscopic preparations. At
the stage when the spirem has the double row of chromatin
granules and when it is much thicker there is usually no syn-
izesis unless the material has been very poorly killed. The sexual
attraction continues very strong between the synaptic mates,
holding them in telo-synapsis at the point of union of the pairs
much more strongly than the union with the next pair in the
skein, as shown by the subsequent behavior. After the forces
which produce the extended spirem and which apparently act
in opposition to the synaptic attraction are expended and the
spirem is shortening and developing the chromatin loops the
synaptic attraction again acts very strongly and throws the
mates into longitudinal often twisted loops or fold, into the
true para-synaptic position. Next the force that has held the
chromosomes together in a continuous chain disappears just as
in a vegetative division and the chromosomes fall apart except

at the ends where the pairs were originally held together in
telosynapsis in addition to the ordinary union. The sexuality
of the synaptic mates becomes much intensified at this stage
resulting in such a close union of the bivalents and their daugh-
ter halves that they usually appear like single chromosomes.
But just as the primary sexual state disappears in the united
gametes when the nuclei have fused so the synaptic mates lose
their + and − condition and by the time they have been brought
into the mother star with the spindle fibers properly attached,
they normally become promptly and completely desexualized
and are separated to the opposite poles much like daughter
chromosomes are in vegetative karyokinesis, except that each
univalent is made up of two longitudinal daughter halves as it
arrives at the pole. However, sometimes the attraction contin-
ues beyond the usual stage in some synaptic pair, resulting in
irregular chromosome distributions. The sexual state of the
synaptic mates may also disappear too early, again making
abnormal distributions possible. As indicated, the segregated
univalents are already in the longitudinally divided condition
and this probably is the cause of the prompt development of
the second spindle, often before the nucleus has advanced very
far toward the resting condition. The second division of meiosis
is, therefore, a necessary consequence of the modification of the
karyokinesis brought about by the synapsis of the chromo-
somes in the first division.

The reduction division is then an ordinary division modified
by the development of primary sexual states in the individual
chromosomes, leading them into synapsis and there is appar-
ently nothing peculiar in the reduction division except what is
consequent to the sexualization of the synaptic mates. There is
nothing mysterious in the reduction division itself but, as
Strassburger pointed out long ago, it is a necessary consequence
of fertilization if a sexual organism is to perpetuate a working
or workable mechanism. The mystery at present lies with the
sexual states, both primary and secondary. The important
peculiarities which are the result of sexualization are first, the
concentrations and movements of the chromatin giving rise to
the protochrosomes, often rather definite masses; second, the
strong bond of union in telosynapsis of the synaptic mates; and
third the further attractive process at the looping stage by
which the two fused chromosomes are drawn together in a close

lateral union or parasynapsis, which for a time may entirely obliterate any indication of the actual duality of the structure.

Karyokimeses in which there is no sexualization of the chromosomes, whether taking place with haploid, diploid, triploid, or tetraploid complements of chromosomes are essentially the same in character. But the presence of a multiple set or complement of chromosomes greater than diploid must necessarily give rise to possible new Mendelian ratios or to abnormal deviations.

The writer first discovered the important processes in the reduction division in Lilium philadelphicum (10) in 1897, and later in Erythronium in 1901 (11), in Lilium tigrinum in 1906 (12), and in Agave virginica in 1908 (13). In 1905 Mottier (9) found the process essentially the same in Podophyllum peltatum; and Miss McAvoy's study of Fuchsia (6) and of Oenothera biennis in 1913 (7) showed that a similar succession of stages was present in these species, and not merely a telosynapsis as reported for "Lamarckiana" mutants by Gates (3 and 4) and others. From 1903 on a large number of investigators, especially Farmer and Moore (15), confirmed the earlier conclusions. DaCruz (2) found a very beautiful series of figures in Lilium tenuifolium. In the meantime the "parasynaptists" were writing another story. But any one acquainted with the cytology of the higher plants knows that there are no two normal types of reduction as represented by "telosynaptists" and "parasynaptists." It is a matter of divergent psychology or rather cytological cults or sects. But as stated in the beginning, in the higher plants at least, when the reduction is normal, there is both telosynapsis and a real parasynapsis. There are no two types in Lilium for example; the one group of priests or the other is worshiping a false god. According to the Morgan scheme of crossing over, a very definite telosynapsis is demanded if the scheme is to work; for in the following parasynapsis the corresponding parts of the chromosomes must always be in juxtaposition. If the chromosomes are differentiated as to the two ends such a definite mode of telosynapsis may normally take place. But such a method of crossing over as proposed by the Morgan school of geneticists appears too impossible to be taken seriously at the present time. Crossing over can be explained on entirely different assumptions which agree much better with the cytological evidence.

In case of incomplete sexualization of the synaptic mates, parasynapsis may be absent or nearly so. This appears to be the case in the parthenogenetic diploid Leontodon (Taraxacum) as reported by Sears (14). Sears has described under the term "Ameiosis" a process in which the univalents are slow in pairing. "Synaptic pairing is end to end but takes place so slowly that spindle fibers become attached to each of the halves of each univalent instead of the univalents as a whole. In consequence the pairs come to metaphase thirteen in number, but with components still end to end and transversely oriented. . . . The division is qualitative, if ordinary canons be right." Here it is evident that chromosomes in synapsis may begin to lose their primary sexual states before synapsis is complete. In extreme cases synapsis might become so intense and be so prolonged that non-disjunction would result.

That partial loss of the property of sexualization of the chromosomes in reduction may be an important cause in the increase of chromosome numbers is strongly indicated by the discoveries of Longley and Darrow (5) in raspberries. They found that all the raspberries studied by them can be separated into two groups; those with seven haploid chromosomes and those with more than seven. Furthermore, they found that the typical species with seven haploid chromosomes have their somatic univalents pairing very promptly in the prophase of the first reduction division and that these bivalent chromosomes divide regularly and promptly in both the first and second divisions. Sometimes however, in rare cases, there was a little tardiness in pairing of univalent chromosomes, or occasionally a single chromosome lagged behind its associates in reaching the pole. They also found that the polyploid raspberries showed characteristic irregularities in the distribution of their chromosomes during meiosis. In these, prompt pairing of the chromosomes in reduction was absent. There were irregular distributions of the chromosomes, some of which lagged on the spindle and were extruded from the daughter nuclei. The authors believe that such behavior indicates a hybrid origin. There is probably both specific incompatibility and imperfect sexualization due to the hybrid condition of the nuclei.

There is probably no question but that incomplete sexualization of any set or of any complete complement of chromosomes,

leading to incomplete synapsis is one of the several causes of the origin of polyploid sets and complements of chromosomes.

Whether there is a partial loss of the synaptic property in certain Oenothera lamarckiana mutants which might modify the later part of the process of synaptic union and thus account for the slight discrepancy in the reduction as reported by Gates on the one hand and by Miss McAvoy for OE. biennis and Fuchsia on the other is a question that only further, careful cytological studies can answer.

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