"In extreme cases the nuclear division may give four to five generative nuclei and thereby kill the pollen grain, much as the excessive mitosis of a tumour may kill an animal" (Darlington and Mather 1949). Supernumerary chromosomes in rye bring about lowered fertility (Müntzing 1946).

Special consequences of differences in gametogenesis in higher plants and animals

At this point, the meiotic and post-meiotic cycles in higher plants and animals will be reviewed paying special attention to differences which affect the transmission of certain chromosomal aberrations; and also affect the results from radiation experiments. Although there are many variations of the meiotic and post-meiotic cycle in higher plants (see Maheshwari 1950, page 86, ff), the sequences shown in Figures 2 and 3 are found in many of our crop plants. Meiosis; micro- and megasporogenesis. Each microspore-mother-cell (pollen-mother-cell or P. M. C.) in the anthers undergoes two meiotic divisions to produce a quartet of microspores, as shown in Figure 2A.

Likewise the megaspore-mother cell in the ovary undergoes two meiotic divisions but produces a linear quartet of megaspores as shown in Figure 3A.

Each of the four spores from microsporogenesis, and each of the four from megasporogenesis, has one of the chromatids from the tetrad of chromatids present originally in each of the pairs of chromosomes and hence contains the n number of chromosomes. Reduction is completed during the two meiotic divisions. In many species (dicotyledons especially), both nuclear divisions are completed before cell division occurs. In other species (for example the cereals) cell division occurs at the end of the first and second meiotic divisions. In these latter the first and second division planes may be distinguished in the spore quartet immediately after division II. This has been useful in cytological studies of crossing over and chromosome segregation (page 75).

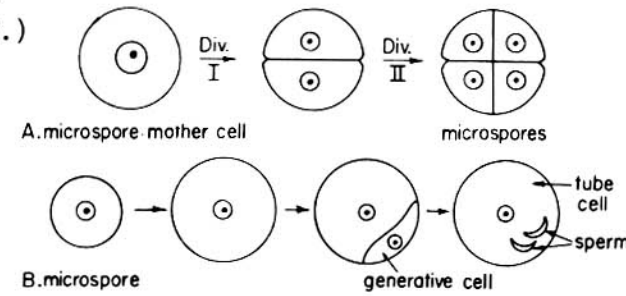

FIG. 2. Schematic diagrams:
A. Microsporogenesis in a species in which cytokinesis occurs after division I.
B. Post-meiotic divisions of the microspore to form the pollen grain.

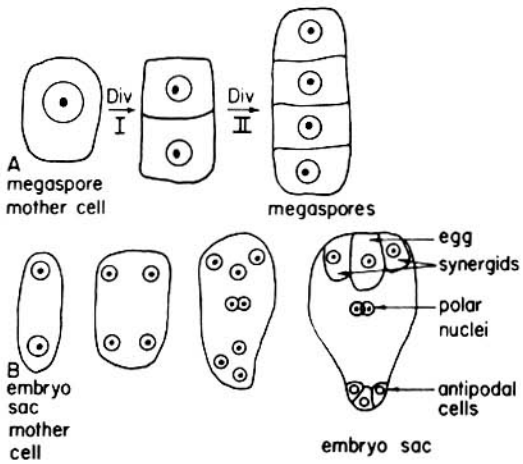

FIG. 3. Schematic diagrams:
A. Megasporogenesis.
B. Post-meiotic divisions in the development of the embryo sac (megagametophyte). Usually the functional megaspore is the one at the chalazal end of the quartet but in certain species it is the one at the micropylar end.

Post meiotic (somatic) divisions and subsequent events in plants

THE MALE GAMETOPHYTE. As shown in Figure 2B, the microspore divides to produce the tube and generative cell. This is the first post meiotic division. The generative cell then divides to form the two

sperms. In certain species (e.g. the cereals) this second post meiotic division has occurred by the time the pollen is shed, in others it occurs in the pollen tube after pollination.

THE FEMALE GAMETOPHYTE. As shown in Figure 3 B, the nucleus of one of the four megaspores, usually the one toward the chalazal end of the nucellus, divides once and the two resulting nuclei migrate to opposite poles of the cell. Each of them undergoes two nuclear divisions, resulting in a group of four at each pole. One nucleus from each group passes to the middle of the cell. These two are called the polar nuclei or the primary endosperm nuclei. The three remaining at the pole toward the micropyle are differentiated into the egg cell and two synergids, also termed the egg apparatus. The three at the other pole form the antipodal cells. This 8-nucleate structure is the mature embryo sac, and is the female gametophyte.

Note that the nuclei within a particular ♂ or ♀ gametophyte are genetically identical, since each arises by a series of somatic divisions of a single spore. One of the variants in certain species is that in which the four megaspores take part in the development of the embryo sac. There the nuclei are expected to be genetically different in a plant that is heterozygous (see Maheshwari (1950) for other modes of gametophyte formation).

POLLINATION AND FERTILIZATION. When a pollen grain falls on a stigma it germinates and produces the pollen tube. This grows down the style and finally through the micropyle and into the nucellus. The two sperms which have been near the tip of the tube as it grows, are now released. One of the sperm nuclei unites with the egg to form the 2n zygote, the other sperm unites with the two primary endosperm nuclei to form the 3n endosperm nucleus. Since each of the two sperms is involved in a fertilization, the process is termed double fertilization. Note that the endosperm has received 2n chromosomes from the female parent, 1n from the male. For those endosperm characters whose expression is affected by dosage, reciprocal crosses between two stocks carrying contrasting alleles will have a different phenotype. For example, for "floury" vs "flinty" endosperm in corn, since two doses of either are dominant over one dose of the other; floury x flinty ♂ gives a floury ear and flinty x floury ♂ gives a flinty ear. Segregation on the ears of F_1 plants is 1:1.

Gametogenesis and subsequent events in animals vs. plants

In animals, also, meiosis consists of two divisions during which reduction occurs. The one important difference from higher plants is that the products of meiosis are transformed directly into the gametes. That is, the four cells from the spermatocyte are transformed into sperms without any additional nuclear divisions. Likewise for the divisions of the oocyte, one of the four cells becomes the egg, the other three are the polar bodies. In animals, sperms and eggs that are deficient for segments of chromosomes or even a whole chromosome are capable of functioning in fertilization. The zygotes thus produced are deficient, heterozygous for the deficiency if fertilized by a normal gamete; and may not be able to develop normally. In Drosophila and in mice individuals heterozygous for certain chromosome abnormalities such as inversions and interchanges may show reduced egg hatch (Drosophila) or reduced litter size (mice). A similar deficiency in higher plants usually prevents the development of a normal gametophyte and results in aborted pollen grains and embryo sacs. In maize such pollen grains have little or no starch and the aborted embryo sacs show up as missing kernels on the ears. This behavior in plants sets up a gametophyte screen against deficiencies; a screen not found in animals. Most deficiencies in plants are not transmitted through ♀ or ♂ , some are transmitted through the ♀ only, and some relatively small ones may be transmitted through both. Apparently the nutritive surroundings are better in the ♀ and thus enable some deficiencies to survive that cannot survive through the ♂ . One consequence of the absence of an effective gametophyte screen in animals is that certain experiments can be carried out which are impos-

sible in plants. For example, in Drosophila if certain deficiencies are expected, matings can be planned with a stock known to produce a duplication that will cover that deficiency. If the proper genetic markers are used, the frequencies of the various types of deficient gametes can be determined (see page 45, Chapter 3, and page 84, Chapter 4).

The fact that the products of meiosis are in linear order in megasporogenesis in higher plants and in oogenesis in Drosophila is of importance when dealing with meiotic divisions in which dicentric chromosomes are involved. These dicentrics form a bridge as the chromosomes separate at anaphase. This bridge under certain conditions and in certain species may act as a chromatid tie which orients the crossover chromatids toward the middle cells of the linear quartet. Hence the deficient chromatids do not pass into a terminal cell which is the one that functions either as an embryo-sac mother cell in plants, or as an egg in Drosophila. Since the crossovers are not oriented so as to be recovered, crossing over is reduced without the expected reduction in fertility (see page 44, for further details).

In spite of the gametophyte screen in higher plants, pollinations made with irradiated pollen do produce progeny heterozygous for deficiencies which are not transmissible to the next generation. Presumably this could result from pollen grains in which the treatment had not affected the tube nucleus but had affected the other cell(s) present, either the sperm cells or the generative cell, depending on the species.

In animals, the treatment of sperm produces deficiencies only part of which may be transmissible to the immediate progeny. Eggs fertilized by sperms carrying deficiences may be unable to hatch or to develop further into adults.

An additional hurdle in higher plants is imposed by the necessity of the pollen grain to produce a pollen tube as a part of the development of the gametophyte, before fertilization can take place. Its ability to germinate and produce a tube that grows normally may be impaired by the chromosomal constitution of the pollen grain. If the plant is heterozygous, one type of pollen may produce pollen tubes that grow faster than others. In general pollen grains with additional chromosome material, n + 1, n + fragment, or 2n are at a handicap in competition with pollen having the n number. Interactions between the genotypes of the pollen tube and of the style may also affect the behavior of the tubes. Hence transmission through the pollen and ovules may differ and as a consequence genetic ratios in reciprocal crosses may differ.

Behavior of univalent chromosomes

There are a few facts about the behavior of univalents at meiosis which also will be helpful when considering the cytogenetic effects of the various kinds of changes in chromosome structure and number. Univalents may pass to one pole without dividing at the first division of meiosis and divide normally at the second; but there is a strong tendency for them to lag at the first division. At times they may divide at the first division and then lag at the second. In either case, the lagging chromosomes usually are not included in the nuclei resulting from meiosis, but appear as micro-nuclei in the quartet of spores. The final percentage of cells that receive the univalent may be about 25%, (as in wheat monosomics) but it is not the result of a 50-50 chance of the univalent passing to one pole or the other at both divisions. A univalent which passes to one pole without dividing probably divides normally at the second division. When lagging occurs, usually neither nucleus receives the univalent.

The behavior of univalents at the prophase stages of meiosis illustrates another point, the tendency for parts of chromosomes to be associated 2-by-2. In a plant monosomic for chromosome 10 in maize, McClintock (1933) discovered that the usual appearance of this chromosome involved some form of folding of the chromosome to bring non-homologous

parts together. The folding frequently began at the centromere, but there was a tendency also for the ends to be associated. At times, there were several foldback points. She observed this in all plants in which univalents occurred, including trisomics (2n + 1), and plants with one or three supernumerary 'B' chromosomes. She presented evidence also that exchanges occur occasionally between non-homologous parts that are associated at prophase, and produce chomosomes with a different structure.

Genetic control of chromosome behavior

Species differ with regard to chiasma position at meiosis. In some their position appears to be at random along the chromosome pair. In certain species they may be localized near the centromere (Darlington 1935, White 1936 in Mecostethus and Merioptera). A gene for control of interstitial localization of chiasmata in Allium fistulosum and in the cross of A. cepa x A. fistulosum was reported by Emsweller and Jones (1935). Chromosome length may be under genetic control by individual chromosomes in certain species hybrids as mentioned earlier.

Also there are recessive genes that affect the apparent length of chromosomes at various stages. One in barley causes abnormally short chromosomes at all stages of meiosis (Moh and Nilan 1954). One for "long chromosomes" in barley (Burnham 1946, McLennan 1947) and in Mattiola (Lesley and Frost 1927) results in a high frequency of elongated rod bivalents on the metaphase I plate. Univalent frequency is also higher. This has been ascribed in Matthiola to a lower frequency of chiasmata (Philp and Huskins 1931).

As described by Thomas (1936), one line among the breeding material of Lolium perenne had metaphase I chromosomes about a fourth of the normal size. A male sterile plant in that line produced, by outcrossing, two seedlings. The chromosomes of one of these were normal in size, those of the other were double the size at metaphase I of meiosis.

Strains of maize differ in the ease with which smear preparations showing well-spread pachytene chromosomes can be made (Wellwood and Randolph 1957).

The study of a collection of maize stocks segregating for gene-determined male sterility revealed that in most of them abortion occurred after meiosis, but in a few, aberrant meiotic behavior was the cause of the sterility (Beadle 1932b). One gene caused the chromosomes to stick together during the stages of meiosis ("sticky", Beadle 1932c, 1937). At anaphase I, the members of a pair were stretched as they pulled apart, and when they broke, the free broken ends extended polewards beyond the centromere bearing portion, much as a rubber band would behave when stretched until it breaks. The leaves of such plants showed streaks of chlorophyll-deficient tissue, probably the result of deficiencies. In another of the male-steriles, "polymitotic", the cells resulting from meiosis continued to divide (Beadle 1933a). The "variable-sterile" type was characterized by the failure of cell division at meiosis (Beadle 1932a).

Genes for a lack of synapsis (asynapsis) have been reported in maize (Beadle 1933), wheat (Li et al. 1945), Datura (Bergner et al. 1934), cotton (Beasley and Brown 1942), barley (Enns and Larter 1960) and in many other species of plants; also in Drosophila (Gowen 1933) (see Gaul 1954, for an extensive review).

Another type described in maize has divergent spindles at metaphase I and in occasional divisions of the microspores (Clark 1940). Since pollen sterility ranged from 13 to 90% in the 7 plants observed, the expression of the character seems to have been extremely

variable. In another, termed "elongate" the chromosomes are uncoiled at meiosis (Rhoades 1956), see p. 175.

One strain of barley segregated plants whose pollen mother cells had chromosome numbers varying in multiples of 7, i.e. from 14 to 56 and higher (Smith 1942). The multiploid sporocytes arose from the absence of cell walls from two or more adjacent cells in the sporogenous tissue. Metaphase I plates with polyploid number of chromosomes were observed.

There is evidence that in wheat (Triticum vulgare and Triticum durum) a genetic constitution has evolved that reduces the frequency of pairing of chromosomes that are partially homologous (homoeologous) (Riley 1958, Sears and Okamoto 1958).

Thus there is a wide range of mutant forms in which chromosome behavior is modified. With diligent search and with the aid of radiation treatment the various types might be found within the same species.

Further study of these types in comparable backgrounds and in different species should contribute badly needed information. The intriguing possibilities in stocks which combine these mutants in two's and three's in various combinations still await investigation.

CHAPTER 1. INTRODUCTION

Evidence for sister-strand meiotic crossing over has been reported in maize (Schwartz, 1953) and by Miles (1971) using ring chromosomes.

Genes that reduce recombination and others that promote recombination have been reported in Neurospora (Catcheside, D. E. A., 1974, Catcheside, D. G. et al., 1964).

Most of the DNA is synthesized during the premeiotic S-phase, but a small amount is synthesized at pachynema (Hotta et al., 1966). The latter is a repair synthesis (Howell and Stern, 1971). The homologous chromosomes come together at their ends and then loose association occurs between the unreplicated segments scattered along the chromosomes. The synaptonemal complex first described by Moses, (1956), is formed during replication of those segments. This complex holds the four chromatids together in a rigid form and apparently allows for crossing over to occur in an efficient manner. In oocyte nuclei from Drosophila females homozygous for an asynaptic gene the synaptonemal core structures were absent (Meyer, 1964).

Models. Whitehouse (1963, 1967) proposed models for crossing over that involve breakage of complementary nucleotide chains, molecular hybridization, and repair synthesis. They offer possible explanations for the major results of experiments on genetic crossing over as well as gene conversion and other unusual or rare events.

Chromosome morphology

Secondary constriction. The nucleolus organizer is the site of the secondary constriction. It is also the chromosomal site of ribosomal RNA synthesis. A series of interchanges with the break in 6 at different positions in the nucleolar organizer and also duplications for different portions of the organizer produced from Type 2 b intercrosses between the interchange stocks (see p. 107) were used to study the rRNA gene content and also the role of different segments of the organizer in nucleolus formation (Givens, 1974; Givens and Phillips, 1976).

Satellites. The results from tests with maize interchanges that have the break in 6 at different positions in the satellite indicate that the gene for polymitotic (po) is in the satellite (Phillips et al., 1977, and unpublished).

Effect of supernumerary 'B' chromosomes, knobs, and abnormal-10 (K-10) in maize.

Crossing over is increased when 'B' chromosomes are present. For the A2-Bt region in chromosome 3, crossing over values for plants with 0, 1, and 2 B's were 5.9, 6.9, and 8.8%, respectively (Nel, 1973). When knobs are present, crossing over is higher in the male than in the female (Rhoades, 1978).

In microspores with 2 or more 'B' chromsomes disjunction of chromosomes that have a knob is affected. The whole chromosome may be lost or only portions of it. The mechanism appears to be late replication of the knob which results in bridge formation, followed by loss or breakage and loss. This also initiates a bridge-breakage-fusion cycle in the endosperm (Rhoades and Dempsey, 1971, 1973).

In the presence of K10, neocentromeres form at the knobs. In a chromosome heterozygous for a knob, crossing over between the knob and the centromere produces four chromatids in which the two knob-carrying chromatids are non-sisters at the centromeres. The neocentric activity at the knobs directs them to the megaspores at opposite ends of the quartet. Hence there is preferential recovery of the knob. For the A1 locus this is about 70% (Rhoades, 1958).

In tomato, cultivars vary as to the length of the satellite which is heterochromatic. Association with the nucleolus is at one point in the short and long satellite races, at two points in the very long satellite (Lesley, 1938).