A First View of the Meiotic Process [and Discussion]

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A first view of the meiotic process

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In this introductory paper we have highlighted some aspects of the meiotic process which seem important to us and about which some especially interesting features have been discovered. These include the switch from mitosis to meiosis, premeiotic DNA synthesis, association of the chromosomes with the synaptonemal complex, the nature of chromosome homology in relation to chromosome pairing, the process of chromosome pairing, the regulation of meiosis as a developmental process and the process of recombination. We have indulged in speculation in the hope that it will stimulate additional discussion and research into these crucial meiotic cell divisions which link the generations in higher organisms.

In the recent past valuable new knowledge has been provided about some of the processes that together make up meiosis. However, we cannot feel satisfied that as yet we have other than a rather perfunctory understanding of the cell divisions which link the generations in higher organisms. This discussion meeting was organized to provide an opportunity for an assessment of the present state of our understanding and in the hope that at the same time it would provide indications of the most important directions for future research. In this introduction our aim is to highlight a few of the aspects of the meiotic process that seem important to us. We shall speculate about particular meiotic phenomena with the hope of stimulating active discussion throughout the meeting. It must be emphasized that we make no particular claims for the originality of the ideas contained in the paper and ask indulgence at the outset if we have failed in any attributions.

By *meiosis* is implied those cell divisions which either lead to the production of gametes with balanced but reduced chromosome complements or which give rise to an alternate generation with a reduced or 'haploid' chromosome complement. The nucleus is changed from the 4*C* to the 1*C* state by sequential reductional and equational divisions. But, so far as we are aware, there is little evidence about the cause of the switch from the sequence of somatic cell cycles to meiotic division. In some fungi, the conversion can be manipulated by changing the environment (Lu 1974*a*; Rao & Niederpruem 1969; Esposito & Esposito 1974). Whatever its nature, the developmental switch from mitotic to meiotic divisions is very effectively protected from error, probably because the conversion involves very many integrated steps. No example has been reported of meiotic divisions being displaced morphologically, spatially or temporally in eukaryotes. This is true even of organisms with totipotent cells. Occasionally, however, a particular consequence of meiosis such as recombination or chromosome reduction may be achieved by non-meiotic means.

There is evidence that conversion from mitosis to meiosis is not achieved abruptly but may be approached over several somatic cell generations. This gradual build up to meiosis has been reported for several species including mouse (Monesi 1962; Kofman-Alfaro & Chandley 1970), and *Triturus* (Callan 1972). In wheat (Bennett, Rao, Smith & Bayliss 1973) the three somatic cell cycles preceding meiosis were estimated to take 25, 35 and 55 h respectively at 20 °C in continuous light.

Mitotic–meiotic switch

Although the build up to meiosis is gradual in some organisms, there is only limited evidence as to the period over which the commitment to meiotic development becomes irreversible. The classical evidence is that of Stern & Hotta (1969), which showed that in lily, provided leptotene had not been initiated, cells which would normally proceed to meiosis could be induced to revert to a mitotic division. The reversion occurred despite its having been preceded by the prolonged DNA replication period that is normally a preliminary to meiosis. It may be significant that, in lily, there is a clear G2 period of between 6 and 12 h separating S and leptotene.

Our comprehension of the mitotic–meiotic switch is not made clearer by evidence that the pattern of meiosis can be affected by events occurring before the premeiotic S (Buss & Henderson 1971; Bayliss & Riley 1972*a*, *b*; Simchen, Pinon & Salts 1972; Dover & Riley 1973). There is apparently a distinction between meiotic readiness and meiotic commitment. Perhaps this helps in the definition of the information that we need, namely the separate cellular changes that constitute readiness for, and those that mark an irrevocable commitment to, meiosis. In yeast, however, if meiosis is interrupted, diploid recombinants can be obtained that have not gone through the reductional division (Esposito & Esposito 1974). Thus in this organism at least there is not an irrevocable commitment to the meiotic division until after the recombination events have been initiated.

Premeiotic DNA synthesis

The duration of the period of DNA replication in the prolonged premeiotic cell cycles may be of particular importance to the understanding of meiosis. Bennett, Chapman & Riley (1971) reported that the immediately premeiotic S of wheat lasts for at least 8 h at 20 °C compared with an S period of about 3.5 h in somatic cell cycles in the root. Callan (1972) also reported a much longer S phase (200 h at 18 °C) immediately prior to meiosis in *Triturus vulgaris* than in blastula cells (1 h) and investigated the process by DNA fibre autoradiography (Huberman & Riggs 1968). He showed that the greater period of premeiotic synthesis results from wider distances than in somatic cells between the points in the DNA molecule at which replication is initiated. The rates of progress of replication from the initiation points are rather similar. Another difference is that, in the premeiotic synthesis, replication is predominantly in a single direction from the point of initiation.

A further indication of the distinctiveness of premeiotic DNA synthesis has been uncovered in *Coprinus lagopus* by Lu & Jeng (1975) and in *Saccharomyces cerevisiae* by Esposito & Esposito (1974). In *Coprinus* high temperature and continuous light inhibit premeiotic DNA synthesis but these conditions do not inhibit somatic DNA replication. In yeast, meiotic mutants have been isolated which are blocked in premeiotic DNA replication while somatic DNA synthesis is unaffected. DNA synthesis in yeast may also derive its metabolic precursors from different pools (Simchen *et al.* 1972). Premeiotic and premitotic S are therefore subject to different controls. It may be noted, incidentally, that a 3 h delay of premeiotic S by high temperatures will increase recombination in *Coprinus* even though the chromosomes between which recombination is to occur are at that time in different nuclei (Lu 1974*b*).

In *Lilium* another distinctive feature of the immediately premeiotic S has been demonstrated by Hotta & Stern (1971). This is that approximately 0.3 % of the total DNA is not replicated. Replication of this fraction, which has a distinctive base composition, is delayed until zygotene and chromosome pairing fails in the absence of the replication (Stern & Hotta 1967, 1973).

Perhaps the most striking properties of the nucleus of an early meiotic cell are that each chromosome must be organized to permit (i) an association at leptotene with lateral components that participate in synaptonemal complexes at zygotene, (ii) the recognition of and pairing with its homologue and (iii) chiasma formation involving 4 strand exchanges. It may be that the changed pattern of chromosome replication is related to the preparation of meiotic chromatin for participation in these events. DNA may be packed or coiled differently in meiotic chromosomes. It is reasonable to conclude, as Callan did (1972), that the very different number of replication initiation points in premeiotic chromosomes reflects a different chromatin structure.

Lateral components and the synaptonemal complex

By the end of leptotene, lateral components have been formed in the interval between the two chromatids of unpaired chromosomes (for references see Westergaard & von Wettstein 1972). Subsequently, as partner chromosomes synapse in zygotene the lateral components attached to the partners associate with a central core to form the synaptonemal complex. Westergaard & von Wettstein (1972) have drawn attention to the results which show that in *Neurospora* the total length per nucleus of the synaptonemal complex is about 50μm whereas the length of the DNA molecules is about 16 mm, so only 0.3 % of the total length of DNA double helix is matched by the length of the lateral component. In *Drosophila* the complex is 110 μm and the DNA length 61 mm, so the lateral component only covers 0.2 % of the double helix. Gillies (1973) has shown that in maize the lateral component is equivalent to between 0.017 and 0.014 % of the length of DNA double helix. Thus we must conclude that only a small proportion of chromosomal DNA can be looped into, or entrapped within, the synaptonemal complex, if a speculation of chromatin-component association of this kind is valid. It may be that only regions of DNA around certain kinds of nucleotide sequences can become entrapped within the lateral components. Many studies on recombination in fungi, suggest that recombination processes are initiated by an endonuclease nicking the DNA at specific sites (Holliday 1974). Genetic evidence suggests that recombination can occur at an extremely large number of sites on each chromosome in different cells. Which particular regions of the DNA, containing recombination-specific sites, are incorporated into the lateral component in any one meiotic cell may be determined largely at random. The DNA or chromatin segments incorporated into the synaptonemal complex after association with the lateral component may have a distinctive tertiary or quaternary structure that is established premeiotically. This suggestion again emphasizes special events, crucial to meiosis, that may occur during or after premeiotic DNA replication or even earlier.

It seems likely that regions of the DNA molecule of both chromatids become associated with the lateral component at different points along its length. This would explain the tightness of the association of both chromatids with the component in a way that prevents the recognition of chromatids by light microscopy during the prophase of meiosis prior to diplotene. Also, if the insertion of DNA molecules into the lateral component is a prerequisite for bringing DNA of partner chromosomes sufficiently close together in the synaptonemal complex for recombination to occur, then all four chromatids must participate for crossing over to be of the four strand type.

Chromosome homology

Chromosome synapsis is the next important meiotic event that follows the synthesis and assembly of the lateral components. The lateral components of different chromosomes are unpaired at the end of leptotene (La Cour & Wells 1971; Moens 1969; Westergaard & von Wettstein 1972). Chromosome pairing commences in *Locusta* with the rough alignment of lateral elements of potential partners which are about 300 nm apart (Moens 1973). Subsequently when lateral elements are separated by about 100 nm the synaptonemal complexes are formed, being initiated simultaneously at several different places along the chromosome (Moens 1969, 1973; Westergaard & von Wettstein 1972).

Since synaptonemal complexes that are apparently quite normal in appearance can be formed between chromosomes that are genetically dissimilar (Gillies 1973), it must be concluded that the complex is not particularly specific. The association together of unrelated chromosomes by a synaptonemal complex does not lead to chiasma-formation and crossing over for example in haploids of *Antirrhinum* or maize (Sen 1970; Ting 1971). In addition, close pachytene pairing in haploid barley does not lead to chiasma-formation and crossing over (Sadasivaiah & Kasha 1971). So pairing and complex formation are in themselves insufficient preparation for recombination even though they are necessary preliminaries, at least in meiosis. It may be speculated that recombination can only occur when linearly corresponding parts of DNA molecules are brought into proximity in the central core by both being trapped in the lateral components of homologous chromosomes. Presumably the juxtaposition of similar base sequences rarely occurs when pairing and complex formation takes place between unrelated chromosomes.

From this the question is immediately raised of the nature of the similarities and differences between chromosomes that are defined by calling them *homologous* or *non-homologous*. Apparently chromosomes that are either homologous or non-homologous can pair and be joined by synaptonemal complexes. But in the presence of homologous chromosomes or chromosome segments, non-homologous chromosomes do not pair or form complexes, complex formation is confined to homologues. In an attempt to understand this situation it is appropriate to consider the properties of chromosomes that may permit them to be described as 'homologous'. Homologous chromosomes or chromosome segments would usually have a common origin in evolution from the same chromosome of an ancestral species and overall morphological similarity for example in arm lengths, the distribution of secondary constructions and the distribution of heterochromatic and other discernible bands or regions. However, all of these morphological properties may be modified by structural rearrangement. On a more detailed comparison, homologous chromosomes would probably have the same structural and regulatory genes arranged in the same linear order. These genes may be modified by mutation and selection but lengths of very similar nucleotide sequences would remain. These sequences would probably result in a similar array of histone and non-histone protein being attached to the DNA, thus causing the chromosomes to have similar coiling or condensation patterns along their length. Chromosome homology, in relation to chromosome pairing, may crucially depend upon chromatin configuration.

It is reasonable to assume that homologous chromosomes first recognize each other, not by detailed matching of all the DNA sequences in their chromosomes, but by comparison of a rather few sequences or blocks of sequences scattered along the chromosomes. These sequences may be in special chromatin configurations during premeiosis and meiotic prophase. For this reason chromosomes which are similar only in a gross way, and not in fine structure could pair in meiosis. Now that we know that the genomes of higher organisms carry many families of repeated nucleotide sequences possibly distributed singly or in blocks at many places throughout the genome, it is possible to explain the pairing of non-homologues in meiosis, by the hypothesis that the limited number of sequences used in chromosome recognition include repeated sequences, which may be identical or very similar in non-homologues. It should be pointed out that it is only in plants that we have detailed knowledge of the pairing of non-homologues in haploids, and plants have large proportions of their genomes as reiterated sequences (Flavell, Bennett, Smith & Smith 1974). Since the distribution of different families of repeated sequences is always likely to be more similar in homologues than in non-homologues this hypothesis does not imply that in the presence of true homologues, non-homologous chromosomes would be paired. Chromosome homology, for meiotic pairing purposes is not then the same thing as nucleotide sequence homology throughout a chromosome or chromosome segment; although rather precise nucleotide sequence homology is surely necessary for recombination to occur after pairing.

Chromosome pairing

A property of meiosis that must be allowed for in any attempt at an explanation of chromosome pairing is that the interlocking of bivalents is extremely rare (Barber 1942). Why is it so rare in bivalents with two or more chiasmata, to find an unrelated chromosome inserted between partner homologues ? It seems unlikely that within the period of zygotene an entire complement of chromosomes, each member of which is randomly placed and in an elongated state, could be disentangled and paired, without interlocking. Alternatively, some co-orientation of potential partner chromosomes might be established before synapsis. This would imply some means of premeiotic homologue recognition. The recognition might be of potential partners for each other or of both partners for a common site within the nucleus.

Chromosomes are usually attached at certain points, principally the telomeres and heterochromatic blocks, to the nuclear membrane (Franke 1974). Moens (1973) could detect no special pattern in the attachment positions on nuclear envelopes of the ends of lateral elements in *Locusta*. Nevertheless, homologue recognition may in part derive from the correspondencies of membrane attachment sites. However the initiation of synaptonemal complex formation is not confined to the periphery of the nucleus (Moens 1973) so co-orientation, if it occurs, must also depend upon homologue to homologue recognition. If this model is correct it must be reinforced by the suggestion that, as a preliminary to synapsis, homologue recognition is sustained by physical attachments. This has been suggested by others (e.g. Holliday 1968; Comings & Riggs 1971; Maguire 1974) and is illustrated in the contribution of Majorie Maguire (this volume). Hints concerning the nature of the attachments may be contained in the observations that chromosome pairing can be disrupted in wheat by premeiotic colchicine treatment (Dover & Riley 1973) and the recognition that, at the same stage of development, fibrillar material (resembling microtubules) may be detected in the wheat nucleus (Bennett, Stern & Woodward 1974). We may speculate that the materials that attach chromosomes to each other do so by association with specific attachment sites which are spaced from each other along the chromosome in a way which corresponds for homologues.

At this meeting we have no contribution specifically devoted to the subject of 'distributive pairing'. This is a phenomenon that is recognized in *Drosophila* by means of genetical rather than cytological evidence (see Grell 1969). Distributive pairing is distinguished from 'exchange pairing' in that the latter is considered to depend on homology and crossing over whereas distributive pairing is related to chromosome length and may depend upon post-synaptic association. Alternatively, as described by Novitsky (1964) and Portin (1975), distributive pairing might result from associations between non-homologous regions initially established in the chromocentre during the premeiotic interphase.

Irrespective of the precise causes of distributive pairing it is one of a range of examples of reductional separation that takes place during meiosis in the absence of chiasma formation. There is a general problem here and as yet there is inadequate understanding of the molecular basis for the stabilization of bivalents in the absence of chiasmata. In *Drosophila* males for example the synaptonemal complex is not assembled and so is not responsible for the organization of bivalents to permit reductional separation (Gillies, Rasmussen & von Wettstein 1973) as appears to be the case in female *Bombyx* (Rasmussen 1977, this volume). Alternatively, suggestions have been made that pairing stability and regular reduction in male *Drosophila* may depend upon specific pairing sites in the basal heterochromatin (Lindsley & Sandler 1958; Cooper 1964; Peacock 1965). Baker & Carpenter (1972) have pointed out that mutants affecting the first part of the meiotic division in female *Drosophila* modify the behaviour of all chromosomes in affected flies but have no effect on male meiosis. Mutants affecting male meiosis are similarly sex specific but in this case they usually affect only one chromosome pair and not the entire complement. This evidence that male and female meiosis are under different genetic controls may provide a key to the better understanding of the meiotic process in *Drosophila* and perhaps we shall hear more of this during the meeting.

Regulation of meiosis

Many components of the meiotic process can be disturbed by environmental effects, by genetic anomaly or by manipulative procedures. Change may affect the contraction and congression of chromosomes, their pairing and disjunction, the formation of the spindle, chromosome movement and many other attributes. Generally these sorts of anomalies do not interfere with the course of the division. However, inhibition of protein synthesis with cycloheximide or DNA synthesis by deoxyadenosine during meiosis does halt the course of meiosis (Stern & Hotta 1967; Parchman & Stern 1969; Flavell & Walker 1973). Thus it would appear that some events in meiosis are an integrated part of the overall control of the developmental process while others are not. Many events may be pre-programmed premeiotically and are consequently not affected by internal anomalies while other events may depend upon being triggered by other normal processes during the cell cycles. It seems reasonable to presume that the developmental process depends critically on the induction of specific proteins, e.g. spindle proteins, recombination enzymes, and synaptonemal complex proteins and of RNA and DNA synthesis at specific times.

Recombination and information flow

We have referred to recombination earlier in considering the association between the DNA of both chromatids of the chromosome and the lateral component. The availability of sites for recombination requires the occurrence of single strand scission in the DNA molecules of homologous chromosomes. Evidence for single strand nicking of DNA has been provided for lily (Hotta & Stern 1974) and for *Saccharomyces cerevisiae* (Jacobson, Pinon, Esposito & Esposito 1975). In the latter organism the single strand scissions are reported to occur in both the newly synthesized DNA strand and in the template strand. Repair DNA synthesis is well known for the pachytene period. We need to know whether there is DNA entrapped in the lateral component and, so to speak, offered for recombination, in a way that makes it peculiarly available for single strand nicking. In a very general view of meiosis and recombination such a notion has considerable appeal.

Meiosis leads, except in total homozygotes, to the production of genetically distinct offspring. For the new genotype to be expressed there must be the minimum opportunity for the translation of messages transcribed before recombination and segregation took place. It is by no means certain, as yet, how the new genotype so quickly acquires its autonomy. However, as is well known from segregation in maize pollen (Longley 1925; Demerec 1924), and gametophytic incompatibility, pollen grains can speedily display phenotypes that are autonomously determined and distinct from the phenotype of the sporophyte. The nature of the change in information transfer subsequent to meiosis requires further study. Is there carry over of messenger from the diploid to the haploid daughter cells? If so how, and how quickly, are the old carry over messages cleared from the cell?

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Discussion

K. **Jones** (*Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey*). Professor Riley talked of synaptonemal complexes appearing in non-homologous associations as in haploids. I would like to mention that in my experience there are species of plants which undeniably have all the chromosome attributes of diploids but which in fact turn out to be tetraploid and this situation may prove to be more widespread than we think.

B. C. **Lamb** (*Botany Department, Imperial College, London SW7 2BB*). Professor Riley mentioned that only 0.3 % of the meiotic DNA could be matched in the lateral components of the synaptonemal complex in the fungus *Neurospora*, and only 0.015 % in a higher plant. The question then arises as to whether different regions of DNA get into the matched regions at random or selectively.

I want to draw attention to the value of gene conversion studies in establishing the frequency with which hybrid DNA, and therefore intimate pairing, can occur in particular regions of DNA. In the fungus *Ascobolus immersus*, gene conversion frequencies of 18 % and more have been recorded at the *w*-10 and *w*-78 sites (Emerson & Yu-Sun 1967; B. C. Lamb & Wickramaratne, unpublished), and these are minimum estimates of hybrid DNA formation because hybrid DNA giving normal 4:4 or aberrant 4:4 segregations would not have been detected. If – as seems likely from studies on many organisms – only a very small proportion of total DNA can be matched in the lateral components of the synaptonemal complex, and yet hybrid DNA formation at particular sites can be very frequent, then either there must be very selective incorporation of DNA into the lateral components, or detailed DNA matching must occur mainly outside the lateral components, although it could be initiated within them.

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