Studies of Mitosis and Meiosis in Comparison

VI. The meiosis, its relation to mitosis

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Introduction

DARLINGTON (1932) says: "Now meiosis has always been recognized as a form—a complicated form—of mitosis, since like mitosis, it effects the separation to pairs of daughter-nuclei of longitudinally split halves of chromosomes. The immediate problem of meiosis is therefore the problem of how it is related to mitosis and how it can have been derived from it". He put forward the well-known cytological theory of meiosis, the precocity theory, and has interpreted how it can have been derived from it. The problem is, however, one wrapped in mystery and working hypotheses from various points of view seem necessary for the investigation into the whole problem. In the comparative investigations of mitosis and meiosis (especially KUWADA, 1940; KUWADA and NAKAMURA, 1941) which were supported by the Scientific Research Expenditure of the Department of Education, some form of hypothesis was suggested and here this is presented in a brief form.

I. General Description of Meiosis in Comparison with Mitosis

It is convenient first to describe the essential feature of mitosis. The observation of *Tradescantia* staminate hairs in water medium (KUWADA and NAKAMURA, 1941) seems to show that there is a preparatory stage

(a) immediately preceding the beginning of mitosis. In this stage, in the water medium, the nucleus shows now a diffuse and now an aggregate structure, changing from one to the other from time to time, indicating that there take place in this period changes in water relation in the nucleus. In the very beginning of mitosis interchromosomal spaces become visible, and consequently in the case of nuclei of elongated shapes the general straight arrangement becomes conspicuous, probably owing to the contraction of each chromosome—the contraction stage (b). In the medium of liquid paraffin the change in the preparatory stage is not remarkable as in the water medium. This result of observation with liquid paraffin may indicate that the change visible in this stage in the water medium is simply an effect of the water used as medium, but in the paraffin medium also the very beginning of mitosis is generally characterized by the twisted configuration (dehydration or contracted configuration, KUWADA and NAKAMURA, 1940) and the straight arrangement, of the chromonema threads. Then the nucleus becomes hydrated and the water comes to occupy first the interchromosomal spaces, so that the latter are rendered more conspicuous. During this period, the chromatids (cf. KUWADA and NAKAMURA, 1941) are also hydrated, and as a result the spiral configuration of the chromonemata becomes clearly visible—the spiral stage or the hydration stage (c). The nuclear hydration goes further, and in the cooperation of this hydration with the respiralization which is observed in the spiral stage (AISIMA, 1941), the old spirals become drawn out, and a diffuse stage comes to appear again. In this stage, the general appearance of the nucleus very much resembles that of the resting nucleus of diffuse structure, excepting that the nuclear threads are much thicker than in the latter. This stage (d) may be called the first diffuse stage, since the second diffuse stage may occur in a later stage (e), though this is of an abnormal occurrence in mitosis. In the e stage when the old spirals have almost completely been drawn out, the new spirals are usually not visible in the living state and the spiral structure of the chromosomes is generally obscure, but in water medium it often becomes visible as a result of abnormal hydration. If the nucleus is of an elongated form, the general straight arrangement of chromosomes is very conspicuous in this stage as in the spiral stage. In the next stage (f), the chromosomes are much thicker than in the foregoing stages, and in this stage the chromosome split is first visible in the living state. At this stage the polar caps are developed, and the nuclear contraction takes place which apparently corresponds to the “third contraction” in meiosis.

In the f stage (in prophase) and in anaphase, the general appearance of the chromosomes is alike, and in anaphase the longitudinal split is visible in the chromosomes, which corresponds to the “tertiary split” in

meiosis. This split is said by some authors to be visible in fixed material in the late prophase. This fact is significant when meiosis is compared with mitosis.

In the beginning of telophase a third contraction is observed, the tassement polaire. Then the telophasic groups of chromosomes become hydrated and nuclei are reconstructed. In this late telophase two chromatids are clearly observed in each chromosome, but later each chromosome territory becomes indistinguishable and the nuclei come to present a diffuse structure.

In meiosis too, nearly the same series of chromosome changes can follow one after another with the same sequence. The pre-leptotene stage is subjected to some variations, but this seems to be a question of degree. Namely, the chromosome contraction is stronger in some cases and weaker in others, indicating that in meiosis the nucleus is more sensitive to the change in water-relation than in mitosis. This stage is followed by the "unravelling stage" (*c*) to reach the leptotene. In leptotene, the spirals are drawn out, at least to some extent, and the nucleus shows a diffuse structure as in the *d* stage in mitosis. One thing which appears in the early prophase of meiosis to differ from mitosis is the difference in the stage at which the respiralization takes place. While in mitosis it has taken place already in the *c* stage (AISIMA, 1941), it is generally considered in meiosis to be postponed to a later stage. The earliest stage in meiosis at which the new spirals have been observed is the pachytene (SINKE, 1934). In meiosis, therefore, the respiralization is probably to take place at a stage that immediately precedes the pachytene. The *d* stage in mitosis is the stage that follows the respiralization as pachytene, and at the same time the stage that follows the drawing-out of the spirals as leptotene. If the respiralization and the drawing-out occur in meiosis in successive order, the stages from leptotene to pachytene will then roughly be comparable to the *d* stage in mitosis. The *d* stage in mitosis is, therefore, regarded as the stage at which a change takes place in meiosis which gives rise to its characteristic phenomenon, the chromosome pairing.

In meiosis, the so-called "diffuse stage" occurs in diplotene, and in mitosis such can occur in the *e* stage (KUWADA and NAKAMURA, 1941). The two stages, the diplotene and the *e* stage, are therefore, probably comparable, the difference between meiosis and mitosis being only in the fact that in the former the diffusion takes place as a normal process while in the latter it does only as an abnormal one, indicating here also that in meiosis the nucleus is more sensitive to the change in water relation than in mitosis (KUWADA and NAKAMURA, 1941). In meiosis, at the end of diakinesis a nuclear contraction takes place, and in mitosis it takes place at the end of the *f* stage. This contraction may signify simply

something connected with the formation of polar caps¹, but the two stages at which it occurs immediately preceding the process of chromosome separation may probably be compared. The meiotic prophase is thus comparable to the mitotic prophase, or we may say that the process that takes place in the mitotic prophase takes place also in the meiotic prophase.

In higher plants the mitotic anaphase and telophase correspond to the anaphase and telophase of the second division in meiosis respectively and, therefore, the stages from the first metaphase to the second metaphase may be taken as comparable to the mitotic metaphase. The "tertiary split" has been observed in diakinesis (HUSKINS and SMITH, 1935), I anaphase (KATO and IWATA, 1935; cf. KUWADA, 1939) and interkinesis (SINKE, 1934), and the corresponding split in the late prophase or metaphase in mitosis (KAUFMANN, 1926; SHARP, 1929). In meiosis, therefore, all the stages in mitosis can be followed with the same sequence. If in meiosis the chromosome pairing and the disjunction phenomenon are disregarded, the meiosis would be essentially a mitosis.

II. Meiosis as a Double Division Cycle and a Possible Process of its Occurrence

In meiosis, while the mitotic process goes on, the chromosome pairing begins to take place in amphitene at which the nuclear contents or threads are very liable to contraction (synizesis) or to some definite orientation (bouquet, cf. HIRAOKA, 1941). The pairing is completed in pachytene. In diplotene, the chromosome split becomes visible and at the same time the chiasmata also, which have been formed between the paired chromosomes. In most cases, the diakinesis is characterized by the formation of major spirals that may indicate a strong contraction or a change in water-relation of the chromosomes and a change into the twisted or dehydration configuration, or a lengthening, of the minor spirals (cf. WILSON and HUSKINS, 1939). The chiasmata may be terminalized before metaphase, since the spirals are covered with a matrix sheath of smooth surface, but some of them may remain at metaphase. The major spirals may remain as such through almost all later stages of meiosis, but may have completely been drawn out before the late prophase of the second division. These characteristic features make the meiosis appear very much different from the mitosis.

Another characteristic feature of meiosis as compared with mitosis is the existence of an additional chromosome separation mechanism or nuclear division. While in mitosis there takes place only one nuclear division in one mitotic cycle, in meiosis two nuclear divisions take place in its cycle in successive order with a pause called interkinesis between

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¹ In meiosis the two polar caps are continuous to form a hollow sphere.

them. One division is the chromosome separation of mitotic nature and the other is the disjunction of the paired chromosomes.

The chromosome pairing and the disjunction form the reduction division. The meiosis, therefore, consists of two division processes, the mitosis and the reduction division, and they both go parallel with each other, hence the meiosis is a double division taking place in one mitotic cycle.

A suggestion may be made as to the possible process of occurrence of the double division in one mitotic cycle, as follows:—Under a certain condition, the homologous chromosomes were paired in early prophase of mitosis, and as a consequence a leisureliness in mitotic development of chromosomes was caused. Thus the normal chromosome separation process (the first division) was too early for the divided chromosomes, but in time for the paired chromosomes. An additional separation process (the second division) was then introduced for the divided chromosomes to complete the division (KUWADA, 1940).

In the modern forms, the stages of leptotene and synizetic contraction and also an apparent diakinesis, all connected in various manners with the change in water-relation, can occur in the absence of chromosome pairing, and the two successive divisions take place as in the normal case of meiosis (HEUN, 1939; ROSENBERG, 1917). This fact indicates that these stages and the two successive division, or double division characters of meiosis, occur in no direct connection with the chromosome pairing, but are fixed as the characters of meiosis which may originally have occurred as suggested above, to appear irrespective of whether the chromosome pairing takes place or not. The occurrence of meiosis is, therefore, subject to a certain condition which brings these characters of double division into development. A mere chromosome pairing alone cannot alter the mitotic nature of nuclear division into the meiotic. The “scheinbare Geminibildung” (the somatic syndesis) may occur, but the nuclear division is still a mitosis in the essential feature (*Ricinus*, NĚMEC, 1910; *Culex*, cited from AGAR, 1920).

III. The Origin of the Interkinesis Nucleus

The possible process of occurrence of meiosis which we have suggested postulates that in the primitive type of meiosis the chromosomes in interkinesis are as compact in form and texture as in metaphase and anaphase, and are free from the nuclear vesicle as in these stages, and that the cases where the nuclear vesicle is formed are advanced types. The case of this primitive type is known to occur generally in animal oögenesis, and in some animals in spermatogenesis. In plants, TUAN (1931) has observed this case in *Gasteria* as an abnormal case—probably a reversion. In the advanced type, there are variations in regard to the chromosome structure. These cases have been observed in plants. In plants the

chromosomes are mostly of double coiled structure in the first division. In the simplest case, this structure is maintained in the interkinesis, and consequently in all later stages too. This case is found in *Sagittaria*, *Fritillaria* and other plants, and may be called the *Sagittaria* type. In the second case, the major spirals are drawn out, but the minor spirals remain intact. This case is found in *Lilium*, and may be called the *Lilium* type, though in this plant the change in chromosome structure is subject to some variation. The third case is the *Tradescantia* type found in *Tradescantia* and some other plants, and in this type not only the major spirals but also the minor spirals undergo a change and the general structure of the nucleus appears like a resting nucleus (see (KUWADA, 1939, p. 232)). This is the deepest one of the primary changes which we can imagine, and no other type is to be expected to occur, so far as the primary changes are concerned.

In short, in the interkinesis all possible cases of variation in texture and structure of chromosomes from the chromosome as such to the structure as a nucleus in the resting stage are found. These variations in the interkinesis show that in this stage the chromosome as the form in the dividing stage tends to take the form in the resting stage, or in other words that the interkinesis as one of the dividing stages is developing towards becoming a resting stage. There are other evidences to indicate the existence of this tendency in interkinesis.

In mitosis, two successive divisions are characterized by the formation of a resting (interphase) nucleus between them. In meiosis too, this is generally the case, but it appears to be only superficially so, because in the original type of meiosis it is to be assumed that the mitosis which takes place parallel with the reduction division undergoes the process of chromosome separation first in the second division, hence after a "resting stage" at interkinesis. It seems, then, that the interkinesis is a stage comparable to the diffuse stage in prophase. We have, however, facts to show that there are in interkinesis both cases signifying a superficial and the true rest.

In the normal mitosis, katachromasis takes place in the telophase, and the division cycle ends with it. Experimentally it has been shown that a similar phenomenon can take place at any stage of prophase also (KUWADA and NAKAMURA, 1941). In these cases all later stages are obliterated, and accordingly such a mitosis may be called an abbreviated mitosis. In this abbreviated mitosis the process of mitosis is abbreviated, but the cycle has ended. Before the cell is activated for a new mitosis, no mitotic process can take place. If the interkinesis is only superficially a resting stage and is in reality nothing more than a mere diffuse stage occurring in the division cycle, both the first and second divisions which are in this case division stages in one and the same cycle will be obliterated.

ed when an abbreviation (restitution) occurs at the first prophase. In this case the result is naturally the formation of monads. This case has been shown by BARBER (1940) in *Fritillaria* in a heating experiment. If, on the other hand, the interkinesis demarcates between two division cycles as does the interphase, the result will be the formation of dyads, because in this case the second division can start independently of the restitution in the first division. This case has been observed by ROSENBERG (1927) in the case of prophasic restitution in *Hieracium* as in *Fritillaria* observed by BARBER. The two cases of interkinesis exist, therefore.

Thus in the *Hieracium* meiosis, the cycle of the first division ends with the interkinesis, or we may say that the cycle of meiotic mitosis has been divided into two division cycles each with a half mitotic process, of which the first cycle is comparable to an "innere Teilung" and the second cycle to the somatic reduction division (comp. Sect. VII). In *Fritillaria*, on the other hand, the mitosis keeps up its integrity as one division cycle. The *Fritillaria* interkinesis may thus be regarded as a primitive type as compared with the *Hieracium* interkinesis, as is the *Sagittaria* type of interkinesis to the *Lilium* or *Tradescantia* type in respect to nuclear structure.

The tendency toward the interphase in mitosis of the interkinesis which is regarded as originally a mere period of pause in the dividing stage is, therefore, shown not only by the formation and the change in structure, of the nucleus, but also by the change in nature of chromosome diffusion as indicated by the result of restitution. It must be here noted, however, that the apparent parallelism in *Fritillaria* (*Sagittaria* type) and *Hieracium* (probably *Lilium* type) interkinesis shown between the changes in nuclear structure and in the nature of diffusion whether temporary or division-terminating may not necessarily exist in all cases, because in the case of true katachromasis in mitosis too the change in structure and texture of chromosomes may be in a similar degree to the case of *Fritillaria* interkinesis, as inferable from the structure of *Triton* or *Triturus* erythrocyte nucleus (KUWADA and NAKAMURA, 1941). In *Triton* erythrocytes the nuclear threads are as thick as the anaphasic chromosomes (SEIFRIZ, 1930; cf. KUWADA, 1939) and in *Triturus* erythrocytes the nuclear structure can artificially be made much finer (SINKE, 1941). We may probably say that even the type of meiosis in which the interkinesis shows no chromosome change in texture and structure, may be an advanced type. It seems likely that the two progressive changes toward the resting stage have occurred quite independently.

How then was a nuclear vesicle formation possible in the interkinesis? Normally, chromosomes undergo the katachromatic or division-terminating diffusion in telophase. In mitosis, in prophase also they can undergo an untimely diffusion of this nature, if they are subjected to a certain

condition, and in anaphase too, if here moreover the chromosome separation process is suspended (KUWADA and NAKAMURA, 1941). In metaphase an experimental demonstration of this seems difficult, but in view of the fact that it is successful in all the other stages of mitosis, it seems likely that a certain appropriate condition will be suitable for the metaphase chromosomes too, probably provided the chromosome separation process is here also suspended as in the case of anaphase.

The interkinesis is a stage comparable to a part of the metaphase in mitosis, but in this stage the chromosome separation mechanism ceases to exist as in the mitotic telophase. The chromosomes in this stage will, therefore, be able to undergo a diffusion, if a condition arises which causes it. The nature of this diffusion may be division-terminating, but may also be a temporary one, because it has been demonstrated that in mitosis a temporary chromosome diffusion may take place during the course of prophase (KUWADA and NAKAMURA, 1941). As natural phenomenon this kind of diffusion occurs in animal meiosis, especially in oögenesis, and is known as the diffuse stage. A demonstration by the direct experimental method of this chromosome diffusion to bring it about at metaphase is hardly possible, because it is probably a necessary condition as suggested by the abbreviated mitosis experimentally induced, that here also the separation mechanism in work is repressed, and because from this experimentally induced repression an untimely diffusion of the division-terminating nature may result. In the case of interkinesis where this mechanism is absent, however, the inference seems possible that a chromosome diffusion may occur in this stage, which does not interrupt the further process of division.

According to the condition causing the diffusion, the change in texture and structure of chromosomes may vary in degree, as shown by the types of interkinesis occurring in various plants such as *Sagittaria*, *Lilium* and *Tradescantia*. According to IWATA (1940), in *Trillium*, in which the structure of the interkinesis nucleus is nearly of the *Sagittaria* type, the plants sent from the Hokkaido to Kyoto and transplanted in pots showed a structure very much similar to the *Tradescantia* type. The structure of the erythrocyte nucleus in *Triton* and *Triturus* may be seen as affording evidence to admit the assumption that in the normal telophasic karyokinesis in mitosis too, such a variation as seen in the three types of interkinesis, may exist.

In conclusion, we may say that the interkinesis nucleus has originated in a mere chromosome diffusion which is to take place in the course of mitosis, but that in some (or many) cases it has been transformed to signify the division ending.

IV. Pre-reduction Type of Meiosis

In the pre-reduction type the reduction division takes place in the first division, ending with it, and the mitotic division ends with the second division, occupying the whole cycle of meiosis. This is the type which we have assumed as the original one. In this type there are found all possible cases of interkinesis with nuclei of different structures and the chromosome diffusion of different natures, temporary and division-terminating. In the extreme case the cycle of mitosis in the meiosis is divided by the interkinesis into two division cycles which represent each a different part of the original cycle with a complete mitotic process. In the pre-reduction type of meiosis, therefore, it is shown that the meiosis is tending both in structure of chromosomes and in nature of chromosome diffusion in the interkinesis toward becoming two independent division cycles. In the case of post-reduction type this tendency is extended so as to alter the fundamental construction of meiosis as double division.

V. Post-reduction Type of Meiosis

In the post-reduction type, the reduction division takes place in the second division. WILSON (1925) has concluded "that pre-reduction division probably constitutes the general rule, but that changes in the order may readily occur" He states further: "In such cases both divisions may be of mixed type, and the old distinction between the reduction- and the equational-division can only apply to the tetrads considered individually" In plant hybrids, it has been shown that all unpaired chromosomes can behave after the post-reduction type, though in this case the disjunction division is naturally irregular owing to the fact that the chromosomes are unpaired.

In the post-reduction type the mitotic division ends in the first division, hence the second division is free from the process of mitosis. It is only occupied by the later part of the process of reduction division and is of a single division process. In this case, therefore, the whole meiosis is a cycle of two divisions overlapping rather than a double division. Thus a shifting is recognizable in timing relation between the two divisions toward their becoming successive independent single divisions. The post-reduction type of meiosis may, therefore, be regarded as an "advanced" type.

If the first division was originally the separation division of mitosis, but came to work as the disjunction division as a result of the leisureliness of chromosome development owing to pairing, the mitotic division in the case of post-reduction type would be regarded as a case of reversion to normal mitosis. From this point of view, it is seen that in the

post-reduction type the meiosis is regulated to have the original, i.e. the normal, type of mitosis as one of the components of its double form. We have seen that in the pre-reduction type there is a strong tendency of one cycle of double division toward becoming two division cycles, and now see that in the post-reduction type this tendency is more definitely shown by the reversion resulting in the partial separation of the two divisions in double form.

VI. Transformation of Meiosis into Mitosis

If in the case of post-reduction type the reduction division, i.e. the chromosome pairing and the disjunction division (the second division in this case), is obliterated, the mitotic division will remain still to exist. In this case the product is naturally dyads. This division is a normal mitosis in the essential feature, because in the post-reduction type the mitotic division has completed before interkinesis, or in other words, here it takes place in the normal manner without its course being intervened by a nuclear stage. This type of transformation of meiosis into mitosis may be called the transformation by reversion, and may be regarded as being represented by the case of an abnormal meiosis called by GUSTAFSSON the pseudo-homotype division and by those cases of haploids where the chromosomes form a metaphase plate in the first division, in *Matthiola* haploid in most cases (LESLEY and FROST, 1928), in *Datura* (BELLING and BLAKESLEE, 1927), *Nicotiana* (KOSTOFF, 1929) and other true haploids in some few cases. It is very significant that in haploids where the chromosomes are unpaired the second division is commonly omitted when they have already divided in the first division (the pseudo-homotype division). This seems to indicate that it is because the disjunction has not taken place that in the post-reduction type the second division still exists in the condition that the meiotic mitosis is of the reversion type. In the mixed type of meiosis in hybrids with unpaired chromosomes and in such a type in haploids also the second division exists for the same reason. It may also be regarded that in the post-reduction type of meiosis in haploids the second division is simply omitted, as proving the correctness of the assumption that the meiosis is originally a single cycle of mitosis, and also that the second chromosome separation process is an additional one.

If the shifting in timing relation between the mitotic and reduction divisions goes further than is in the case of post-reduction type, and so far that the two divisions are no longer overlapping one upon the other, but a pair of successive divisions taking place directly one after the other, the double division cycle disappears, and hence the divisions are no longer meiosis. The chromosome pairing does not, therefore, take place in this case. The two divisions are each mitosis. Not only the first divi-

sion, but also the second division can perform the normal mitosis, because the chromosome splitting as the antecedent of chromosome division (the "tertiary split") has occurred in the preceding division (the first division) as in normal mitosis. A normal mitosis can follow the second division which is now mitosis, because an inducement of chromosome splitting in the absence of chromosome pairing is indicated by the unpaired chromosomes in hybrids to be possible. While in *Triticum* hybrids the tertiary split remains undivided in the second division, it divides in *Caninae* roses. The latter case probably indicates that in this case the new chromosome splitting has occurred, which in *Triticum* hybrids has not. The actual occurrence of this type of transformation is suggested by the *Pygaera* hybrids (FEDERLEY, 1913), and actual cases are represented by an apogamous haploid fern, *Pteris cretica* var. *albo-lineata* (HEUN, 1939) and by *Lomentaria rosea* in European waters (SVEDELIUS, 1937)—the transformation by progression. It is noted, however, that in the transformed mitoses the tetrad division nature is retained and some characteristic features of double division, such as the synizetic contraction and the diakinesis chromosome contraction, may also be retained, indicating that the meiosis is a sporophytic character with long history of phylogenetic development.

We have the third type of transformation (the case of restitution-nucleus formation in *Hieracium* observed by ROSENBERG). This is the case of transformation by obliteration of the reduction division in the meiosis of the pre-reduction type, hence the reduction division that takes place in the first division. In this case the obliteration of the reduction division is effectuated only by the formation of restitution nucleus, i.e. the nuclear division abbreviation, and consequently the transformation is possible only in the case of meiosis divided into two division cycles, or speaking in respect to the mitosis of meiosis, only in the "advanced type" in which its whole mitotic process is divided into two division cycles. In this case the transformation is not into a real cycle of mitosis, but an apparent cycle consisting of two division cycles each of a half mitotic process, so to speak. This case is a simple obliteration of the reduction division by restitution from the original type of meiosis, and may be called the transformation by reduction. It is significant that while in the case of transformation by reversion the extra division is obliterated simply as a natural consequence of the failure of chromosome pairing, it can be obliterated in the case of transformation by reduction only when restitution occurs.

The transformation of meiosis into the mitosis of a complete cycle is thus possible only in the case of the post-reduction type or in its extreme case. A direct transformation from the pre-reduction type cannot be made into the mitosis of complete cycle. The post-reduction type is,

therefore, regarded as a necessary step toward the true transformation of meiosis into mitosis. This chain of transformation from the pre-reduction type to the post-reduction type, and then to mitosis, is seen in the behaviour of unpaired chromosomes in *Drosera* hybrid (ROSENBERG, 1909), *Triticum* hybrids (KIHARA, 1924) and *Caninae* roses (TÄCKHOLM, 1922), and also in different cases of true haploids (*Datura*, BELLING and BLAKESLEE, 1927; *Capsicum*, NISHIYAMA, 1940; *Pteris*, HEUN, 1939).

The meiosis is originally a mitosis, and hence can regress to mitosis. It is a cycle of double division, and in some or the majority of cases this cycle has developed into two division cycles. These cycles can become two independent cycles, and when this is realized, they both are single cycles and necessarily mitotic. The meiosis can progress to two cycles of mitosis as well as regress to one cycle of mitosis.

VII. A Comparison of Reduction Division in Meiosis and the Somatic Reduction Division

The reduction division in meiosis is a new type of division originating in the pairing of homologous chromosomes. It exists only with mitosis in a double form. When it becomes an independent division, it can no longer be the reduction division, it has been transformed into a mitosis. The reduction division in meiosis is, therefore, not an independent division, but a type of division which can progress to mitosis.

The somatic reduction division is, on the other hand, a nuclear division which is reduced from mitosis. Mitosis consists of two fundamental phenomena, chromosome division and chromosome separation. If the chromosome separation ceases to take place, the mitosis is an endomitosis, and if the chromosome division ceases to occur, it is the somatic reduction division. The somatic reduction division is, therefore, a teratological mitosis, so to speak, in which one of the two fundamental processes of mitosis is lacking. This type of abnormal mitosis can occur only in connection with the other type of abnormal mitosis, the endmitosis or an "innere Teilung". The division is peculiar to certain tissues with definite functions, and does not occur in the meristem of an undifferentiated condition.

Meiosis is a physiological phenomenon connected with reproduction, and hence the mechanism of meiosis must be one that keeps the whole system of regular chromosome distribution in organisms from hindrance, and any phenomenon which is of a teratological nature must not be included in it.

The physiological mechanism for regular chromosome distribution is the mitosis, and the chromosome splitting takes place in the nuclear division (mitosis) at least directly preceding one in which the divided

halves are separated. The complete chromosome cycle consists, therefore, of a pair of mitosis. If the chromosome splitting takes place in the mitosis two cycles prior to separation, it will consist of three consecutive mitotic cycles. In each mitosis, however, both chromosome splitting and separation take place and, therefore, all mitoses must be followed and also preceded by a mitosis. The meiosis is preceded and followed by mitosis and, therefore, it must also be a mitosis, in order that the whole system of regular chromosome distribution may keep good; and yet chromatin reduction must take place in it. This requirement is fulfilled by the addition of a new type of division, the reduction division, into mitosis, thus the original single cycle of division being made double. Here the somatic type of reduction division cannot take part, because it is an abnormal type of mitosis reduced from the normal mitosis and it would not be supposed that two mitoses can exist in a double form. A mere pairing of homologous chromosomes can, on the other hand, take place in the course of mitosis, and this caused a mitosis to be a meiosis. The two reduction divisions are of quite different origin.

They are also of different nature, since the meiotic reduction division is a new mechanism of compensating the chromosome doubling due to the nuclear fusion in fertilization, while the somatic reduction division is simply one which fills up the gap of the process left unperformed by the endomitosis or "innere Teilung" that precedes it and thus makes the whole process of mitosis complete. In the *Hieracium* type of meiosis, the first division is a double division consisting of the meiotic reduction division and an "innere Teilung" of mitotic nature, and the second division is a somatic reduction division in nature.

The somatic reduction division can exist as a single cycle, because it is originally a mitosis which exists as an only mechanism of regular chromosome distribution. But this is not the case with the meiotic reduction division, because it has arisen independently from mitosis. It can exist only in a double form with mitosis. The "monokinetic meiosis" (LEVAN, 1935) is not a single reduction division, but an abbreviated double division resulting from the restitution occurring before the second division (separation), hence the resulting nuclei contain unreduced number of chromosomes. It is noted here that the restitution (mitotic abbreviation) can occur even in the beginning of prophase (KUWADA and NAKAMURA, 1941).

VIII. The Question of the Third Division

DARLINGTON (1931) says: "It is doubtful whether a third division (as in the Ascomycetes) can be an essential part of meiosis" The conclusion on meiosis which we have reached is that the meiosis may appear to be two division cycles, but is originally one which takes place in one

mitotic cycle. This conclusion postulates that the third division is merely the next mitosis to that which has been transformed into meiosis.

This division in Ascomycetes was taken by FRASER (1908) as a reduction division that follows the ordinary meiotic divisions, and called brachymeiosis. This opinion was supported by investigators such as TANDY (1927), GWYNNE-VAUGHAN (1937) and GWYNNE-VAUGHAN and WILLIAMSON (1931, 1932, 1934). In *Pyronema* (TANDY; GWYNNE-VAUGHAN and WILLIAMSON, 1931), *Morchella* (WAKAYAMA, 1930), *Lachnea* (GWYNNE-VAUGHAN, 1937) and other ascomycetes studied by these authors, the chromosomes are very small spherical bodies, and a judgement on the question from the cytological point of view is very difficult, if here the chromosome number which under various circumstances may be subject to variation is not considered. In *Humaria* (FRASER), on the other hand, the chromosomes being very large as those of higher plants, it is possible to draw some inference. The drawings of FRASER show that the chromosomes are in shape heterotypic (major spiral type) in the first division, homotypic (minor spiral type in this case) in the second division, and of the somatic type in the third division. The interkinesis nucleus (between the first and second divisions) shows that it is of a type regardable as belonging to the *Lilium* type. The inference is, therefore, that in *Humaria* studied by FRASER the first two divisions are the meiotic divisions and the third division a mitosis.

FRASER and most of those who hold the view that the third division is a reduction division believe that the nuclear fusion takes place twice, one in the ascogonium and the other in the young ascus, and they assume that the second reduction division in the third division is a compensating mechanism to the chromosome multiplication due to the extra nuclear fusion. In *Humaria*, a nuclear fusion has occasionally been observed by FRASER to occur before and after the second division, and the fusion of the two spindles in the second division has also often been observed in higher plants. In all these cases no compensating reduction division has been observed. KARPECHENKO (1927) has observed an extra nuclear fusion in the course of the first division in meiosis, but no compensating reduction division at all. Chromosome number can be multiplied in diverse ways, but no single case is known where any regular reduction division other than the meiosis can occur as a compensating mechanism. It is most doubtful, therefore, that such a special type of reduction division as brachymeiosis exists, and consequently also that in Ascomycetes two nuclear fusions regularly occur.

Theoretically, the brachymeiosis cannot exist as an independent division, because in brachymeiosis it is implied that the separation of chromosome halves is suppressed. The comparison of meiosis with mitosis

in higher plants shows that the tertiary split in meiosis is an actual occurrence. In lower organisms the mitosis may differ from that in higher organisms in some points of minor importance such as, for instance, in the time of nuclear membrane dissolution (in anaphase in *Cossinodiscus*, IKARI, 1923, in a still later stage in Ascomycetes and the persistence throughout mitosis in Protista) and in the time of chromosome shortening (in anaphase in *Aggregata eberthi* and *Collozoum inerme*, Fig. 27 and 28, BĚLAŘ, 1928), but it is highly improbable that there is a difference between these organisms in such a fundamental point as the time at which the chromosome splitting occurs. In the third division, therefore, the split halves in the meiosis should grow into chromosomes and be ready for separation. If this division is a reduction division, a fourth division must immediately follow it to separate these chromosomes¹) As a physiological process, therefore, a single reduction division cannot exist. An only case of the third division which seems apparently possible as a second reduction division not being followed by a fourth division is that case where it forms a part of meiosis which consists of three divisions. Namely:—The first reduction was accomplished in the first division, but the chromosome pairing for the second reduction took place in the second division in which the divided chromosomes were to be separated, and as a necessary consequence the third chromosome separation process was introduced. In this supposed type of meiosis four homologous chromosomes are to associate in pairs at two different times. If the apparent reduction in chromosome number in the second division in *Pyronema confluens* studied by GWYNNE-VAUGHAN and WILLIAMSON (1931) is due to chromosome pairing, this case of *Pyronema* can be taken as representing this type of meiosis, but the meiosis in tetraploids in higher plants shows that the homologous chromosomes associate at a time into a quadruplet or in groups of variable numbers of chromosomes. In this supposed type of meiosis, moreover, the three divisions should take place in immediate succession, but according to FRASER, "the four nuclei of the ascus now pass into a stage of rest which, as it was frequently encountered, probably lasts for some time" It is therefore hardly assumable that such a peculiar type of meiosis should exist. We must then conclude that there can exist no third division which forms part of meiosis. As a physiological process, the third division can neither be part of meiosis nor the brachymeiosis.

There are, on the other hand, results of observations which conform with the general rule that the reduction division takes place only in the meiotic divisions. According to MOREAU and MOREAU (1931), COLSON (1934), BEATUS (1939) and others, the regular nuclear fusion in Asco-

¹ The fourth division may take place in the spores, but probably with a pause after the third division.

mycetes takes place once only in the young ascus, and according to MOREAU and MOREAU, COLSON, MATSUURA and GONDÔ (1935) and BEATUS the third division is a mitosis. The whole problem of the ascospore formation has been elucidated especially clearly in the case studied by MATSUURA and GONDÔ where an unequal pair of chromosomes exists. The experimental investigation by LINDEGREN (1932) also shows that the third division must be a mitosis.

There may be in the Ascomycetes some complication leading to confusion in regard to chromosome number, but the question seems to be connected with something independent of the nature of the third division whether it is primarily reductional or equational.

As to the probable cause of the apparent reduction in chromosome number in the third division, WAKAYAMA (1930) has made two alternative assumptions: "1) that the chromosomes in the third division constitute so-called 'Sammelchromosomen', pairing in 6 complexes, 2) the results of poor fixation". When we look over the results of GWYNNE-VAUGHAN and WILLIAMSON and WAKAYAMA, it seems that even if the apparent reduction is only a result of "poor" fixation there is an underlying cause which gives rise to it whenever fixation is poor, and the first assumption seems to be most significant among others which might be suggested. Under this assumption, in *Pyronema confluens* studied by GWYNNE-VAUGHAN and WILLIAMSON (1931)¹ the chromosomes are to constitute the "Sammelchromosomen" first in the second division, and *Ascobolus*, *Ascophanus* (GWYNNE-VAUGHAN and WILLIAMSON, 1932, 1934) and *Morchella* (WAKAYAMA, 1930) in the third division. In *Lymantria monacha*², four separate chromosomes in the spermatogonia turn into a large "Sammelchromosom" in the first division in spermatogenesis, and in the interkinesis in the oögenesis, and they are separate chromosomes again after karyogamy. In *Ascaris megalocephala* also, as is well known, after karyogamy, the chromosomes become separated in the ordinary somatic cells into a number of small chromosomes, while in another species of the same genus, *A. lumbricoides*, they do not. If we assume, therefore, that in some Ascomycetes "Sammelchromosomen" occur in both meiotic and haploid phases or in the latter phase, the puzzle will be solved. GWYNNE-VAUGHAN and WILLIAMSON have observed that in *Ascophanus Aurora* the chromosome number which is 4 in the second division is 2 in metaphase and 4 (in total) in anaphase in the third division.

If really the third division is the ordinary mitosis, the four nuclei

¹ According to CLAUSSEN (1912) and MOREAU (1931), in *Pyronema confluens* the third division is an ordinary mitosis and the chromosome number is 12 as in the second division, which is in the same species 6 according to GWYNNE-VAUGHAN and WILLIAMSON. It appears that in this case fixation is responsible for this difference in the two results, though a critical investigation is necessary.

² Cited from BĚLAŘ (1928).

which undergo this division should represent each a spore nucleus. The formation of the spore cells (primary spores) takes place, however, after the third division. In the Ascomycetes, therefore, the development of the spore cells is delayed. It is very interesting in this connection that opposite cases or cases where the developmental process of spores occurs precociously during meiosis are found in the megasporogenesis among angiosperms¹. The well known case is found in *Lilium*. In this case the embryosac development begins already in the first meiotic division, hence both meiotic divisions are the free nuclear division. As a consequence the four nuclei (spores) contribute to the formation of a gametophyte which in the normal type develops from a single spore.

In the normal type the formation and development of the spore occur in succession, but in abnormal types there may be a shifting in this timing relation. When development occurs precociously all the four nuclei or two of them contribute to the formation of a gametophyte, according to the degree of shifting, and when it occurs late after the third division each progeny cell from a spore develops into a gametophyte. A corre-

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¹ RUTGERS (1923) has made an interpretation on the morphological nature of angiospermous embryosacs with different developmental histories, which appears to harmonize two representative opinions of COULTER and ERNST on the problem. In this interpretation of RUTGERS, however, there seems to be some contradiction which seems to us to be chiefly due to the fact that he had laid too great a stress on the vacuolization as one distinguishing between the formation and development of embryosacs. To take up an instance, Type CC which he considers as a bisporic embryosac should logically be a tetrasporic, because there would be no reason, when one recognizes the polysporic nature of an embryosac, to suppose it to be bisporic which contains in the early stage of its development the four nuclei directly derived from the mother cell nucleus.

With ERNST, we should distinguish in the history of embryosac between its formation and development, but as a criterion neither the number of nuclear divisions nor the vacuolization in the embryosac can be taken. COULTER (1908) emphasizes that "it is absolutely necessary to trace the nuclear succession from mother cell to completed embryosac before any safe conclusion can be drawn as to the significance of the conditions observed within the sac." The meiotic divisions, a critical event in the life cycle, cannot be disregarded in the morphological treatment of embryosacs.

In the development of the megaspore into the embryosac there should take place a considerable change in the physiological conditions, and as a result the free nuclear division may occur in connection with a rapid growth of the cell. Here the vacuolization may take place in the cytoplasm, and this may be a criterion distinguishing the development from the formation of embryosac, but in the vacuolate condition of the cell both normal and free nuclear divisions can take place (SINNOTT and BLOTH, 1941). The criterion here in question is the free nuclear division rather than the vacuolization which is also less reliable as a microscopical criterion than the former. In short, in the abnormal types of embryosac the process of formation is overlapped by a precocious development, so that both meiotic divisions, the first and second, or the second one take place in the form of free nuclear division, and in these cases the embryosac is tetra- or bisporic, according to how deep the formation and development are overlapped one over the other. It would be interesting to note in this connection that in one of the two extreme types of fertilization in animals, "the later stages of maturation are overlapped by the earlier stage of fertilization" (WILSON, 1925).

sponding case is found in the development of fertilized eggs too, if the proembryonic divisions are the free nuclear division (*Pinus*, *Ephedra*, for instance). In the latter case the normal sporophytic development is regarded as postponed, because in this case the normal type of cell division giving rise to the ordinary tissue formation is delayed in its occurrence. In both gametophytic and sporophytic developments, therefore, the delay in the normal development results in the multiplication of individuals. In the multicellular organisms "cell division has become a feature of growth" (COULTER, 1914), but in the unicellular stage in the life cycle it often serves the purpose of cell division as the reproduction mechanism in unicellular organisms.

IX. The Origin of Meiosis

ALLEN (1937), re-examining the evolutionary problem of the alternation of generations, has put forward a view in which two methods of evolution are assumed—the duplication and the transfer. In this section we are going to discuss the question of what the meiosis originates in, but on this question the case of *Oedogonium* which ALLEN has taken as a critical case of diploid phase occurring by duplication is most suggestive.

In *Oedogonium* as a primitive type, the zygote undergoes the meiotic divisions in its germinating division. Each spore produced develops into an individual which is haploid and a duplication of the haploid parent. The investigation of MAINX which ALLEN has cited shows that under conditions unfavourable to the occurrence of meiosis the zygote can develop without undergoing meiosis into an individual of duplicated form with diploid chromosome constitution. If in this diploid individual the meiotic divisions take place in a certain period of its ontogenetic history, spores will be produced which develop each into a haploid individual producing gametes. The alternation of the diploid and haploid phases becomes then established. As actual examples that would be expected from an origin of this nature of alternation, *Ulva*, *Enteromorpha*, *Cladophora* and *Chaetomorpha* have been mentioned. The case of *Oedogonium* of MAINX is a result of response to special circumstances. "But if a mutation were to occur affecting the response of the zygote to external conditions a behaviour otherwise exceptional might become the rule," says ALLEN.

The evolutionary process of alternation is essentially the same in both cases of duplication and transfer, excepting that in the latter "the two generations are unlike ("antithetic") from the start."

What is of great significance in the theory postulated by ALLEN, in connection with the problem which we are here dealing with, is that in the first stage of evolutionary history of alternation the meiosis should have taken place in the first two divisions after the formation of the zygote.

This postulation suggests that there was some close connection between the gametic union and meiosis. In the primitive state of organisms where no sexuality exists, cell union is an abnormal phenomenon if it occurs, hence it follows that the original single condition of the cell must be restored in order that the normal life phenomena may be maintained. When sexuality was established, the cell union was required (cf. CULTER, 1914), but at the same time it should have also been required that the double condition arising from it be reduced to the single condition at an earliest opportunity. The mechanism of this reduction is the meiosis. The meiosis must have taken place as a necessary consequence of the gametic union.

In what substantial connection was then the meiosis with the gametic union? One of the essential features of meiosis is the chromosome pairing taking place during the process of mitosis which does not occur in the ordinary mitosis. The chromosome pairing is an attraction phenomenon as is the gametic union, and these two phenomena are connected by the nuclear fusion (karyogamy) which is also an attraction phenomenon, to form a series of events. In modern forms of organisms, no case is known where all these phenomena take place in immediate succession, but the nuclear fusion occurs directly following or preceding (as in Ascomycetes) one of the other two. The latter facts suggest, as also seen from MAINX' case of *Oedogonium*, that the three phenomena can take place in immediate succession, but are prevented from doing so by a certain internal condition developed in organisms, until another condition arises which rouses the attraction put in a dormant condition to activity. It is interesting in this connection that the two cases of nuclear fusion, i.e. the case where it directly follows the gametic union and that where it immediately precedes the meiosis (chromosome pairing) are connected with intermediate cases or cases of gonamery, such as those observed in *Pinus* or more clearly in some Copepoda (HAECKER, 1902), in the first division or in divisions in the first stages of development of fertilized eggs. It is here also interesting that in *Amoeba diploidea* the two nuclei in the gonamery condition fuse together first when two individuals come together to enclose themselves in a common cyst, and then when the fused or zygote nucleus undergoes a process of meiosis¹. The occurrence of events of the same nature in immediate succession suggests that these events are causally very closely connected². Probably, in the evolutionary history the start of meiosis lay in the moment of gametic union, but a condition caused a postponement of its realization as such.

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¹ Cited from AGAR, 1920.

² From this point of view, the investigation of fertilization seems to be significant in relation to the problem of chromosome pairing. Among gymnosperms, it has been described that in the fusion of the male nucleus with the female the former presses

Figs. 1-2. Egg nucleus in *Cycas revoluta* (quotations from IKENO, 1898). 1. Showing depression ("Empfängnishöhle"). Comp. IKENO, Taf. VIII, Fig. 42 a. 2. Showing a state of nuclear fusion. "Nun dringt der Spermakern immer tiefer in den Eikern hinein, bis schließlich sein ganzer Körper innerhalb des letzteren liegt und von ihm völlig umhüllt wird." In a, an "Ansammlung der durch Tinktionsmittel schmutzig und intensiv färbbaren Substanzmasse" (long stretched one in the photograph) which is observed "stets neben dem Spermakern" is seen in the immediate vicinity above the nuclei in fusion. Comp. IKENO, Taf. VIII, Fig. 44, tr. b. Highly magnified to show the granules (faintly stained) near the sperm nucleus.

If the depression of the egg nucleus is regardable as due to a local reduction of surface tension as the effect of an electric charge (BAYLISS, 1918), the two facts mentioned above may be regarded as phenomena of the same category, and as suggesting something fundamental lying in the complex mechanism of nuclear fusion in fertilization, and perhaps also of chromosome pairing (cf. MANTON, 1939).

inward the membrane of the latter. In *Cycas revoluta* this depression of the egg-nuclear membrane is observed before the nuclear fusion or even before the spermatozoid reaches the egg (IKENO, 1898), a phenomenon which seems to be due to a local change in surface tension of the nuclear membrane. An analogous case is found in the entrance cone in animal eggs. LILLIE (1919) has assumed that "the spermatozoon causes a local diminution of surface tension of the egg." In this case of the animal egg, the surrounding medium, being water, is naturally less viscous than the cytoplasm inside the cell, and consequently a local diminution of surface tension will cause a cone, but in the case of *Cycas* egg nucleus the cytoplasm appears to be much denser than the karyoplasm (Fig. 1), and would cause a depression. The phenomenon is protrusion in one case and depression in the other, but the primary cause seems to be common.

There is another phenomenon in fertilization in the egg in *Cycas*, which seems to be interesting in connection with the local diminution of surface tension of the egg. When the egg nucleus is entire in contour, hence it is in the stage before insemination, the nuclear contents are evenly distributed, but when the nucleus is depressed on the side toward the sperm entrance, "die dichte feinkörnige Substanz" becomes gathered in the depressed region (IKENO, 1898), reminding us of a cataphoresis which might here take place (Fig. 1). In the egg nucleus peculiar granules of somewhat irregular shapes and sizes are found, the nature of which has not been determined. These granules are also found near the depression when it is formed. In Fig. 2 "die dichte feinkörnige Substanz" and these granules are found surrounding the male nucleus in the process of fusion with the egg nucleus.

The haploid plants arising among higher plants (cf. especially JØRGENSEN, 1928, among others) show, on the other hand, that the meiosis can occur in plants of parthenogenetic origin too. In these plants (true haploids), chromosomes are unpaired, and naturally the disjunction does not take place; but the nuclear division may occur, which is too early for the separation of divided chromosomes, and is followed by the second division, as in the normal meiosis (cf. BELLING and BLAKESLEE, 1926). These are characteristic features of meiosis. We must then conclude that in higher plants meiosis ontogenetically has no origin in fertilization. Probably, the meiosis had occurred phylogenetically in a direct connection with gametic union, but the double nuclear division process as one of its fundamental features became fixed as a sporophytic character independent of the gametic union. That the meiosis which we observe to-day is no longer a simple double division which might be induced directly by chromosome pairing, but a morphological integrity developed as a sporophytic character, is seen from its complex nature shown by various types of meiosis, and also from the fact that the tetrad division exists even in the case where the gametophytic generation is entirely lost to existence (*Lomentaria rosea* in European waters). So far as a plant is sporophyte, it has this character irrespective of whether it be haploid or diploid. Probably, a condition which arises in sporophyte in a certain period of its ontogenetic development gives rise to the occurrence of meiosis. When this condition arises, the meiotic divisions take place irrespective of whether or not there are pairs of chromosomes that can pair.

There is also evidence to show that the synapctic pairing has no direct connection with the gametic union. This is shown by the cases of polyploid plants where only the assumption that they have arisen through the method of WINGE's indirect chromosome binding can give an adequate explanation (NISHIYAMA, 1933¹). In these cases, the synapctic pairs of chromosomes must be the pairs of progeny chromosomes from the sister chromosomes produced by division after the gametic union. These progeny chromosomes from a pair of sister chromosomes can also pair when the meiotic condition arises. Any homologous chromosomes can, therefore, pair, whatever their origin may be. The necessary condition for the pairing of the homologous chromosomes is the meiotic condition that makes a mitotic division to be a double division.

Any regular nuclear division calls for the chromosome pairing whether

¹ From the result which he obtained, NISHIYAMA has emphasized that in the hypothesis of WINGE it is not a necessary condition that the parents have different genomes. It seems highly probable that the indirect chromosome binding is due to the restitution phenomenon occurring at some early stage of development before meiosis. There may be a higher possibility of this phenomenon occurring in hybrids, but the phenomenon may also occur in pure plants according to environmental conditions.

its origin be in division or syndesis. In meiosis, one chromosome pairing by division exists, but it needs another pairing, since it is a double division. The meiosis is, however, one mitotic cycle, and consequently no more pairing by division is to occur, and the lacking pairing is fulfilled by the synaptic pairing as a response to the meiotic condition. This interpretation of the fulfilment of the lacking pairing with synaptic pairing coincides with DARLINGTON's cytological theory of meiosis, so far as it is concerned with the point that the synaptic pairing takes place in the nuclear division in which the chromosome division has not occurred.

In lower organisms in which meiosis takes place in the germinating divisions of zygotes, the meiotic condition occurs after a dormant period. In higher organisms it occurs in a later period of the sporophytic development. In higher plants the gametic union (plasmogamy) or the approach of the male nucleus to the female is directly followed by a nuclear fusion (karyogamy), and the nuclear fusion may occur quickly or slowly. In *Pinus* it occurs slowly. When the nuclear contents of both origins become mingled, the homologous chromosomes come to show paired arrangement. In *Yucca rupicola* the paired arrangement occurs quickly and is recognizable already in young embryo cells (WATKINS, 1935). There exists, therefore, an attraction or affinity between these chromosomes as between the gametic cells or nuclei. In Ascomycetes in which the nuclear fusion is postponed this attraction may be shown to exist between nuclei by their paired condition. No further approach is made, however. In these conditions, all nuclear division is mitosis. But, when the meiotic condition arises, the attraction or affinity is strengthened (cf. STEBBINS, 1935. STRAUB, 1938), and the chromosome pairing is first made to perform the complete meiosis regularly. In some instances (*Ricinus*, *Culex*), the chromosomes show a pairing in some close approximation in mitosis. This may indicate that in these cases the pairing affinity is strengthened, but the division cannot be a meiosis, because it is of a single division process. In the modern forms of organisms the chromosome pairing alone cannot be a cause of meiosis, it is merely a cytological response in the result, of the affinity to the meiotic condition which may be replaced by some other condition so far as the chromosome pairing only is concerned.

The meiotic condition develops in a definite tissue or organ in the sporophyte. It seems unlikely that this condition developed with a long history to arise in a definite tissue can be substituted by some other which has no such history, to cause a meiosis in the ordinary somatic tissues. ROSENBERG (1909) has observed a meiotic division in *Drosera* anther wall tissue stabbed by an insect, but it is a tissue which is derived from the archesporial cells (COULTER and CHAMBERLAIN, 1909).

The meiosis has phylogenetically its origin probably in the establishment of sexuality or gametic union, but ontogenetically not in fertiliza-

tion. It is determined by a post-zygotic or a sporophytic character which produces the meiotic condition, a character which was acquired in the phylogenetic development of sporophytes probably in a causal relation to the gametic union in the early evolutionary history of sexuality. The diploid condition of the nucleus is not a factor of inducing meiosis, as it is not one producing sporophytic characters. In no diploid gametophyte meiosis takes place, while in the haploid sporophyte it does. The meiosis is also a sporophytic character as are the ordinary characters of sporophyte.

X. Conclusion

The interpretation of meiosis in relation to mitosis which we have attempted above is briefly as follows:—

In the organisms in which mitosis is observed, mitosis is the only physiological mechanism of regular chromosome distribution in nuclear division, and in higher plants one chromosome cycle extends over at least two mitotic cycles. Every mitosis is, therefore, followed by a mitosis to complete the chromosome cycle and is preceded by another one in which the chromosome splitting as the antecedent of the chromosome separation takes place, or we may say that as the physiological process every nuclear division is mitosis. In these organisms, therefore, the system of nuclear multiplication is a chain of mitosis after mitosis. Meiosis as a physiological phenomenon is preceded and followed by mitosis, and therefore, it also must be essentially a mitosis.

In the early stage of phylogenetic development of organisms the meiosis occurred probably in the first nuclear division after the gametic union. The gametic union was followed by the nuclear fusion and the nuclear fusion was followed by the chromosome pairing. In the first mitosis, therefore, the synaptic pairing was performed, and as a consequence the mitosis was forced to assume a form of double division consisting of the mitotic process and a disjunction process of paired chromosomes or the reduction division. During the phylogenetic development, this double division was fixed as a sporophytic character to arise under a certain condition in the sporophyte.

In modern organisms, the chromosome pairing does not directly follow the gametic union, but the meiotic condition or the double division inducing condition develops as a sporophytic character in a certain period of their ontogenetic development in a definite tissue. When the double division begins, the synaptic pairing is induced to substitute the lacking pairing by chromosome division, and thus the meiosis of the modern form is performed.

In meiosis as a double division, the two divisions are superimposed one upon the other. This is the original type. The two separation proc-

esses, the disjunction and the mitotic separation, take place successively one after the other, because two divisions cannot take place simultaneously in the bipolar system of chromosome separation in mitosis. In the original type no nuclear stage is found between the two divisions, but in advanced types the nuclear stage (interkinesis) is found with a series of different nuclear structures, from the case where the chromosomes undergo scarcely a change to that where they form a complete nucleus with a structure very similar to that of the interphase nucleus in somatic cells. The results of prophasic restitution indicate also that there are two types in the interkinesis, in one of which it is merely a diffusion stage occurring as a stage in the course of nuclear division and in another of which it signifies the termination of division cycle as does the resting stage. Thus, meiosis which originally represents one cycle of mitotic division shows a tendency toward developing into two cycles of division. The post-reduction type of meiosis, in which the reduction division is shifted in timing relation to overlap upon the mitosis, also shows a further step toward two independent division cycles each with a complete division process.

This tendency of the shifting in the post-reduction type is, however, prevented from going further, so far as the divisions are meiosis by which the normal physiological system of nuclear multiplication as a chain of mitosis after mitosis is maintained. If the shifting goes further and the two single division cycles really occur, this system will be broken up; since the second division thus arising is not a mitosis. This second division without the chromosome division can exist as an independent physiological division only when it is transformed into mitosis by gaining the chromosome pairing by division which may be induced by the development in the process of nuclear division in the absence of synaptic pairing. The meiosis is then actually transformed into independent cycles of mitosis.

The meiosis is originally a double division as a modified mitosis, representing a mitotic cycle. No other division takes part. The double nature has developed toward becoming two independent cycles, and the double state can actually be transformed into two mitoses each with a complete cycle. The reduction division or an incomplete division as a mitosis can, therefore, be transformed into a complete mitosis with chromosome division, and it can exist as an independent division only when this transformation is complete. The mitosis is the only mechanism of nuclear division. All the nuclear divisions are mitosis and its modifications or derivatives. The amitosis in the original sense should not exist as a physiological method of nuclear division.

The meiosis may have originated in the gametic union in the evolutionary history, but it was fixed as a post-zygotic or a sporophytic character during the phylogenetic development of organisms. It is determined by the condition or conditions developing in the post-zygotic phase or in the

sporophyte—the meiotic condition. In DARLINGTON's precocity theory and the theories of HUSKINS (1933), J. and K. SAX (1935) and GUSTAFSSON (1935) a precocity or some retardation phenomena in certain mitotic processes (which may be regarded as cytological responses of mitosis to these conditions) are taken as inducing the chromosome pairing, while in the theory presented above it is assumed that the meiotic condition or the double division condition is responsible for inducing the chromosome syndesis. In the absence of homologous chromosomes, the pairing naturally does not take place, but the double division can occur. Any division is, therefore, regarded as meiosis, so far as it is of the type of double division irrespective of whether the syndetic chromosome pairing takes place or not. The normal meiosis can take place only in the presence of homologous chromosomes which have by their nature the affinity to pair under a certain condition. The important factors for the normal meiosis are, therefore, the chromosome affinity and the meiotic condition. The ultimate object of the physiological part of our investigations in which Dr. SINKE is in charge is to contribute something to the question of the nature of this meiotic condition.

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