Chromosome behavior, breeding characteristics, and seed set of partially sterile lines of barley, Hordeum vulgare L.

by Cheng-Wou Yu

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirement for the degree of MASTER OF SCIENCE in Agronomy
Montana State University

Abstract:
The chromosome behavior and the breeding characteristics of partially sterile barley Betzes has been studied. Most of the cyto-logical configurations which have been observed are of rod type chromosomes, univalent, and quadivalents in metaphase I; of lagging chromosomes, non-disjunction, one bridge only, bridge and fragment, and fragment only in anaphase I and anaphase II. The fertility of these partially sterile plants ranges from 33.8% to 87% with most of them having a 75%, or 50% seed set.

Using the meiotic configuration, percentage of seed set, and segregation ratio of fertile:partially sterile plants from the partially sterile plants, the partial sterility can be classified into six different types as follows: Type 1 partial sterility Translocation Type 2 partial sterility Inversion Type 3 partial sterility Deletion, viable pollen and egg, lethal in endosperm Type 4 partial sterility Deletion, viable pollen but lethal in egg Type 5 partial sterility Recessive lethal genes in a "balanced lethality" Type 6 partial sterility Unknown lethal factor

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Date December 3, 1971

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Abstract

The chromosome behavior and the breeding characteristics of partially sterile barley Betzes has been studied. Most of the cytological configurations which have been observed are of rod type chromosomes, univalent, and quadivalents in metaphase I; of lagging chromosomes, non-disjunction, one bridge only, bridge and fragment, and fragment only in anaphase I and anaphase II. The fertility of these partially sterile plants ranges from 33.8% to 87% with most of them having a 75% or 50% seed set.

Using the meiotic configuration, percentage of seed set, and segregation ratio of fertile:partially sterile plants from the partially sterile F_1 plants, the partial sterility can be classified into six different types as follows:

Type 1 partial sterility	Translocation
Type 2 partial sterility	Inversion
Type 3 partial sterility	Deletion, viable pollen and egg, lethal in endosperm
Type 4 partial sterility	Deletion, viable pollen but lethal in egg
Type 5 partial sterility	Recessive lethal genes in a "balanced lethality"
Type 6 partial sterility	Unknown lethal factor

INTRODUCTION

Barley has been widely cultured in the world and has been used rather extensively in genetic studies. 'Betzes', a barley variety grown in northwestern United States, produces some partially sterile plants for which the causes are unknown, (Hockett and Eslick, 1969). In plant populations the occurrence of partial sterility may be caused by 1) Chromosomal structural changes such as heterozygosity for segmental interchange, inversion, duplication, and deficiency (Müntzing and Pakken, 1941); 2) Chromosomal number change such as euploidy and aneuploidy (Swanson, 1957); 3) Genetic factors (Beadle, 1932, Mangelsdorf, 1926); 4) Extra-chromosomal influence (or cytoplasmic influence, Rhoades, 1933); and 5) Environmental influence (Mangelsdorf, 1926, Müntzing, 1930).

A discussion of sterility in barley has applications to both practical and theoretical problems. One aspect is related to breeding programs for the production of hybrid barley and for producing improved varieties. It is of practical value to determine and eliminate causes of sterility in a barley variety so that ergot and smut are not troublesome.

Sterility may be elicited by environmental as well as genetic factors. Cytological and genetic studies can distinguish the hereditary causes from the non-hereditary reasons. The hereditary sterility of plants will be transmitted to succeeding generations. The genetic and chromosomal constitution of the plant has been used as a

productive tool in genetic studies on barley such as translocations (Ramage, 1963) and point mutations (Hagberg and Persson, 1963) There is also a theoretical interest in the use of partial sterility in plant breeding associated with cytological and genetic studies.

The object of this study is to determine the cause(s) for the partial sterility in these barley lines. This will be done by cytological observations of chromosome configurations at meiosis; determination of seed set percentage on field grown plants; and counting segregation ratios of fertile and partially sterile plants. Unfortunately, an examination of pollen was not made in this study. The hypotheses presented here will not be confirmed until the necessary crosses and pollen fertility examinations are completed.

REVIEW OF LITERATURE

Among the crop species, barley is one of the leaders in the number of loci plotted on linkage maps, Smith (1951). Three hundred and ninety-six translocation break points have also been reported (Kreft, 1969). Extensive cytological studies of barley have made it possible to identify the seven chromosomes of barley, Sarvella, Holmgren and Nilan (1958) and Nilan (1964), and to assign the seven linkage groups to the individual chromosomes, Robertson et al. (1965).

Stadler (1930) induced chromosome breakage by ionizing radiation and found that the subsequent chromosome rearrangement greatly reduced the seed set of plants. This established that a chromosome structural change could influence the fertility of a plant.

Chromosome aberrations leading to rearrangement in the linear order of genes were grouped into four classes by Swanson (1957): 1) deficiences, 2) duplications, 3) inversions, and 4) translocations. Generally the first three involve only a single chromosome while translocations may involve, one, two, or more chromosomes.

Chromosomal Deficiences

Bridges (1917) discovered the phenomena of chromosomal deficiencies. He reported that the location of a deficiency in Drosophila can be determined with considerable accuracy by using salivary gland chromosomes. In plants, McClintock (1931) reported that it is difficult to determine the break region where the deficiency occurred.

Deficiences involve the loss of genetic material, with the

effect depending on the amount and quality of material lost, according to Swanson (1957). Most of the deficiencies have been identified in Drosophila; however, McClintock (1938b, 1941) showed that viable mutants in maize can be produced if deficiencies are minute homozygous. Burnham (1962) pointed out that even the deficiencies existing in heterozygotes have their size limits in maize, while Datura can stand the loss of a whole chromosome to give 2n-1.

In Drosophila, Mackensen (1935) used a deficiency to locate a gene on the salivary gland chromosome. According to Swanson (1957) deficiencies in plants usually can not be detected cytologically.

Chromosomal Duplications

Sturtevant (1925) found duplications in Drosophila chromosomes. As might be expected, duplications are more frequent and less lethal to the individual than are deficiencies. Most of the work has been done with Drosophila, Swanson (1957). Few studies of duplication have been reported in barley; however, Hagberg (1962) obtained a duplication of a large piece of the short arm of chromosome 6 by crossing the barley translocation stocks $T6\text{-}7_a$ and $T6\text{-}7_d$. Ramage (1963) estimated that an increased dosage of certain genes may increase disease or insect resistance, enzymatic activity in malting barley.

Chromosomal Inversions

An inversion caused by mutagens was reported by McClintock (1931) in maize, by Sax (1937) in Paeonia suffruticosa, by Swanson (1940) in Tradescantia, and by Smith (1941) in barley. Inversions in barley can also be caused by spontaneous mutation according to Powell and Nilan (1968). The first cytological analysis of an inversion was reported by McClintock (1931).

Sax (1937) found the frequency with which crossovers take place in inversions depends upon the length of the inverted segment, its location in the chromsome, and the crossover characteristics of the individual. The frequency of crossovers which have been found in PMCs is variable. Sax (1937) found frequencies of 12% in a clone of Trillium erectum, 66% in the Bussey plants and less than 10% in many of the Arboretum plants of Paeonia suffruticosa.

McClintock (1938a) estimated the relative fertility of plants by counting the number of abnormal spores in an anther. Swanson (1940) indicated that sterility in Tradescantia was always higher than could be accounted for on the basis of meiotic irregularity.

In an inversion barley plant, Holm (1960) found pollen fertility to vary from 26-84%. A high percentage of seed set was reported by Smith (1941), Holm (1960), and Ekberg (1969) for barley which had an inversion.

Powell and Nilan (1963) observed that temperature will influence

the rate of crossover in inversions. They showed the crossing over in inversion heterozygotes of barley was optimal between 15°C and 21°C. Plants heterozygous for inversions induced by irradication had a frequency of cells carrying bridges and fragments of about 8 to 11% (Powell and Nilan, 1968).

Sax (1937) showed that a long fragment will be produced by a short inversion near the fiber attachment, and a short fragment is formed by crossing over in the loop formed by a short distal inversion in Paeonia suffruticosa. Newman (1966) divided fragment length into three classes small (1-5u), medium (6-10u), and large (11-15u) in Podophyllum peltatum inversions. Fragment size was also related to the type of bridge. Cells with a long fragment have a thin bridge, and cells with short fragments have a thick bridge. Smith (1951), Holm (1960), and Powell and Nilan (1968) nearly always found small fragments in barley inversion because of terminal chiasmata.

Other cytological configurations of bridge and fragment due to a breakage and reunion of the chromosomes have been reported by Walters (1950) in Bromtus trinii, by Heneen (1963) in Elymus farctus, by Newman (1966) in Podophyllum peltatum, and by Haga (1953) in Paris.

Burnham (1962) summarized the use of inversions in both Drosophila and plants. The inversion has been widely used in plants for genetic linkage tests and to produce duplications for known regions

of chromosomes.

Chromosomal Translocation

The first cytological study of a translocation in Drosophila was made by Stern (1926). He found a piece of the X-chromosome attached to one end of the Y-chromosome. Burnham (1934), while studying the sterility of translocated maize plants by determining the frequency of inviable seeds or defective pollen, found sterility to be near 50%. In barley, a higher fertility was reported by Smith (1941), Burnham, White, and Livers (1954), and Ekberg (1969). Burnham et al. (1954) found almost 29% spore abortion in barley, whereas, Barton (1954) found pollen abortion of 27 to 32% in tomato plants heterozygous for a single reciprocal translocation.

Burnham (1934) in a cross of two translocated plants got a "highly sterile" plant with 75% sterility; these plants have two rings of four chromosomes. Walters (1942) found a translocation complex in Paeonia california where all the chromosomes are attached to form a ring.

Translocations have been widely used in plant cytogenetic studies and still are one of the most useful tools for barley genetic studies. Burnham et al. (1954) and Ramage, Burnham, and Hagberg (1961) reported that the translocation can be used to produce trisomics. By using translocation break points the seven barley linkage groups were pointed by Robertson et al. (1955 and 1963), Burnham et al.

(1954), and Ramage et al. (1961)

Genetic Factors

Beadle (1931) reported the phenomena of asynapsis in maize where the chromosomes were unable to pair in meiosis. Examination of the micropsorocytes in diakinesis showed cells having from zero to ten bivalents with distribution of chromosomes at anaphase highly irregular. This will cause a high percentage of sterility. Prakken (1943) made a similar observation in rye. A similar effect named asynapsis was reported by Li, Pao, and Li (1945) in wheat, and by Clark (1942), and Nelson and Clary (1952) in maize. The genes responsible for asynapsis can affect the development of both megaspores and microspores (Beadle, 1933, and Clary, 1952).

Many of the genes affect only one type of gamete. The genes in maize which affect only microspores are variable sterile-2, Va_2, male sterile, ms-6, (Beadle, 1932); small pollen-1 gene, sp, (Singleton and Mangelsdorf, 1940); and pollen abortion gene, pa, (Burnham, 1941). The behavior of these genes is variable. Beadle (1932) reported that the variable sterile-2 gene in maize acted as a single recessive character and caused most of the anthers to fail to shed their contents. Burnham (1941) reported that the pollen abortion gene is lethal, or nearly so, to pollen carrying it. A count of the pollen sterility on 24 plants showed wide variability (from 33 to 67.9%) with an average of 49.2%. Most of the pollen lethal genes

were simple recessive genes, while Singleton and Mangelsdorf (1940) reported that the small pollen-1 gene, sp, acted both like a gene and a deficiency. The genes mentioned above only affect the microspores but are transmitted through the megaspores.

In maize, Singleton and Mangelsdorf (1940) found a lethal ovule factor (lo) which caused the abortion of any megaspores in which it is present. Another lethal ovule factor (lo_2) which affected ear semi-sterility of maize was also found by Nelson and Clary (1952). Lethals may affect gametes or zygotes, which is termed 'haplontic' and 'diplontic' by Müntzing (1930). Manglesdorf (1926) found defective seeds are due to lethal or semi-lethal characters which affect the development of the endosperm and embryo between the time of fertilization and maturity. Genes affecting the development of the embryosac and embryo in apple was also found by Bryant (1935). Lethals which cause abortion in 25% or 50% of the seeds in heterozygous plants of barley were reported by Ekberg (1969).

Environmental Influence

Clark (1942) in an investigation of ear semi-sterility (50%) in hybrid and pollen semi-sterility in corn inbreds found that chromosomal aberrations, gene-controlled meiotic abnormalities, and environmental influence were all predisposing factors in different cases. Certain environmental conditions, especially a high temperature, may be decisive in altering the meiotic process and thus causing

some degree of sterility in plants which are otherwise normal (Li, Pao, and Li, 1945; Nelson and Clary, 1952). Müntzing (1930) in a study of sterility of genus Galeopsis, reported that lack of nutrients and unfavorable weather condition will cause low pollen fertility. Mangelsdorf (1926) reported that higher humidity of the atmosphere would injure the pollen and decrease the fertility. In maize, other than the weather condition, environmental factors such as age of silks and age of pollen will influence the appearance of parthenocarpic defectives which were reported by Mangelsdorf (1926). The position of the flower (Müntzing, 1930) and disease or insect injury (Clark, 1942) will give some missing seed in the plant.

MATERIALS AND METHODS

Spontaneous sterile lines of Hordeum vulgare L. were collected from different sources and grown in the field at Bozeman, Montana[1/] in 1969. Seeds harvested from partially sterile plants of these plantings resulted in 70 lines of barley being planted in the greenhouse in November 1969. Most of the lines are from the variety 'Betzes' (CI 6398), and one each from CI 12233, 'Firlbecks III' (CI 10088) and 'Piroline' (CI 9558). In order that the probability of not getting at least one partially sterile plant would be less than 1% (Mather, 1938), seven greenhouse seedlings per line were selected for cytological examination . This probability is based on an expectation of a 1:1 ration of fertile:partially sterile plants.

Several spikes of each plant were collected during sporogenesis. The material was then fixed in an acetic-alcohol solution (1 part glacial acetic acid and 3 parts 95% alcohol). Other tillers on the plant were allowed to bloom and set seeds. At maturity, the heads of each plant were scored for seed set to allow classification of fertile or partially sterile plants. The seed was harvested from the partially sterile plants for planting the next year. The remaining vegetative portion of the partially sterile plants was kept in the greenhouse and allowed to regenerate tillers for a recheck of partial sterility.

[1/] Lines 1-39 were obtained from R. F. Eslick, Department of Plant and Soil Science, Montana State University; lines 40-70 were obtained from E. A. Hockett, U.S.D.A., A.R.S., Bozeman, Montana.

Since plants from line 1, 3, and 4 were completely sterile, and plants from line 13, 18, 20, 22, 23, 35, and 40 were completely fertile in the greenhouse, no seeds were collected from these lines. Therefore, only 60 lines were studied in the field in 1970. The number of partially sterile plants found in the greenhouse in each line varied from 1 to 7. Seeds harvested from each individual partially sterile plant in the 60 lines were planted separately as a sub-line in the field in May 1970. A total of 187 field-planted sub-lines were utilized in determining if the partial sterility shown in the greenhouse was due to the greenhouse environment.

After harvesting the sub-lines, the segregation into fertile and partially sterile plants was recorded. Subsequently, a chi-square test was applied to the fit of observed to expected ratio of fertile to partially sterile plants.

The percentage of seed set of the partially sterile plants in each sub-line was determined by counting the number of filled and empty spikelets within 20 spikes randomly collected from all partially sterile plants in the row.

The meiotic chromosome configurations were analyzed by observing the pollen mother cells (PMCs) of one fertile plant and one or two plant(s) in each of 60 different lines of the greenhouse grown partially sterile plants. An acetocarmine smear technique (2% of acetocarmine) was used for examination of the PMCs. All PMCs were examined

in detail under a Zeiss light microscope (Carl Zeiss 4004604). Photomicrographs were taken with a Pentex 135 camera(SP 2541067) under 1200 X.

RESULTS

A. Cytological studies

The meiotic chromosome behavior is shown in Table 1. The configurations shown in the different stages were recorded as follows:

I. Configurations in metaphase I (MI)

Chromosome pairings in most cells are in the form of either ring or rod bivalents with most of the chiasmata in the terminal position. If a rod bivalent was present, usually only a single pair of rod bivalents was observed in one cell (Figure 1). The number of rod bivalents varied from 1 to 3 while the percentage of pairs present in each line varies from 0 to 32.6 (Table 1).

Univalent chromosomes were also seen at metaphase. The number of univalent chromosomes varied from 2 to 4 (Figures 2 and 3), and the frequency of the univalents present in the cells was low (Table 1). Another rod type chromosomes caused by neo-centromere effect was also observed (Figures 4, 5, and 6). The number of neo-centromere pairs varied from 1 to 7 (Figure 5) in a PMC.

A multivalent present as ring-of-four (Figures 7, 8, 9, and 10) or chain-of-four (Figures 11 and 12) was observed at diakinesis (Figure 13) and at metaphase in line 46. Other abnormal chromosome behavior, such as unpaired chromosomes

(Figure 14) and broken chromosomes (Figure 15) were occasionally present.

II. Configurations in anaphase I and telophase I

Lagging chromosomes were found with a high frequency in certain lines. Either two univalent lagging chromosomes with a separate chromatid (Figure 16) or two lagging bivalent chromosomes (Figure 17) were observed. The type of non-disjunction found was always a 6:8 chromosomes distribution (Figure 18).

Various types of bridges were observed in anaphase I. A single bridge only (Figures 19 and 20), a bridge with a free fragment (Figure 21), two bridges only (Figure 22), and two bridges with three free fragments (Figure 23) were noted. A free fragment only in anaphase I was also found (Figure 24); this fragment is different from the lagging chromosomes which appear in Figure 16 since the fragment is apparently much smaller in size.

The lagging chromosome shown in Figure 16 may result in: 1) the chromosome stays in the cytoplasm and will not go to either pole during the chromosome separation in anaphase I or telophase I (Figure 25) and 2), the chromatids separate later and move to different poles, and hence, sometimes may become a micronuclei (Figure 26). Behavior similar to that described above is also true for the transition from Figure 17 to either

Figure 27 or 28.

III. Configurations in anaphase II and telophase II

Bridges and lagging chromosomes were usually found in anaphase II in certain lines. One bridge only in one of the dyads is shown in Figures 29 and 30; a bridge with a free fragment in the opposite or same cell of the dyads is shown in Figures 31 and 32. Although a bridge rarely breaks at anaphase II sometimes it remains through telophase II (Figure 33).

Lagging chromosomes were also present in anaphase II in certain lines (Figure 34). The lagging chromosomes, having the same behavior as in anaphase I, lead to configurations which are shown in Figure 35 and Figure 36. A bridge-like configuration with a free fragment was observed in anaphase II (Figure 37). However, these PMCs seldom appeared in certain lines. Several PMCs were observed with numerous univalent chromosomes (Figure 38).

B. Statistical studies

The fertile Betzes check and all 60 lines were evaluated for percentage seed set and segregation for fertile to partially sterile plants (Table 2). The range of percentage seed set varied from 33.8 in line 30 to 87.6 in line 59. A histogram of percentage seed set in these 60 lines is shown in Figure 39.

Most frequent levels of seed set were 50-60% and 70-80%.

Since the segregation ratios vary, a chi-square test for the fit to various estimated segregation ratios was calculated (Table 2). A heterogeneity chi-square test for each sub-line within in the lines was also made.

The percentage of seed set and segregation of fertile: partially sterile plants data obtained from E. A. Hockett and R. F. Eslick (unpublished) is shown in Table 3. The pre-1970 segregation data was obtained from three or more years for each family. It is not known if the year to year data is homogeneous. A homogeneity test has not been calculated for the data from pre-1970 and 1970. The pre-1970 data in Table 3 was included to illustrate that segregation had been observed in previous years for the barley lines included in this study.

DISCUSSION

From the cytological and field data in Table 1 and 2, it can be seen that the partially sterile plants show a different response than the fertile type in both chromosome and breeding behavior. It is possible to distinguish several types of partial sterility among the 60 lines. Following the classification set up by Ekberg (1969), the different types of partial sterility will be presented and discussed separately in the following sections.

A. Type 1 partial sterility caused by a translocation

For the translocation heterozygote in line 46, a multivalent can be seen at diakinesis and metaphase (Figure 7). The components of this multivalent either associate at their ends to form a ring, or break at one end to become a chain.

The breeding behavior of partially sterile barley is based on "segmental interchange between non-homologous chromosome" (Burnham, 1962). If two pairs of chromosomes have a segmental interchange, the translocation heterozygote shows 1 IV + 5 II at metaphase; thus, a ring-of-four or a chain-of-four will be observed.

The orientation of ring-of-four at meiotic metaphase is either "open" (Figure 8) or "zigzag" (Figure 9) (i.e., adjacent or alternate). When the four chromosomes are oriented toward the poles, theoretically the configuration of "open" rings will be three times more frequent than the "zigzag" rings (c.f. Burnham, 1962). Several configurations of non-coorientation of the centrameres of two chromosomes in alternate

position in the ring have been observed (Figure 10). When the chromosome segregation occurs in anaphase, most of the rings, especially the non-coorientation type, may produce a 3-1 segregation from the ring. This will cause a lagging chromosome (Figures 16 and 17) and non-disjunction chromosome behavior (Figure 18) in anaphase I.

There are three types of chromosome separation with translocations:alternate (zigzag), adjacent 1 and adjacent 2. Within an alternate and an adjacent 1 orientation segregation, the homologous centromeres separate and pass to opposite poles; whereas, in adjacent 2 segregation, they pass to the same pole. If the three kinds of segregation occur, six kinds of gametes will be produced at the end of meiosis. Viable gametes are only expected following a zigzag orientation, whereas open rings (adjacent 1 and adjacent 2) lead to a non-functional gamete containing duplications and deficiencies (Burnham, 1962 and Ramage, 1963). Chain-of-four chromosomes instead of rings were also observed in a high frequency in the experimental material. This is represented by either J type (Figure 11), which breaks at one end from an open ring, or Z type (Figure 12), which breaks at one end from a zigzag ring.

In barley an excess of zigzag configuration has been observed by Smith (1941) and Gelin (1956); this excess of zigzag configuration should increase the number of viable gametes. Barley translocations average about 29% of spore abortion (Burnham et al., 1954). This

indicates that alternate orientation predominantly exists in barley and the percentage of seed set should increase over that expected with random orientation; a 70-80% of seed set has been found by Smith (1941), by Holm (1960), and by Ekberg (1969).

The occurrence of the ring-of-four may result in lagging chromosomes in anaphase I (Figures 16 and 17) or in telophase (Figures 25 and 26). Hagberg (1962) pointed out that this abnormality usually causes a separation of the chromatids in anaphase I (Figure 16) which in turn causes a formation of micronuclei at the later telophase I (Figure 26) and tetrad stage (Figure 36).

Since the functional gametes which form from a zigzag orientation of a translocation heterozygote are a pair of heterozygous chromosomes and a pair of homozygous interchange chromosomes, the translocation heterozygotes are expected to segregate in a ratio of 1 standard normal:2 heterozygous translocations:1 homozygous translocation. Since standard normals and homozygous translocations both have normal fertility, and heterozygous translocations exhibit partial sterility, a phenotypic ratio of 1 fertile:1 partially sterile is expected (Burnham, 1962 and Ramage, 1963).

In my experiment, line 46 was the only line which had quadrivalents at metaphase. Both ring-of-four chromosomes and chain-of-four chromosomes were observed (Figures 7 and 12). In anaphase I a high frequency of lagging chromosomes and non-disjunction configurations

were obtained. The percentage of seed set for line 46 was about 69.3 (Table 2) and a good agreement of the chi-square test for 1 fertile:1 partially sterile plant segregation ratio was also obtained (Table 2). Therefore, the cytological observations and field data indicate that line 46 is a translocation heterozygote. Furthermore, from the diakinesis analysis, it can clearly be seen that the segmental interchange occurred in chromosome 6 since it is the nucleolar chromosome (Figure 13).

Since the translocated plants have a 1 fertile:1 partially sterile segregation ratio upon selfing, translocations are widely used in plant breeding. When crossed with normals, partial sterility behaves as if it was a dominant character, i.e., plants heterozygous for the translocation are partially sterile. In barley, translocation break points can be used as markers and plotted on linkage maps (Joachim, 1947). Translocations can also be used in linkage studies (Robertson et al., 1955), as a source of trisomics (Burnham et al., 1954), and to duplicate several genes in chromosomes leading to increased dosages of certain genes (Ramage, 1963).

B. Type 2 partial sterility caused by an inversion

Inversions were also considered as a source of partial sterility. Two kinds of inversions are well known: paracentric and pericentric. The paracentric form is most commonly encountered. Chromosomes heterozygous for an inversion may show homologous pairing at all loci to

form a loop, or pair non-homologously in the inverted region to form a rod. The longer the inversion, the greater is the amount of homologous pairing.

For the paracentric inversion, if no crossover occurs within the inversion and no cytological evidences can be seen in the PMCs, a crossing over within the homologous pairing region of a heterozygous inversion will cause a visible configuration at anaphase I (McClintock, 1931, and Sax, 1937). Sax (1937) pointed out that crossing over in heterozygous inversions paired non-homologously could produce anaphase figures which appeared normal, but that two of the four chromatids would carry a deficiency. A homologous pairing is necessary for inversion caused bridge(s). Furthermore, a paracentric inversion followed by crossing over is always related to bridges(s) and fragments(s). Observations of bridge and fragment configurations have been used extensively as a direct evidence for the presence of paracentric inversions.

Crossovers may occur at random positions within the paracentric inversion loop. However, there are four different types of crossover which can be recognized from eight different configurations shown in anaphase I and anaphase II (McClintock, 1938a and Figure 40). A summary of these four types of crossover is presented in Table 4.

Sax (1937) reported that in individuals heterozygous for inverted segments the fertility is reduced, crossing over is reduced, and "non-

disjunction" of chromosomes is frequent. However, inversions in barley show a high seed set, according to Smith (1941), Holm (1960), and Ekberg (1969). A segregation of 1 fertile:1 partially sterile plant in the offspring of a partially sterile plant was also reported by Ekberg (1969).

In my experiment, a single bridge and a free fragment in anaphase I (Figure 21) was observed in lines 11, 31, 36, 41, 49, and 59. In addition, a normal anaphase II with a free fragment in one of the dyads was also identified in each line (Table 1). The above observations lead us to suspect that a paracentric inversion exists in these lines. A further study of the field data indicated that all lines mentioned above, except line 41, have a rather high percentage of seed set ranging from 74% to 87% (Table 2). This seed set places these lines among the highest ranking lines. The chi-square test shows a probability of a good fit to a segregation ratio of 1 fertile:1 partially sterile plant. Therefore, we may conclude there is a paracentric inversion present in lines 11, 31, 36, 41, 49, and 59. Referring to Figure 40 and Table 4, we know that the crossover present in the said lines belongs to "type a" crossover, a single crossover within the paracentric inversion loop.

Instead of bridges, an anaphase I free fragment was observed in line 41 (Figure 24). Confirming this observation, a configuration of a bridge in one of the dyads and a free fragment in either one of the

dyads also appeared in anaphase II (Figures 31 and 32) and telophase II (Figure 33). Those abnormal configurations indicated the existence of a "type c" crossover - a single crossover within the paracentric inversion loop (Figure 40 and Table 4). The cytological data in Table 1 indicates a fairly high percentage of abnormal meiotic configurations in line 41. This is less than in line 46 which is from a translocation partially sterile plant but still ranks second high among the 60 lines. The high frequency of abnormal PMC showing up with a bridge and fragment emphasizes my observation that the two types of crossover, "type a" and "type c" are present in line 41. The presence of these two types of crossovers will lead to a higher frequency of abnormal cells which will reduce the percentage of seed set.

Another interesting chromosome configuration in the PMC of line 41 is the PMC showing two bridges and three free fragments at anaphase I (Figure 23). If the thick bridge, pointed out by an arrow, was not due to stickiness then possibly two "type a" crossovers plus one "type c" crossover occurred in this paracentric inversion. The two "type a" crossovers within the paracentric inversion loop are indicated by the two bridges and two free fragments present in anaphase I, while the "type c" crossover, one within and one out of the paracentric inversion, is indicated by the free fragment showing in Figure 23. However, since only one isolated cell has this configuration, the thick bridge may be due to stickiness.

In my data, the frequency of bridges observed in anaphase I is very low (Table 1), and the fragments found in a paracentric inversion configuration is also extremely small in size. However, the frequency of bridges is relative to the size of the inverted segment of chromosome, so that the larger the inverted segment size the higher the frequency of bridges. On the other hand, a small fragment has been attributed to a single crossover within a small paracentric loop located along the end of the chromosomes, and the frequency of crossovers can be related to the size and location of the inverted segments (Sax, 1937, Swanson, 1940 and Walters, 1950). A small terminal inversion loop will produce the small fragment and a low percentage of inversion bridge configuration. This might explain the fact that in my experiment I find a low bridge frequency in anaphase I. All the phenomena, shown both in photomicrographs and in the cytological data on Table 1, indicated that the inverted segments are short and probably located near the end of the chromosome. Furthermore, crossing over two times within the loop of an extremely small inverted chromosome with homologous pairing has a very small probability of occurring. This might explain the reason the"b type" crossover in the paracentric inversions i.e., 4 strand double crossover, and/or a "type d" crossover i.e., a triple crossover, were not observed in my material.

In a pericentric inversion, a single crossover within the inversion loop does not give rise to a dicentric chromatid and an acentric

fragment, but instead produces two new chromatids each of whose ends are identical in genic content. Duplication and deficiency result, and sterility would ensue. Since this type of inversion can be cytologically detected only in the pachytene stage of meiosis and does not cause abnormal configurations in anaphase - other than by counting the long arm and short arm in one pole (Brandham, 1970) it will not be discussed here.

A high number of bridges without fragment configurations was found both in anaphase I (Figures 19, 20, and 22) and in anaphase II (Figures 29 and 30). A similar bridge has been observed by Haga (1953), Walters (1950), and Kreft (1969). The reasons for bridges without fragments are many. However, these bridges can not be explained by the inversion hypothesis. An extremely small inverted segment is likely to pair non-homologously. An almost terminal breakage of these paired chromosomes followed by a fusion of the ends of the two chromatids might result in a bridge and form a minute, microscopically invisible fragment. This breakage and reunion phenomenan has been described by Walters (1950). Spontaneous chromosome breakage during meiosis has been reported in a variety of materials: Walters (1942) in Paeonia, Haga (1953) in Paris, and Heneen (1963) in Elymus farctus. Although the ordinary frequency of spontaneous breaks is, in general, low, a high frequency of spontaneous chromosome breakage has been found in Elymus farctus by Heneen (1963). He theorized such breakage was caused

by a disturbance in the genetic balance.

Stickiness is also considered to be a factor in the formation of such bridges without fragments (named sticky bridge) in anaphase I. When stickiness appears in some microsporocytes, it gives rise to an adhesion between two or more chromosomes. When the chromosomes or chromatids associated in such adhesions move to opposite spindle poles at anaphase I, sticky bridges were found. When a bridge is formed in early anaphase I, it is difficult to distinguish with certainty whether a certain configuration was a result of stickiness or whether it was a dicentric chromatid. However, due to the "tear-off" of this pair of chromosomes, an unequal portion chromosome might be formed or a small portion of chromosome might be broken and might not be moving to the pole (Figure 19). This "tear-off" might give rise to a deficiency in the chromosome and lead to sterility. In my experiment, there are many lines having a bridge without any fragment (Table 1).

C. Type 3 partially sterile caused by deletion

Many of the lines shown in Table 2 do not segregate in a ratio of 1 fertile:1 partially sterile plant. For many of these lines, a segregation of 1 fertile:2 partially sterile plants is the rule. Along with the changed ratio, an increased seed set was also observed (Table 2). A hypothesis of a deletion which is viable in the pollen and egg and lethal in the endosperm will be applied to explain this phenomena.

In other words, the deletion gives rise to a dosage effect on the endosperm.

According to the hypothesis given above, the deletion will affect the development of the caryopsis from zygote to mature caryopsis. The genetic constitution assumed for the diploid embryo and the triploid endosperm (in parenthesis) in the seeds of a partially sterile plant is explained in the scheme below:

If a gene A were deleted spontaneously in one of the sister chromosomes, two kinds of gametes would be formed during meiosis. The normal gamete is represented by A and the deletion gamete is represented by O.

φ / σ	A	O
A(AA)	AA(AAA)	AO(AAO)
O(OO)	OA(OOA)	OO(OOO) lethal

The hypothesis gives rise to an assumption that the development of the endosperm will be related to the dosage of O. All seeds except OO(OOO) are functional. Self fertilization of heterozygous plants will result in a fertility of 75%.

Plants grown from the seeds having the constitution AA(AAA) will be fertile and will breed true in the next generation. Plants grown from the seeds having the constitution AO(AAO) or OA(OOA) will be partially sterile and segregate in the next generation

in a ratio of 1 fertile:2 partially sterile plants. A similar type of endosperm deficient seed in barley was observed by Harlan and Pope (1925). They reported a seed set of approximately 75% on the partially sterile plant with a segregation ratio of fertile:partially sterile plants of 1:2.

The experimental data in Table 2 shows that lines 6, 19, 24, 26, 27, 28, 32, 50, 53, 56, 60, 61, 62, 65, 67, 69, and 70 have a high seed set ranging from 67 percent in line 56 to 80 percent in line 67 (an exception is line 70 which has only 42.4% seed set). According to the chi-square goodness of fit test none of these lines segregated in a ratio of 1 fertile:1 partially sterile plant (Table 2). With the exception of lines 28, 53, 62, and 67, all the lines have a good fit to a 1 fertile:2 partially sterile plant segregation (Table 2).

The hypothesis is based on a deletion and dependent upon the number of deleted chromosomes in the endosperm. If the deletion dosage effect exists in the endosperm, the seeds having an endosperm constitution (AAO) or (OOA) would have a lower viability than those seeds without deletions. In this case those seeds may contain a very small amount of endosperm which may by miscounted as empty spikelets. On the other hand, the small endosperm seeds containing a deletion might not grow as well as the normal seeds, especially in an unsuitable environment. In maize, a similar type of seed, named miniature seed, was reported by Lowe and Nelson (1946) to contain a lesser amount of

endosperm than the normal. Those seeds, with few exceptions, when sown in the field either did not germinate or led to a partially sterile plant. Should this happen, the number of partially sterile plants observed would be less than expected. Therefore, the segregation ratio will be slightly lower than 1:2. In barley the ratios tend to be somewhere between 1:1 and 1:2 (Ekberg, 1969).

Lines 28, 53, 62, and 67, as shown on Table 2, have a shortage of plants in the partial sterility class when a fit is attempted to a 1:2 ratio of fertile:partially sterile plants. The ratio for these lines is between 1:1 and 1:2.

Cytological observations show an increase of aberrant cells at anaphase in the 17 lines listed above. Most of these lines have a large fragment and lagging chromosomes in anaphase I configuration (Figures 16 and 17, and Table 1). The abnormal cells ratio shown in these lines at anaphase range from 0.53% in line 53 to 6.33% in line 60. The frequencies of abnormal cells shown for each line are in general small. It can not be proved that there is a relationship between the presence of a lagging chromosome and a large fragment in high numbers at anaphase, and the presence of this type of deletion. However, in contrast to the lines mentioned in type 4 partial sterility (see next section), the lines in type 3 partial sterility give rise to lagging chromosomes. In the case of this type of deletion, i.e., viability in pollen and egg and lethality in endosperm, the

mobility of one pair of chromosomes might be retarded or show no movement at all, in comparison with normal chromosomes during meiotic anaphase.

D. Type 4 partial sterility caused by deletion

The most frequent percentage of seed set in these experimental lines is 50-60 and 70-80 percent (Figure 39). Most of these lines, except for those discussed under translocations and inversions, contain almost no abnormal cells in meiotic division (Table 1). Evidently the cause of the partial sterility for these lines must be other than gross chromosome aberration. Therefore, since most of the genetically controlled forms of sterility are not associated with meiotic abnormalities, sterility in these lines is probably gene controlled.

Deletion, a mechanical deficiency in the chromosome, may serve as the main factor causing the partial sterility. My hypothesis for the type 4 partial sterility is a deletion of gene or genes in the locus or loci of the sister chromosome that will lead to viability in pollen and lethality in egg.

Just as for type 3 sterility normal gamete is represented by A and the deleted gamete is represented by O. The genetic constitutiom assumed for the diploid embryo and the triploid endosperm (in parenthesis) in seeds of a partially sterile plant are listed in the scheme below:

♀ \ ♂	A	O
A(AA)	AA(AAA)	AO(AAO)
O(OO)	OA(OOA) lethal	OO(OOO) lethal

Since we assume the deletion will be lethal in the egg than all the combinations containing a female deleted gamete, OA(OOA) and OO(OOO), will lead to lethality and will cause abortion in 50% of the seeds. The non-aborting seeds should give rise to a ratio of 1 fertile AA(AAA) to 1 partially sterile AO(AAO) plants.

The chi-square fitness test for a 1:1 segregation of fertile: partially sterile plants in Table 2 shows a satisfactory fit for lines other than the translocation, inversion and Type 3 lines mentioned earlier. These lines are 5, 7, 8, 9, 10, 12, 17, 21, 29, 33, 34, 37, 39, 40, 43, 44, 45, 51, 52, 55, 63, 64, 66. and 68.

The percentage seed set of these lines is around 50 except for lines 21, 29, 34, 52, and 66, which range from 65.9% to 75.9% fertility. Furthermore, the cytological data in Table 1 indicate these 24 lines have a quite normal meiotic metaphase and anaphase. Occasionally, a few PMCs exhibit a rod bivalent (e.g. lines 39 and 44) at anaphase; yet the frequencies for those abnormal cells is fairly low (Table 1). These bridges may have occurred due to stickiness and breakage of

chromosomes.

The hypothesis for deletion (type 4 partial sterility) is based on the supposition that the deletion will give rise to lethality in the ovules, i.e. a lethal gene. In maize, a lethal ovule gene has been reported by Singleton and Mangelsdorf (1940), Clark (1942), and Nelson and Clary (1952). Similar results have been reported in barley by Ekberg (1969).

E. Type 5 partial sterility caused by lethal genes in a "balanced lethality"

Several lines in this experiment only produced offspring of partially sterile plants. These are lines 2, 14, 25, 30, 38, 42, and 58 shown in Table 2. In these lines a fairly high frequency of abnormal anaphase I configurations, especially bridge formations, was found (Figures 19 and 20 and Table 1). The percentage of seed set ranged from 33.8 to 77.3% (Table 2). A hypothesis of two recessive lethal genes linked in a system of permanent heterozygosity which will elicit lethality when either gene is exposed in a double recessive pair may be applied to this situation.

The genetics of this embryo lethality is explained in the scheme below. If these two lethal genes are L_1 and L_2, the heterozygous condition will be (L_1l_2/l_1L_2).

♂ \ ♀	L_1l_2	l_1L_2
L_1l_2	L_1l_2/L_1l_2 (lethal)	L_1l_2/l_1L_2 (viable)
l_1L_2	l_1L_2/L_1l_2 (viable)	l_1L_2/l_1L_2 (lethal)

Seeds having the heterozygous genotype, L_1l_2/l_1L_2 and l_1L_2/l_1L_2 are phenotypically normal. However, their progeny planting will segregate lethal homozygotes and be partially sterile. Thus, the partially sterile plants (heterozygotes) will always produce partially sterile plants only. Embryos having the genetic constitution L_1l_2/L_1l_2 or l_1L_2/l_1L_2 will be inviable due to the double recessive lethal gene l_1l_1 or l_2l_2. Therefore, the theoretical seed set will be 50%.

The lethals in systems of balanced lethality may act zygotically or gametically, or partly zygotically and partly gametically in one or the other sex. In all such cases only the heterozygous genotype L_1l_2/l_1L_2 is viable. If both lethals are zygotic lethals, the fertility is reduced to 50%; if one is zygotic, the other gametic in the female in action, the fertility is 25%. Furthermore, recombination may occur between the heterozygous loci concerned. A rare crossover will give rise to recombination gametes of the types l_1l_2 and L_1L_2. Thus, an excess of the gametes l_1l_2 will result in a slight decrease in the percentage of seed set while an excess of L_1L_2 will bring

about the union of two L_1L_2 gametes, or a completely fertile plant. Therefore, a higher seed set of 77.3% in line 38, a lower seed set of 33.8% in line 30 and a number of fertile plants found in lines 2, 14, 30, and 38 are all explainable. This type of partial sterility is probably not the partial sterility caused by a single recessive male sterile gene due to its high percentage of seed set. In male sterile lines of barley the highest percentage of seed set reported so far is 30.7% (Hockett and Eslick, 1971). In my experiment the percentage seed set of these lines (except for line 30 with 33%) varied from 42.8% in line 25 to 77.3% in line 38.

The presence of these two pairs of heterozygous genes may give rise to a stickiness between the chromosomes. A sticky adhesion between two chromosomes will produce a visible bridge in anaphase I and anaphase II.

Lethals are often maintained at a high frequency in natural populations by various genetic mechanisms. Balanced lethality was first seen by Muller (1917) in Drosophila.

F. Type 6 partial sterility caused by unknown gene(s)

There are other lines in this experiment which do not give a satisfactory fit by the chi-square test to a 1:1, 1:2, or 0:1 ratio of fertile:partially sterile plants. The lines which segregated more fertile:less partially sterile plants are the following lines: 15, 47, 54, and 57 (Table 2). The segregation ratio for these lines

ranges from 2:1 to 3:1 in fertile:partially sterile plants. There is no obvious cytological aberration in the PMCs of these lines. Since not all genetic sterility is associated with chromosomal abnormalities, a gene mutation rather than a chromosome abnormality will be considered as the factor producing partial sterility here.

By viewing the field data in Table 2, the four lines can be divided into three groups.

Group 1, line 15, having a 53.2% seed set and a segregation ratio of 3:1 of fertile: partially sterile plants.

Group 2, line 57, having a seed set percentage of 82.9 and a segragation ratio of about 2:1 of fertile: partially sterile plants.

Group 3, lines 47 and 54, having a percentage of seed set of about 70% and a segration ratio of 3:1 of fertile: partially sterile plants.

Since the segregation ratio is different and the percentage of seed set varies the gene or genes corresponding to the groups is still unknown. Attempts will be made to classify the characteristics of those lethal gene or genes which give rise to a different expression in these lines. The lethal gene may be classified in the following three ways.

1. According to their degree of penetration:

Lethal of these three groups are all subvitals, or detrimental mutations, causing the death of less than 50% of the carriers

(about 10 to 50% lethality).

2. According to their phase of activity:

In Group 1, lethal genes will cause the death of gametes and prevent zygote formation. When they affect the female gamete seed set will only be 50%. In Groups 2 and 3, lethal genes will act on the zygote and lead to the death of the zygote at some stage of development. Depending upon the lethal effect, the seed set will range from 60-90%.

3. According to the influence of the external and internal environment:

Lethal genes that produce Group 1 lethality are conditional lethals, their action may depend on the growth or environmental conditions. This hypothesis may be supported by examining the data on line 15 in Table 3. Both the percentage of seed set and the segregation ratio are quite different from those displayed in Table 2. A change of the environment may bring about the different results. Lethal genes that produce Group 2 and Group 3 lethality might be unconditional lethals. The expressivity may not be influenced by environmental circumstances. The previous data on seed set percentage and segregation ratio are shown to be a reasonable match to those obtained in 1970.

By using induced mutations Ekberg (1969) found 50 lines with translocations, 3 lines with inversions, 26 lines with a lethal gene causing 25% seed abortion, and 5 lines with a lethal gene causing 50% seed abortion in the partially sterile barley obtained. In my experiment with a spontaneous source of mutations I found, 1 line with a translocation, 6 lines with inversions, 17 lines with a deletion causing 25% seed abortion, and 24 lines with a deletion causing 50% seed abortion. Comparing these two results we found that ionizing radiations and chemical mutagens will mainly induce chromosome rearrangements, while spontaneous mutations will give rise to more gene mutations than chromosome rearrangements in barley.

G. Suggestions for further experiments

I. Pachytene chromosome analysis for the determination of translocation break point

During the past 20 years careful studies of the cytogenetics of cultivated barley have made it possible to identify the seven chromosomes. Knowledge of translocation break points has played an important role in linkage tests by serving as markers. In our experiment, line 46 is a reciprocal translocation heterozygote with an interchange segment occurring in chromosome 4. A detailed pachytene morphological study and a linkage and break point test will make it possible to identify

the break points of this translocation heterozygote.

II. Testing the hypotheses advanced

1. For type 2 sterility the segregation from an inversion heterogyzote will be 1 fertile:1 partially sterile plant. The genetic make up of the fertile progeny may be either normal chromosomes or a pair of chromosomes with a segment inverted. Crosses of the fertile progeny to a mother variety will identify the genetic constitution. If the normal gamete is represented by N and the inverted chromosome gamete is represented by I. The crosses are shown in the scheme below.

♀ \ ♂	N	N
N	NN	NN
N	NN	NN

(Fertile)

or

♀ \ ♂	I	I
N	NI	NI
N	NI	NI

(Partially sterile)

Pollen from the normal fertile progeny will produce fertile F_1s, while pollen from the inverted fertile progeny will give partially sterile F_1s. If crosses are made with at least seven fertile plants from each inversion heterozygote's progeny, and at least seven F_1 plants are grown from each cross, the probability of not detecting a 1:1 ratio of fertile plants (NN:II) or a 1:1 ratio in the F_1 (NN:NI) is less than 1%.

2. For type 4 partial sterility, pollen fertility should be studied since the hypothesis is based on lethality only if the ovules. Pollen germination studies and microspore staining should show pollen behavior similar to the fertile normal. If one pollinates a fertile plant with the pollen of a partially sterile plant and obtains a fertile F_1, the hypothesis will be supported.

3. As a further test for type 4 and type 3 partial sterility, reciprocal crosses can give an indication of the genetic constitution of these plants. Reciprocal crosses can also be used as a check for those plants in type 3 having a seed set between 60-70% and having a segregation ratio of 1:1.2 to 1:1.1 of fertile:partially sterile plants which may be improperly classified. The behavior expected when the reciprocal crosses are made is as follows:

   a. With type 4 sterility, reciprocal crosses between the partially sterile plants and the mother variety is shown in the scheme below:

♂ / ♀	A(A)
A(AA)	AA(AAA) (fertile)
0(00)	A0(00A) (lethal)

♂ / ♀	A(A)	0(0)
A(AA)	AA(AAA) (fertile)	A0(AA0) (partially sterile)

A cross where partially sterile plants were used as females will yield fertile F_1 progeny only, while the reciprocal cross will produce a segregating F_1 progeny.

b. In type 3 sterility, the partially sterile plants function both as male and female in reciprocal crosses that is shown in the scheme below:

♀ \ ♂	O	A
A(AA)	AO(AAO)	AA(AAA)
O(OO)	OO(OOO) (lethal)	OA(OOA)

♀ \ ♂	A	O
O(OO)	OA(OOA)	OO(OOO) (lethal)
A(AA)	AA(AAA)	AO(AAO)

The results from both types of crosses will be a segregating F_1 progeny. Should this be true, it would mean both female and male gametes are viable, and the partially sterile plants are obtained from AO(OOA) as well as from AO(AAO) seeds.

4. As a method of testing for type 5 partial sterility, reciprocal crosses of these partially sterile plants and fertile plants can be made to identify the genetic constitution. The reciprocal cross is shown in the scheme below:

♀ \ ♂	L_1L_2
L_1l_2	L_1L_2/L_1l_2 (partially sterile)
l_1L_2	L_1L_2/l_1L_2 (partially sterile)

♀ \ ♂	L_1l_2	l_1L_2
L_1L_2	L_1l_1/L_1L_2 (partially sterile)	l_1L_2/L_1L_2 (partially sterile)

By using the partially sterile plants as either male or female to cross to a fertile female or male will produce F_1 plants with about 75% seed set. The F_2 segregation expected from these F_1 plants is 1 fertile:2 partially sterile plants. The partially sterile plants found in the F_2 should also have about 75% seed set.

CONCLUSIONS AND SUMMARY

The cytological configurations and breeding behavior of lines of partially sterile barley have been examined and detailed in this study. Combining the cytological and statistical data, I found several types of partial sterility in my experiment. Utilizing the meiotic configurations, the seed set percentages and the segregation ratios, the different types of partial sterility were classified as follows:

A. Type 1 partial sterility caused by translocation

1. At metaphase I a multivalent chromosome in the form of rings or chains, and at anaphase I and anaphase II lagging or non-disjunction chromosomes were found in the PMCs of partially sterile plants.

2. The fertility of partially sterile plants is about 70%.

3. The segregation ratio of fertile:partially sterile plants is 1:1 in offspring of a partially sterile plant.

B. Type 2 partial sterility caused by inversions

1. Normal metaphase and at anaphase I and II bridge(s) and/or fragments(s) were observed in the PMCs of the partially sterile plants.

2. The fertility of the partially sterile plants is about 75% or more.

3. The segregation ratio of fertile:partially sterile plants is 1:1 in the offspring of a partially sterile plant.

C. Type 3 partially sterility caused by deletion viable in pollen, viable in egg, lethal in endosperm

1. A normal meiotic metaphase was found. In some PMCs a few lagging chromosomes or a large fragment was observed in anaphase I and anaphase II.

2. The fertility of a partially sterile plant is about 75%.

3. The segregation ratio of fertile:partially sterile ranges from 1:1.2 to 1:2 in the offspring of a partially sterile plant.

D. Type 4 partial sterility caused by a deletion viable in pollen and lethal in egg

1. A normal meiotic division at metaphase and anaphase I were observed.

2. The fertility of a partially sterile plant is about 50%.

3. The segregation ratio of fertile:partially sterile plants is 1:1 in the offspring of a partially sterile plant..

E. Type 5 partial sterility caused by lethal gene in "balanced lethality"

1. A normal meiotic metaphase I and a few sticky bridges or lagging chromosomes in anaphase I and anaphase II were found.

2. The fertility of a partially sterile plant is about 50% or less.

3. Only partially sterile offspring were obtained from a partially sterile plant.

F. Type 6 partial sterility caused by unknown lethal genes(s)

1. A normal meiostic configuration in metaphase I and anaphase I were observed.

2. Seed set percentage was variable since I found either 50-60% or 70-80%.

3. A segregation ratio of 2:1 or 3:1 in favor of fertile plants was found.

Based on the classification above, we know that Type 1 and 2 sterility are caused by chromosome structural changes while Type 3, 4, 5, and 6 could be caused by deletions or gene mutations. The number of these hereditary types of sterility in my experiment are listed as follows:

Causes of sterility		Sterility type	No. of lines observed
Chromosome rearrangements	(Translocation	1	1
	(Inversion	2	6
Deletions	(25% seed abortion	3	17
	(50% seed abortion	4	24
Lethals	50% seed abortion	5	7
Viable recessive	Recessive factors causing seed abortion in different degree	6	4

Table 1. Aberrent cells found in cytological studies of pollen mother cells at three meiotic stages.

Line[1] number	Metaphase I, no.				Anaphase I, no.					Anaphase II, no.				
	With rod	Other	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%
Fertile	1	-	154	0.64	-	-	-	200	0.00	-	-	-	178	0.00
2 - 5	2	-	112	1.78	5	-	-	90	5.55	-	-	3	57	5.26
5 - 4	3	-	120	2.50	-	-	2	143	1.39	-	-	-	38	0.00
6 - 4	-	-	108	0.00	-	-	5	152	3.28	-	-	1	49	2.04
7 - 6	-	-	82	0.00	-	-	1	131	0.76	-	-	1	74	1.35
8 - 3	2	-	91	2.19	2	-	-	140	0.14	-	-	-	48	0.00
9 - 3	1	1[5]	78	2.56	-	-	3	148	2.02	-	-	-	30	0.00
10 - 7	-	-	62	0.00	-	-	-	109	0.00	-	-	-	47	0.00
11 - 6[2]	1	-	83	1.20	-	4	-	94	4.25	-	-	3[6]	68	4.41
12 - 1	1	-	70	1.42	-	-	1	121	0.82	-	-	-	57	0.00
14 - 4	5	13[7]	102	17.64	4	-	2	107	5.60	-	-	1	43	2.32
15 - 1	7	-	68	10.29	-	-	-	64	0.00	-	-	-	18	0.00
16 - 1	(Fertile)													
17 - 3	9	1[8]	125	8.00	2	-	2	140	2.85	-	-	-	30	0.00

Table 1. (Continued)

Line[1] number	Metaphase I, no.				Anaphase I, no.					Anaphase II, no.				
	With rod	Other	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%
19 - 6	2	-	86	2.32	-	-	4	146	2.73	-	-	1	84	1.19
21 - 1	19	-	193	7.25	-	-	4	164	2.44	-	-	-	41	0.00
24 - 5	10	-	155	6.45	-	-	4	218	1.83	-	-	4	98	4.08
25 - 5	4	-	120	3.33	3	-	5	309	2.66	-	-	1	32	3.12
26 - 1	7	-	107	6.54	-	-	3	120	2.50	-	-	2	92	2.17
27 - 3	3	1[9]	52	7.68	-	-	2	72	2.77	-	-	-	35	0.00
28 - 3	3	-	178	1.68	2	-	2	104	3.84	-	-	-	--	----
29 - 2	5	-	153	3.26	-	-	3	167	1.79	-	-	3	89	3.37
30 - 6	2	12[10]	128	10.93	3	-	5	61	13.11	11	-	9	119	16.80
31 - 2	-	-	108	0.00	-	9	-	86	10.46	-	-	4[11]	63	6.34
32 - 3	-	-	90	0.00	-	-	5	81	6.17	-	-	-	53	0.00
33 - 5	-	-	70	0.00	-	-	1	124	0.80	-	-	-	67	0.00
34 - 7	2	-	103	1.94	-	-	8	127	6.29	-	-	-	58	0.00
36 - 1	3	-	96	3.12	-	4	1	102	4.90	-	-	3[12]	76	3.94

Table 1. (Continued)

Line[1] number	Metaphase I, no. With rod	Other	Observed Total	%	Anaphase I, no. Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%	Anaphase II, no. Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%
37 - 4	-	-	87	0.00	-	-	-	135	0.00	-	-	-	56	0.00
38 - 3	4	-	98	4.08	-	-	4	144	2.77	-	-	1	63	1.58
39 - 2	-	2[13]	82	2.43	2	-	-	102	1.96	-	-	-	82	0.00
40 - 1	6	-	179	3.35	-	-	-	94	0.00	-	-	-	47	0.00
41 - 2	32	-	98	32.65	-	7	28[14]	240	14.58	-	4	14[14]	228	7.89
42 - 1	4	-	117	3.41	5	-	1	104	5.76	-	-	1	48	2.08
43 - 6	-	-	19	0.00	-	-	-	50	0.00	-	-	-	10	0.00
44 - 3	-	-	23	0.00	3	-	6	247	3.64	-	-	6	109	5.55
45 - 5	-	-	78	0.00	-	-	21[15]	244	8.60	2	-	10	143	8.39
46 - 2	156[16]	106[16]	275	95.26	-	-	89[16]	321	27.72	-	-	12	83	14.45
47 - 5	73	-	722	10.11	-	-	-	107	0.00	-	-	-	--	----
49 - 3	1	4[17]	60	8.32	-	2	-	226	0.88	2	-	4[17]	126	4.67
50 - 3	25	1[18]	139	8.69	4	-	1	227	2.22	-	-	-	69	0.00
51 - 5	31	-	104	29.80	-	-	6	169	3.55	-	-	1	92	1.08

Table 1. (Continued)

Line[1] number	Metaphase I, no.				Anaphase I, no.					Anaphase II, no.				
	With rod	Other	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%
52 - 4	1	-	46	2.17	-	-	-	135	0.00	-	-	-	62	0.00
53 - 1	4	-	181	2.20	1	-	-	186	0.53	-	-	-	65	0.00
54 - 2	19	20[19]	335	11.64	3	-	-	207	1.45	-	-	-	26	0.00
55 - 2	14	-	165	8.48	4	-	-	123	3.25	-	-	-	21	0.00
56 - 2	17	2[20]	275	6.90	5	-	2	252	2.77	-	-	-	12	0.00
57 - 4	-	-	96	0.00	3	-	-	103	2.91	-	-	-	27	0.00
58 - 4	9	-	112	8.03	-	-	2	76	2.63	-	-	-	43	0.00
59 - 4	6	-	97	6.18	-	5	-	87	5.74	-	-	2	61	3.27
60 - 5	4	3[21]	74	9.45	-	-	10	158	6.33	-	-	-	31	0.00
61 - 6	12	2[22]	121	11.56	1	-	5	129	4.65	-	-	1	24	4.16
62 - 5	47	-	274	17.15	1	-	2	99	3.03	-	-	-	60	0.00
63 - 6	24	4[23]	315	8.87	1	-	1	144	1.39	-	-	-	20	0.00
64 - 5	53	-	485	10.92	15	-	1	234	6.83	-	-	-	11	0.00
65 - 6	20	-	104	19.23	-	-	4	87	4.60	-	-	-	25	0.00

Table 1. (Continued)

Line[1] number	Metaphase I, no.				Anaphase I, no.					Anaphase II, no.				
	With rod	Other	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%	Bdg[2]	Bdg[3] with frg	Lag[4] chr	Observed Total	%
66 - 7	2	1[24]	62	4.83	2	-	-	73	2.74	-	-	-	40	0.00
67 - 1	15	-	137	10.94	-	-	5	170	2.94	-	-	2	151	1.32
68 - 1	15	-	108	13.88	1	-	-	38	2.63	-	-	-	--	----
69 - 5	12	-	95	12.63	2	-	6	243	3.30	-	-	-	80	0.00
70 - 2	15	-	122	12.29	1	-	4	124	4.03	-	-	3	115	2.60

1/ Under line number, fertile means a fertile plant was used as a check. 2-5 means in family number 2 the 5th plant was used for cytological study. 5-4 means in family number 5 the 4th plant was used for cytological study and so on.

2/ Bridge

3/ Bridge with fragment

4/ Lagging chromosome

5/ One cell having two univalents in MI

6/ Three cells showing fragment in AI

7/ Thirteen cells having two univalents in MI

8/ One cell having two rods in MI

9/ One cell having two rods in MI

10/ Ten cells having two univalent and two cells having two rods in MI
11/ Three cells having fragment and one cell having lagging chromosome in AII
12/ Two cells having fragment and one cell having lagging chromosome(s) in AII
13/ Two cells having two univalents in MI
14/ Six cells having fragment and twenty-two cells having lagging chromosome in AI, four cells having fragment and ten cells having lagging chromosome in AII
15/ Two cells showing non-disjunction and nineteen cells having lagging chromosome(s) in AI
16/ One hundred and fifty-six cells showing ring-of-four and one hundred and six cells showing chain-of-four in MI, fifteen cells having non-disjunction and seventy-four cells having lagging chromosome(s) in AI
17/ Four cells having numerous chromosomes in MI, three cells having fragment and one cell having lagging chromosome (s) in AII
18/ One cell showing complete unpairing in MI
19/ Twenty cells showing two or more rods in MI
20/ Two cells showing fourteen chromosomes in MI
21/ One cell showing seven rods and two cells having fourteen chromosomes in MI
22/ Two cells showing twenty eight chromosomes in MI
23/ Four cells having two univalents in MI
24/ One cell showing a chain-of-four like chromosome in MI

Table 2. Segregations for fertile and partially sterile plants and seed set on partially sterile plants grown in the field at Bozeman, Montana in 1970.

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit>	Homo-geneity P>		Seed set Flowers no.	%
Fertile	20	0	1 : 0				661	97.5
2 - 1	0	47	0 : 1	0.90			532	55.6
2	2	59	0 : 1	0.75			516	64.0
3	0	33	0 : 1	0.90			536	58.0
4	0	49	0 : 1	0.90			513	68.0
5	3	67	0 : 1	0.50			537	49.3
6	0	28	0 : 1	0.90			515	61.2
7	0	23	0 : 1	0.90			492	57.3
Total	5	301	0 : 1	0.75	0.50	avg	520	59.0
5 - 1	21	24	1 : 1	0.50			---	---
4	37	30	1 : 1	0.25			502	43.3
7	18	13	1 : 1	0.25			---	---
Total	76	67	1 : 1	0.25	0.25	avg	502	43.3
6 - 3	23	26	1 : 2	0.25			507	69.6
4	10	22	1 : 2	0.75			501	71.1
5	13	29	1 : 2	0.50			491	74.1
7	22	30	1 : 2	0.10			542	70.5
Total	68	107	1 : 2	0.05	0.05	avg	510	71.3
7 - 1	10	13	1 : 1	0.50			523	57.6
2	28	29	1 : 1	0.90			---	---
4	20	16	1 : 1	0.50			---	---
6	16	14	1 : 1	0.50			---	---
Total	74	72	1 : 1	0.75	0.75	avg	523	57.6
8 - 2	13	14	1 : 1	0.75			489	48.7
3	12	15	1 : 1	0.50			---	---
6	48	45	1 : 1	0.75			503	47.7
Total	73	74	1 : 1	0.90	0.75	avg	496	48.2
9 - 3	15	13	1 : 1	0.50			554	54.7
5	9	6	1 : 1	0.25			---	---
6	1	6	1 : 1	0.05			596	45.3
Total	25	25	1 : 1	0.90	0.10	avg	575	50.0

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit >	Homo-geneity P >		Seed set Flowers no.	%
10 - 7	29	20	1 : 1	0.10			519	55.3
Total	29	20	1 : 1	0.10	---	avg	519	55.3
11 - 4	--	--	-----	---			---	---
5	14	5	1 : 1	0.025			340	82.1
6	5	9	1 : 1	0.25			414	81.6
7	--	--	-----	---			---	---
Total	19	14	1 : 1	0.25	0.25	avg	377	81.8
12 - 1	35	27	1 : 1	0.25			516	47.7
7	13	19	1 : 1	0.25			541	53.4
Total	48	46	1 : 1	0.75	0.10	avg	528	50.6
14 - 1	0	20	0 : 1	0.90			---	---
3	0	44	0 : 1	0.90			---	---
4	7	16	0 : 1	0.10			252	76.3
6	0	28	0 : 1	0.90			500	74.6
7	0	58	0 : 1	0.90			---	---
Total	7	166	0 : 1	0.50	0.10	avg	376	75.4
15 - 1	20	6	3 : 1	0.50			500	53.2
Total	20	6	3 : 1	0.50	---	avg	500	53.2
16 - 7	56	0	-----	---			---	---
Total	(Fertile Plant)						-------	
17 - 2	8	18	1 : 1	0.05			489	56.4
3	11	10	1 : 1	0.50			---	---
6	14	13	1 : 1	0.75			---	---
Total	33	41	1 : 1	0.25	0.10	avg	489	56.4
19 - 3	(All fertile)							
5	7	23	1 : 2	0.10				
6	7	12	1 : 2	0.75			490	72.4
7	21	49	1 : 2	0.50			482	73.7
Total	35	84	1 : 2	0.25	0.50	avg	486	73.0

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit >	Homo-geneity P >		Seed set Flowers no.	%
21 - 1	25	16	1 : 1	0.10			---	---
2	12	8	1 : 1	0.25			---	---
3	23	14	1 : 1	0.10			---	---
4	24	18	1 : 1	0.25			508	68.9
5	25	27	1 : 1	0.90			---	---
6	12	16	1 : 1	0.25			---	---
Total	121	99	1 : 1	0.10	0.50	avg	508	68.9
24 - 1	4	10	1 : 2	0.50			---	---
2	21	39	1 : 2	0.75			489	77.3
3	16	30	1 : 2	0.75			---	---
4	19	50	1 : 2	0.25			467	76.4
5	10	32	1 : 2	0.10			---	---
7	28	56	1 : 2	0.90			---	---
Total	98	217	1 : 2	0.25	0.75	avg	478	76.9
25 - 3	0	51	0 : 1	0.90			---	---
5	0	50	0 : 1	0.90			486	42.8
7	0	43	0 : 1	0.90			---	---
Total	0	144	0 : 1	0.90	0.90	avg	486	42.8
26 - 1	20	49	1 : 2	0.25			---	---
2	25	43	1 : 2	0.50			481	73.8
5	6	8	1 : 2	0.25			516	76.2
6	7	13	1 : 2	0.75			478	75.3
7	30	44	1 : 2	0.10			---	---
Total	88	157	1 : 2	0.10	0.75	avg	491	75.1
27 - 3	4	2	1 : 2	0.05			516	76.7
4	15	34	1 : 2	0.50			458	73.6
Total	19	36	1 : 2	0.75	0.05	avg	488	75.2
28 - 3	24	31	1 : 2	0.10			---	---
4	59	73	1 : 2	0.05			455	72.3
5	28	41	1 : 2	0.10			---	---
6	20	46	1 : 2	0.50			---	---
7	25	20	1 : 2	0.001			429	74.8
Total	156	211	1 : 2	0.001	0.05	avg	442	73.6

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit >	Homo-geneity P >		Seed set Flowers no.	%
29 - 2	28	35	1 : 1	0.25			---	---
4	24	32	1 : 1	0.25			472	65.9
6	11	16	1 : 1	0.25			---	---
Total	63	83	1 : 1	0.05	0.90	avg	472	65.9
30 - 1	0	1	0 : 1	0.90			---	---
2	0	6	0 : 1	0.90			---	---
5	5	5	0 : 1	0.025			---	---
6	0	13	0 : 1	0.90			---	---
7	0	32	0 : 1	0.90			521	33.8
Total	5	57	0 : 1	0.50	0.25	avg	521	33.8
31 - 2	27	32	1 : 1	0.50			---	---
5	23	36	1 : 1	0.05			494	76.5
Total	50	68	1 : 1	0.05	0.25	avg	494	76.5
32 - 1	(All fertile)							
2	12	30	1 : 2	0.50			---	---
3	12	31	1 : 2	0.25			---	---
6	22	28	1 : 2	0.10			465	74.4
7	29	51	1 : 2	0.50			460	73.7
Total	75	140	1 : 2	0.50	0.25	avg	462	74.1
33 - 3	45	23	1 : 1	0.005			440	61.8
5	34	31	1 : 1	0.50			---	---
7	37	42	1 : 1	0.50			443	58.5
Total	116	96	1 : 1	0.10	0.05	avg	441	60.4
34 - 1	49	57	1 : 1	0.25			---	---
7	49	66	1 : 1	0.05			455	71.0
Total	98	123	1 : 1	0.05	0.25	avg	455	71.0
36 - 1	31	22	1 : 1	0.10			390	81.5
2	16	25	1 : 1	0.10			497	70.2
Total	47	47	1 : 1	0.90	0.05	avg	443	75.9
37 - 4	54	36	1 : 1	0.05			544	59.0
Total	54	36	1 : 1	0.05	---	avg	544	59.0

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit >	Homo-geneity P >		Seed set Flowers no.	%
38 - 1	3	47	0 : 1	0.50			---	---
3	17	39	0 : 1	0.01			493	77.3
Total	20	86	0 : 1	0.05	0.10	avg	493	77.3
39 - 1	28	25	1 : 1	0.50			---	---
2	18	27	1 : 1	0.10			498	53.8
4	11	14	1 : 1	0.50			---	---
5	21	27	1 : 1	0.25			---	---
6	15	16	1 : 1	0.75			534	52.8
Total	93	109	1 : 1	0.25	0.75	avg	516	53.3
40 - 1	14	9	1 : 1	0.25			520	54.0
5	31	20	1 : 1	0.10			---	---
Total	45	29	1 : 1	0.05	0.90	avg	520	54.0
41 - 2	21	39	1 : 1	0.01			---	---
5	40	44	1 : 1	0.50			476	53.4
Total	61	83	1 : 1	0.05	0.10	avg	476	53.4
42 - 1	0	59	0 : 1	0.90			459	32.5
7	4	22	0 : 1	0.25			584	62.7
Total	4	81	0 : 1	0.50	0.50	avg	521	47.6
43 - 2	17	8	1 : 1	0.05			500	51.0
6	12	13	1 : 1	0.75			495	47.7
Total	29	21	1 : 1	0.25	0.10	avg	497	49.4
44 - 3	30	21	1 : 1	0.10			---	---
7	46	34	1 : 1	0.10			407	53.8
Total	76	55	1 : 1	0.05	0.75	avg	407	53.8
45 - 5	18	25	1 : 1	0.25			471	59.0
Total	18	25	1 : 1	0.25	---	avg	471	59.0
46 - 2	23	25	1 : 1	0.75			498	69.3
3	18	19	1 : 1	0.75			---	---
Total	41	44	1 : 1	0.50	0.90	avg	498	69.3

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit >	Homo-geneity P >	Seed set Flowers no.	%
47 - 5	54	11	3 : 1	0.10		455	66.8
6	18	13	3 : 1	0.025		484	71.3
Total	72	24	3 : 1	0.90	0.005 avg	469	69.1
49 - 1	(All fertile)						
3	18	14	1 : 1	0.25		498	82.9
(179)	38	43	1 : 1	0.50		416	80.5
Total	56	57	1 : 1	0.90	0.25 avg	457	81.7
50 - 3	26	68	1 : 2	0.25		517	73.3
7	12	32	1 : 2	0.25		---	---
(180)	50	98	1 : 2	0.90		415	74.0
Total	88	198	1 : 2	0.25	0.50 avg	466	73.4
51 - 1	5	10	1 : 1	0.10		513	61.8
5	14	11	1 : 1	0.50		456	59.6
(181)	39	47	1 : 1	0.25		227	55.5
Total	58	68	1 : 1	0.25	0.25 avg	398	59.0
52 - 4	40	17	1 : 1	0.001		434	75.6
(182)	50	49	1 : 1	0.90		481	76.1
Total	90	66	1 : 1	0.05	0.01 avg	457	75.9
53 - 1	26	30	1 : 2	0.025		---	---
4	17	19	1 : 2	0.05		---	---
5	14	24	1 : 2	0.50		486	67.5
6	24	32	1 : 2	0.10		---	---
7	26	34	1 : 2	0.10		---	---
Total	107	139	1 : 2	0.001	0.10 avg	486	67.5
54 - 2	31	7	3 : 1	0.25		494	67.9
Total	31	7	3 : 1	0.25	--- avg	494	67.9
55 - 2	22	17	1 : 1	0.25		---	---
4	15	17	1 : 1	0.50		467	57.8
6	16	17	1 : 1	0.75		---	---
7	53	36	1 : 1	0.05		---	---
Total	106	87	1 : 1	0.10	0.50 avg	467	57.8

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit >	Homogeneity P >		Seed set Flowers no.	%
56 - 2	31	42	1 : 2	0.05			---	---
3	12	15	1 : 2	0.10			---	---
4	16	28	1 : 2	0.50			500	71.6
5	(All fertile)							
6	13	23	1 : 2	0.50			---	---
Total	73	108	1 : 2	0.05	0.50	avg	500	71.6
57 - 4	32	14	2 : 1	0.50			457	78.1
(183)	64	37	2 : 1	0.25			339	87.6
Total	96	51	2 : 1	0.50	0.25	avg	398	82.9
58 - 4	15	34	0 : 1	0.025			485	71.5
5	0	41	0 : 1	0.90			492	76.4
Total	15	75	0 : 1	0.10	0.10	avg	488	74.0
59 - 2	19	10	1 : 1	0.05			454	87.6
Total	19	10	1 : 1	0.05	---	avg	454	87.6
60 - 2	28	59	1 : 2	0.75			478	72.0
4	9	12	1 : 2	0.25			---	---
5	23	33	1 : 2	0.10			477	75.5
7	31	48	1 : 2	0.25			---	---
Total	91	152	1 : 2	0.10	0.50	avg	477	73.8
61 - 5	15	22	1 : 2	0.25			474	75.1
6	14	22	1 : 2	0.25			---	---
7	25	67	1 : 2	0.10			439	76.3
Total	54	111	1 : 2	0.75	0.10	avg	456	75.7
62 - 1	44	45	1 : 2	0.001			---	---
5	31	39	1 : 2	0.05			437	73.7
7	42	71	1 : 2	0.25			458	71.8
(185)	40	59	1 : 2	0.10			386	76.4
Total	157	214	1 : 2	0.001	0.001	avg	427	74.0
63 - 2	32	39	1 : 1	0.25			510	61.8
4	23	31	1 : 1	0.25			---	---
6	18	18	1 : 1	0.90			---	---
Total	73	88	1 : 1	0.10	0.75	avg	510	61.8

Table 2. (Continued)

Line number	Plants, no. Observed Fert	P.S.	Ratio exp	P for fit>	Homo-geneity P>	Seed set Flowers no.	%
64 - 1	33	19	1 : 1	0.05		462	57.8
5	28	36	1 : 1	0.25		471	59.0
6	16	25	1 : 1	0.10		---	---
Total	77	80	1 : 1	0.75	0.025 avg	466	58.4
65 - 2	27	38	1 : 2	0.10		461	69.2
3	0	16	1 : 2	0.001		503	70.1
4	28	35	1 : 2	0.25		492	70.0
5	29	30	1 : 2	0.005		---	---
6	4	49	1 : 2	0.001		479	62.4
Total	88	168	1 : 2	0.50	0.001 avg	483	69.8
66 - 5	6	6	1 : 1	0.90		---	---
6	25	22	1 : 1	0.50		377	69.5
7	52	38	1 : 1	0.10		---	---
Total	83	66	1 : 1	0.10	0.75 avg	377	69.5
67 - 1	12	22	1 : 2	0.75		---	---
6	37	44	1 : 2	0.01		439	77.7
7	39	59	1 : 2	0.10		---	---
(186)	29	40	1 : 2	0.10		412	83.0
Total	117	165	1 : 2	0.001	0.50 avg	425	80.4
68 - 1	20	14	1 : 1	0.25		417	52.5
Total	20	14	1 : 1	0.25	--- avg	417	52.5
69 - 1	23	33	1 : 2	0.10		---	---
2	20	53	1 : 2	0.25		---	---
3	17	59	1 : 2	0.025		---	---
5	45	71	1 : 2	0.10		456	81.1
6	19	44	1 : 2	0.50		---	---
(187)	31	79	1 : 2	0.25		423	73.0
Total	155	339	1 : 2	0.25	0.10 avg	439	77.1
70 - 2	21	34	1 : 2	0.25		514	42.4
5	22	44	1 : 2	0.90		---	---
Total	43	78	1 : 2	0.50	0.50 avg	514	42.4

Table 3. Comparison of field data on segregation for fertile and partially sterile plants and seed set on partially sterile plants grown at Bozeman, Montana[1/].

Line number	Plants, no.				Seed set, %	
	Pre 1970		1970			
	Fert	P.S.	Fert	P.S.	Pre 1970	1970
2	2	19	5	301	44.0	59.0
5	26	11	76	67	75.0	43.3
6	16	14	68	107	85.0	71.3
7	14	13	74	72	58.0	57.6
8	18	15	73	74	54.0	48.2
9	20	19	25	25	48.0	50.0
10	28	8	29	20	----	55.3
11	19	9	19	14	63.0	81.8
12	11	8	48	46	----	50.6
14	11	5	7	166	79.0	75.4
15	21	14	20	6	63.0	53.2
16	35	2	56	0	59.0	----
17	12	18	33	41	85.0	56.4
19	24	16	35	84	44.0	73.0
21	23	12	121	99	61.0	68.9
24	13	24	98	217	68.0	76.9
25	18	14	0	144	62.0	42.8
26	14	24	88	157	75.0	75.1
27	16	23	19	36	64.0	75.2
28	14	21	156	211	77.0	73.6
29	12	23	63	83	72.0	65.9
30	6	29	5	57	37.0	33.8
31	6	15	50	68	74.0	76.5
32	12	33	75	140	76.0	74.1
33	30	15	116	96	44.0	60.4
34	17	23	98	123	67.0	71.0
36	10	33	47	47	71.0	75.9
37	31	11	54	36	68.0	59.0
38	26	15	20	86	71.0	77.3
39	14	13	93	109	61.0	53.3

Table 3. (Continued)

Line number	Plants, no. Pre 1970 Fert	Pre 1970 P.S.	1970 Fert	1970 P.S.	Seed set, % Pre 1970	1970
40	14	13	45	29	----	54.0
41	34	50	61	83	----	53.4
42	2	27	4	81	----	47.6
43	79	62	29	21	----	49.4
44	40	20	76	55	----	53.8
45	13	17	18	25	----	59.0
46	18	15	41	44	----	69.3
47	14	3	72	24	----	69.1
49	14	20	56	57	----	81.7
50	13	19	88	198	----	73.7
51	15	23	58	68	----	59.0
52	17	5	90	66	----	75.9
53	11	24	107	137	----	67.5
54	17	5	31	7	----	61.9
55	18	7	106	87	----	57.8
56	11	25	72	108	----	71.6
57	45	16	96	51	----	82.9
58	15	25	15	75	----	74.0
59	22	10	19	10	----	87.6
60	12	22	91	152	----	73.8
61	13	25	54	111	----	75.7
62	17	23	163	214	----	74.0
63	21	26	73	88	----	61.8
64	22	17	77	80	----	58.4
65	20	18	88	168	----	69.8
66	19	4	83	66	----	69.5
67	15	24	117	165	----	80.4
68	16	10	20	14	----	52.5
69	11	20	155	339	----	77.1
70	35	28	43	78	----	42.4

1/ Pre 1970 unpublished data obtained from E. A. Hockett and R. F. Eslick.

Table 4. Results of four types of crossover in a paracentric inversion.

Type of crossover	Number and Position(s) of the crossover	Cytological Configuration Presented	
		Anaphase I	AnaphaseII
Type a	A single crossover at position 1 or 2 within the inversion loop	A single bridge and a single fragment	A normal appearing anaphase in both cells, with a free fragment in one of the dyads
Type b	4-strand double crossing over at position 1 and 2	A double bridge and two fragments	A normal appearing anaphase in both cells, with two free fragments vari-distributed
Type c	Two crossovers within and outside of the inversion loop at position 2 and 3	A free fragment no bridge	A bridge configuration in one cell and no bridge in the sister cell, with a fragment in either one of the dyads
Type d	A triple crossover at positions 1, 2, and 3	Two fragments and no bridge	A bridge configuration in each sister cell, with two fragments

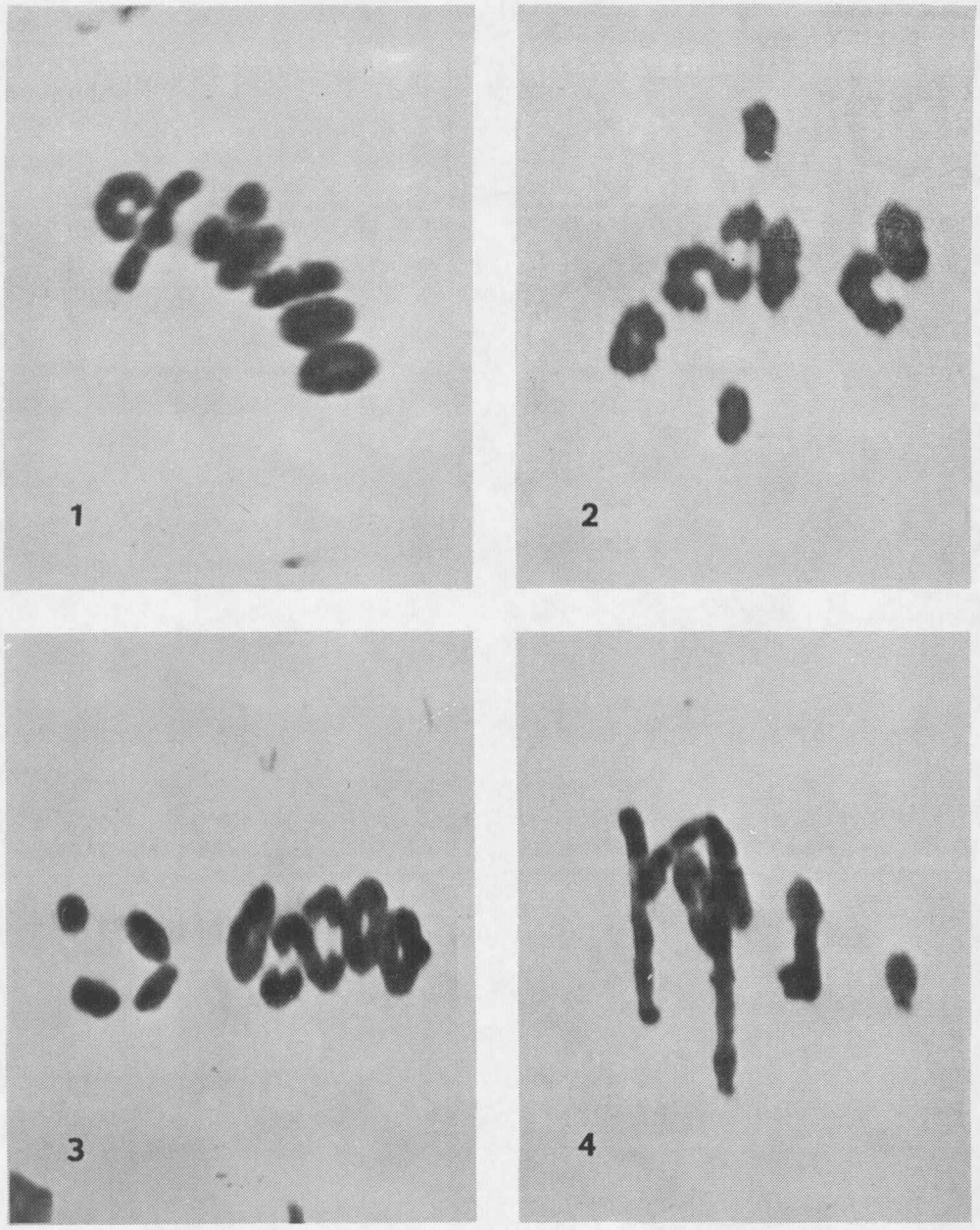


Fig. 1. Metaphase I a rod chromosome and six ring chromosomes
Fig. 2. Metaphase I showing one pair of univalents
Fig. 3. Metaphase I showing two pairs of univalents
Fig. 4. Metaphase I showing one ring and six rods

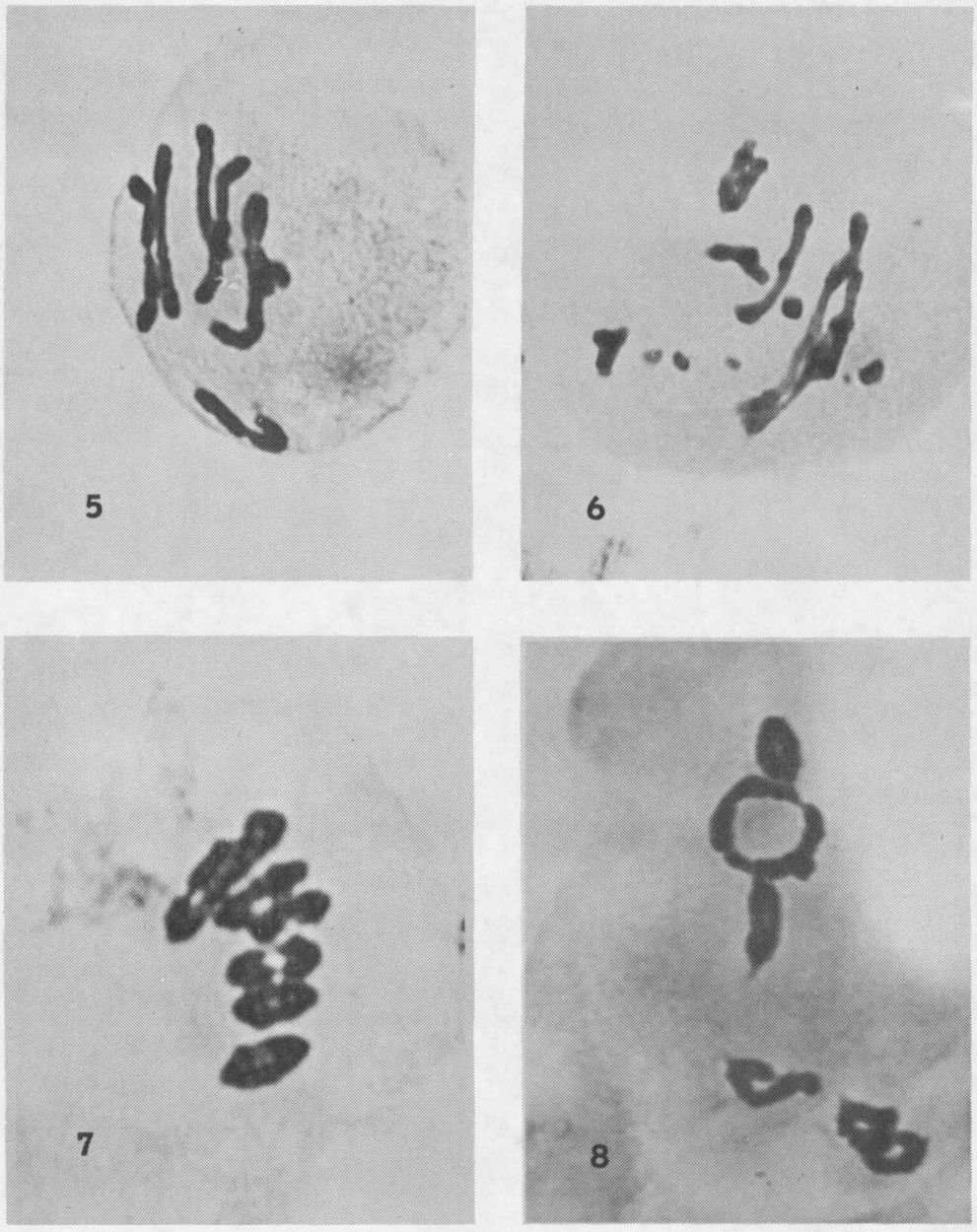
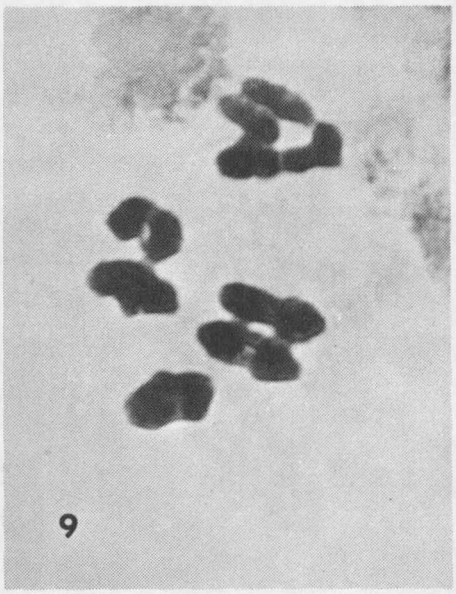
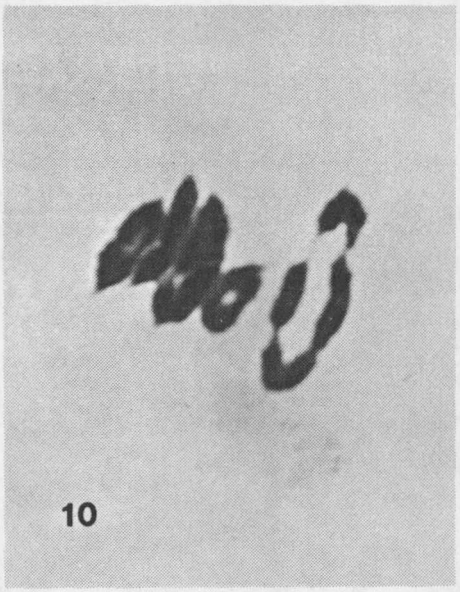
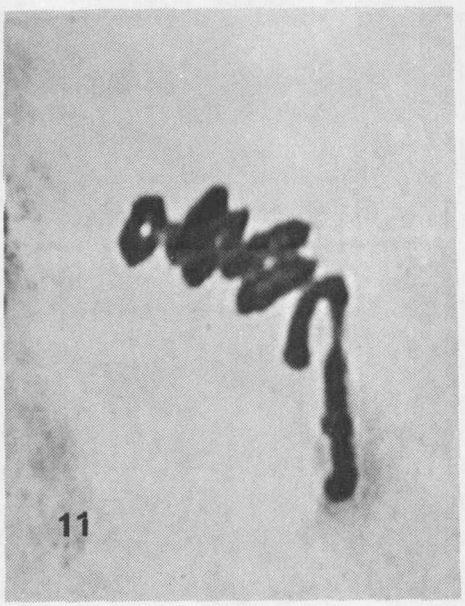


Fig. 5. Metaphase I showing seven rods
Fig. 6. Metaphase I chromosomes showing fragments
Fig. 7. Quadrivalent showing in metaphase I
Fig. 8. An "open" ring in metaphase I







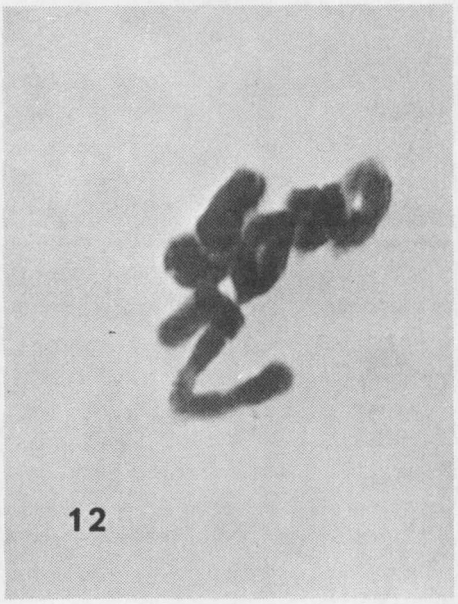
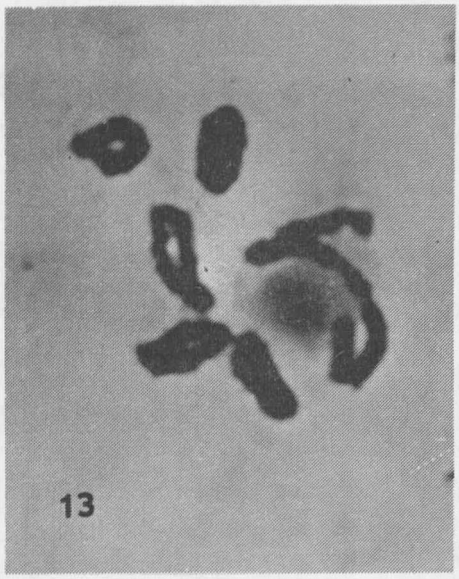
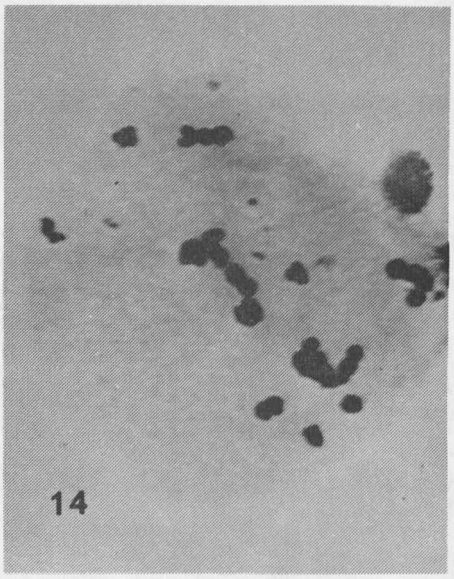
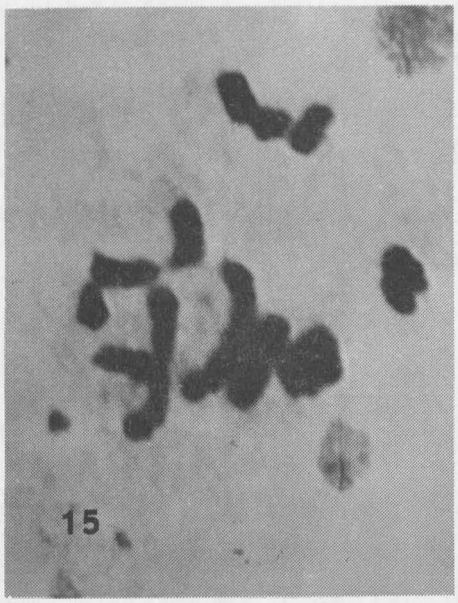


Fig. 9. A "zigzag" ring in metaphase I
Fig. 10. A non-coorientation type ring in metaphase I
Fig. 11. A J type chain of four in metaphase I
Fig. 12. A Z type chain of four in metaphase I







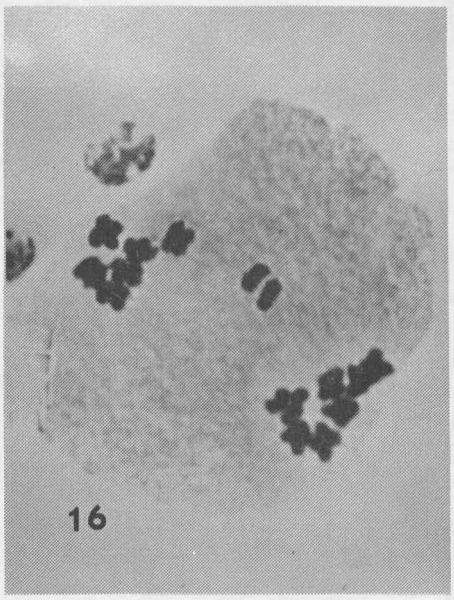
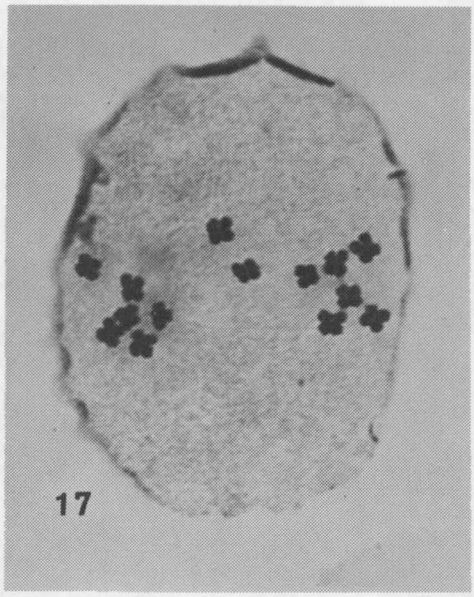
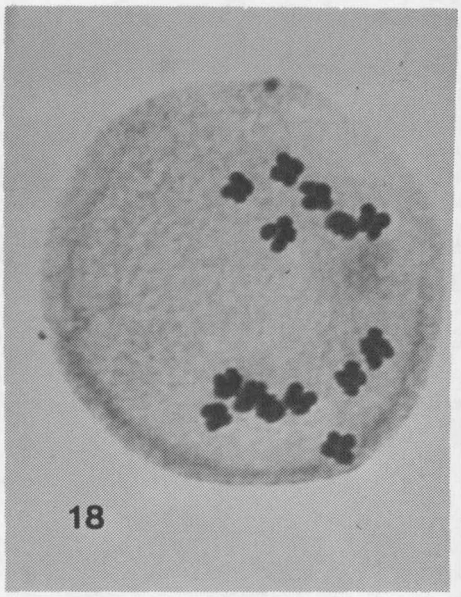
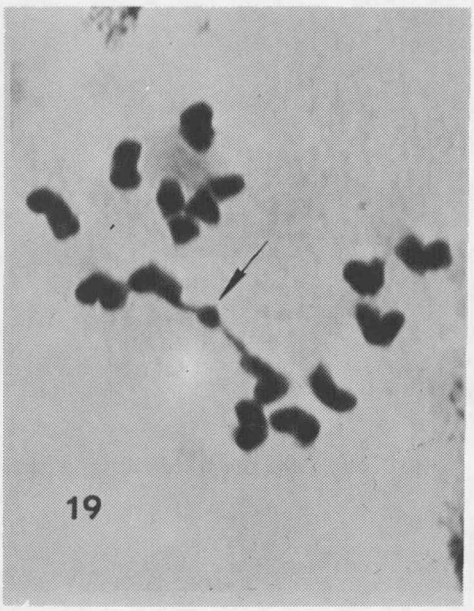


Fig. 13. Quadrivalent showing in diakinesis
Fig. 14. Metaphase I chromosome showing all univalents
Fig. 15. Metaphase I chromosome showing nonpairing
Fig. 16. A lagging chromosome with two separate chromotids showing in anaphase I







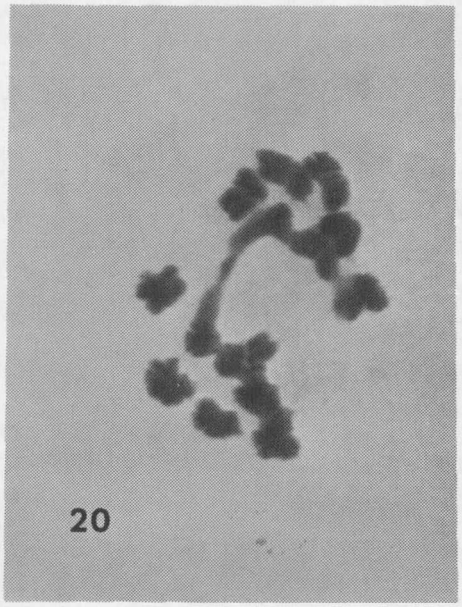
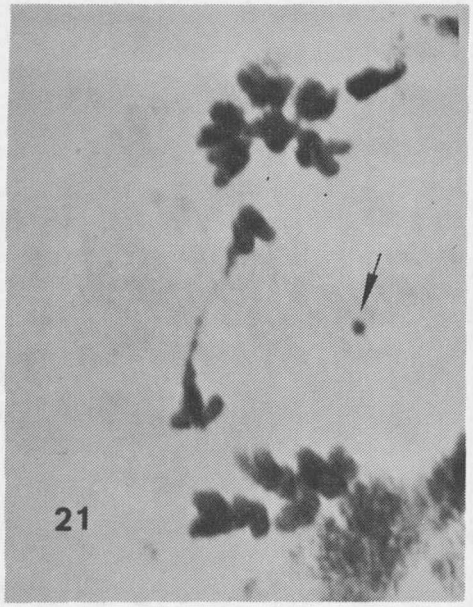
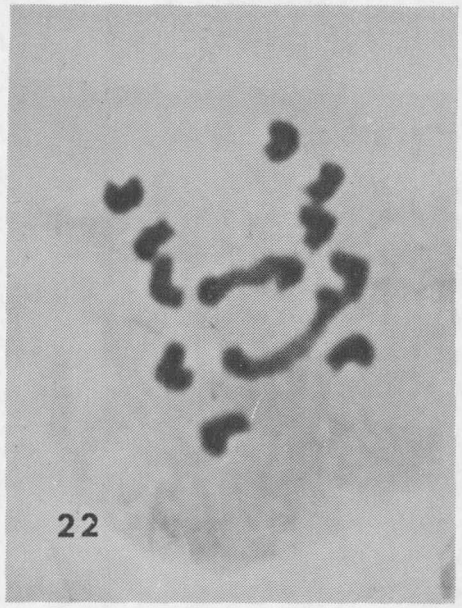
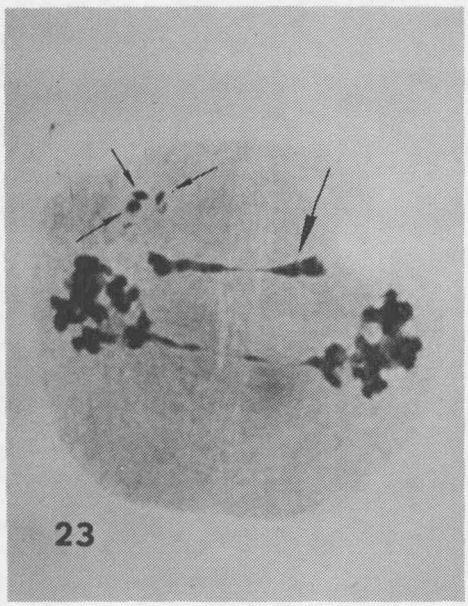


Fig. 17. Two lagging chromosomes in anaphase I
Fig. 18. A 6-8 non-disjunction in anaphase I
Fig. 19. Bridge with a tear off part in anaphase I
Fig. 20. Bridge only in anaphase I







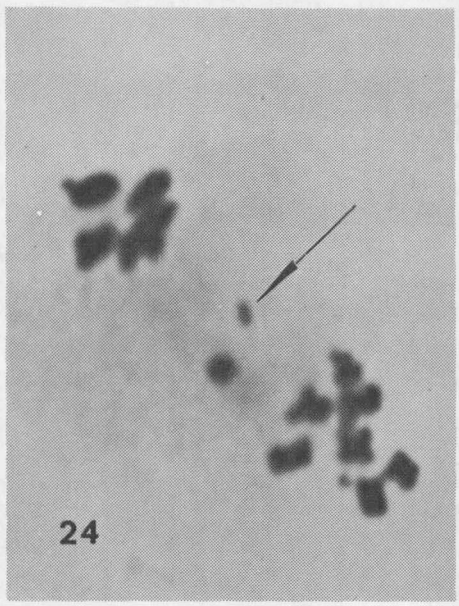


Fig. 21. A bridge and a free fragment at anaphase I
Fig. 22. Two bridges in anaphase I
Fig. 23. Two bridges and three free fragments in anaphase I
Fig. 24. A free fragment only in anaphase I

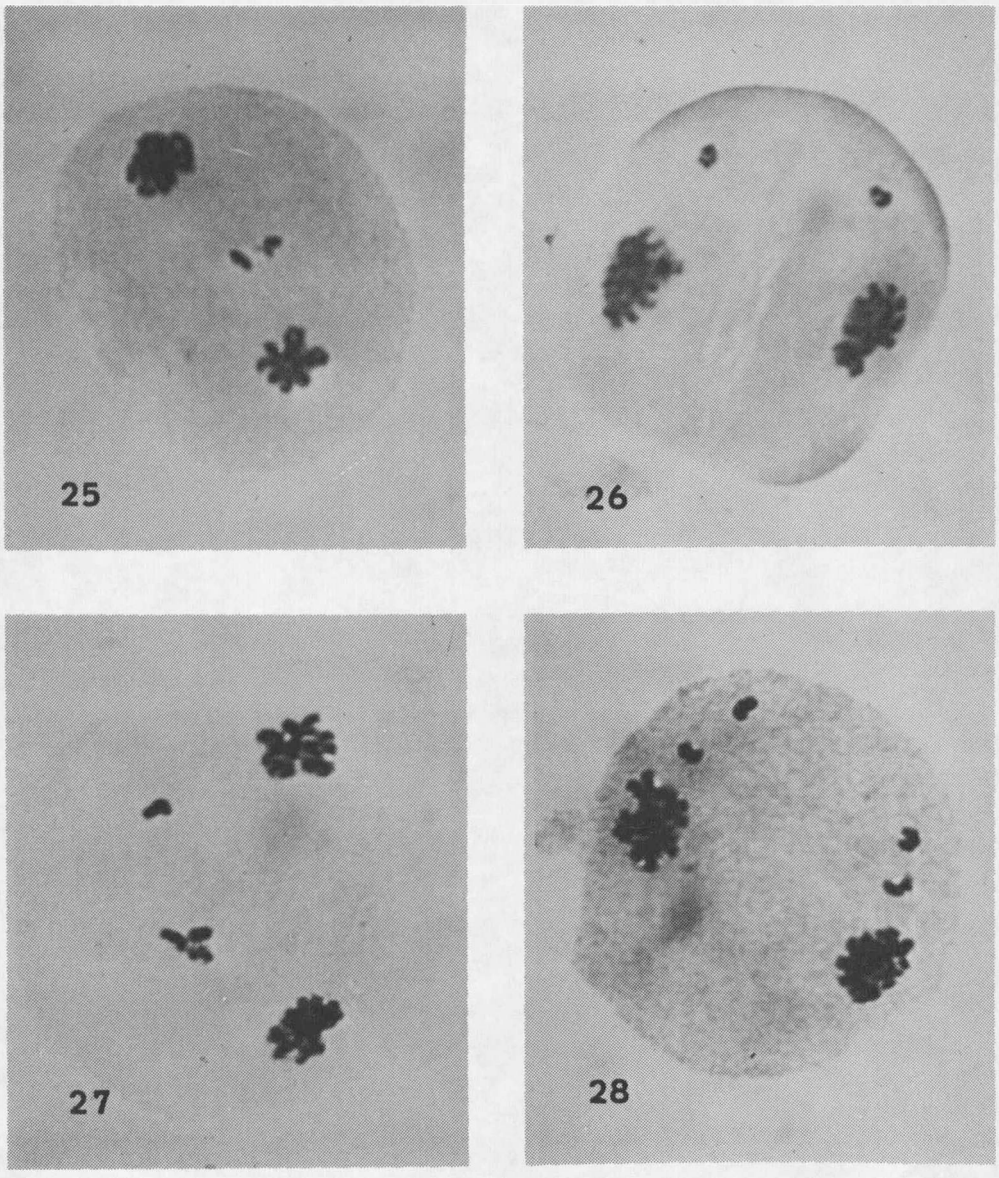


Fig. 25. Lagging chromosome with separate chromatids in early telophase I
Fig. 26. Lagging chromosome forming a micronuclei at both ends of telophase I
Fig. 27. Two pairs of lagging chromosomes with a separate chromatid in later telophase I
Fig. 28. Two pairs of lagging chromosomes in both ends of telophase I

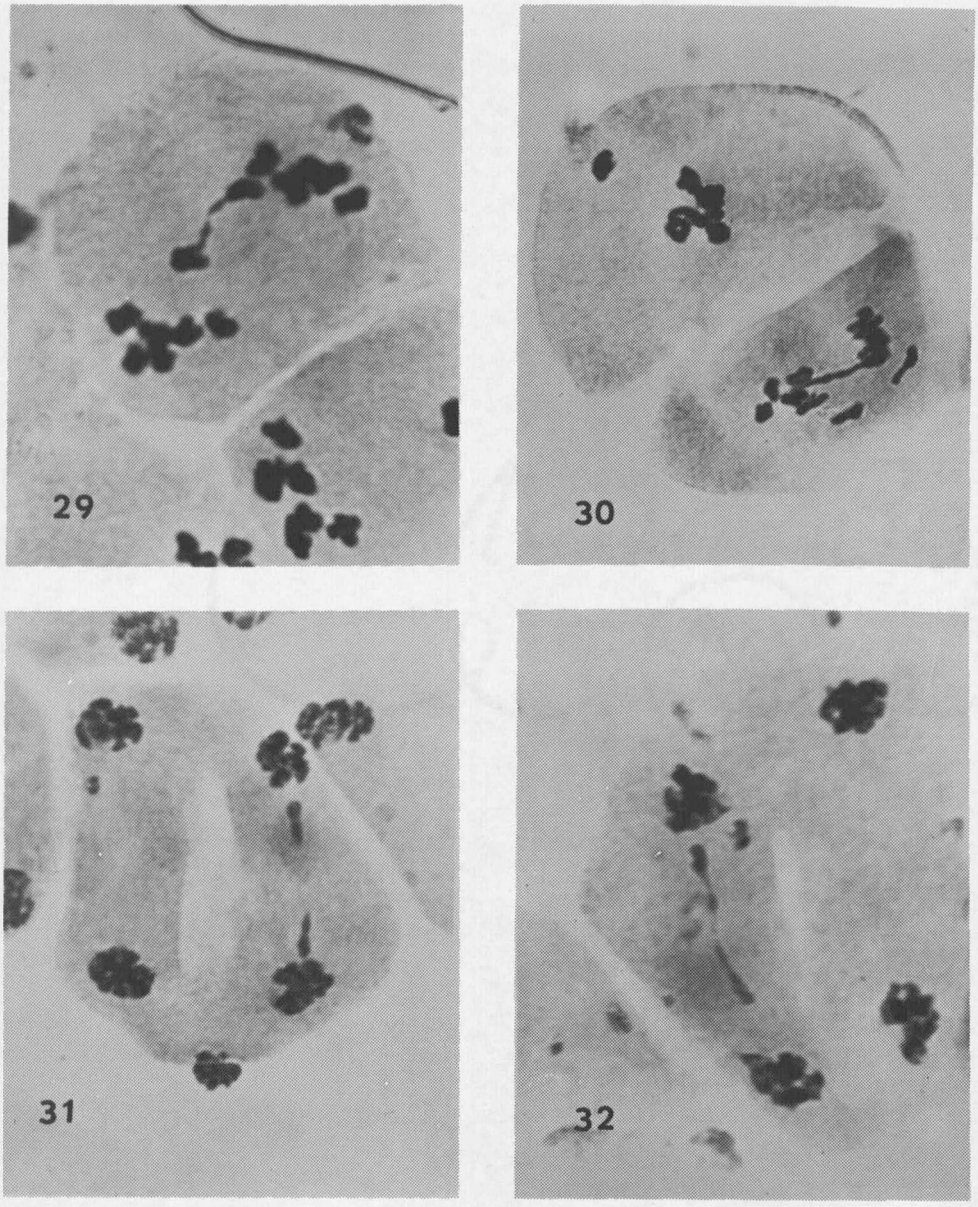
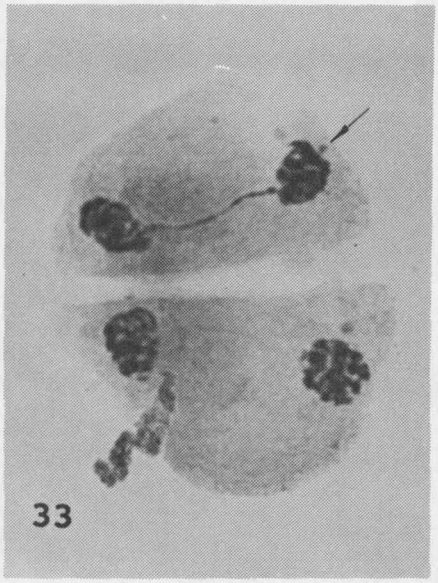
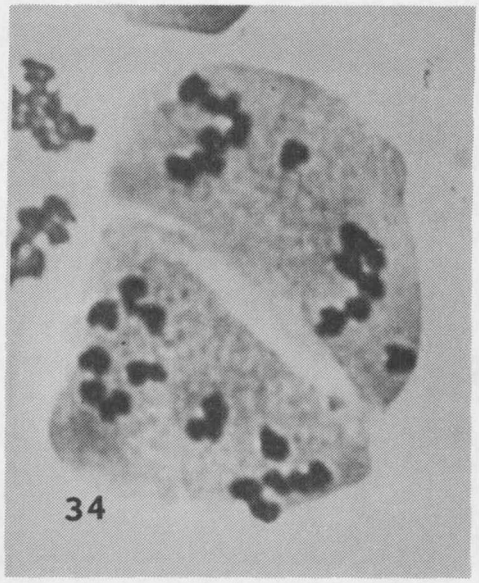
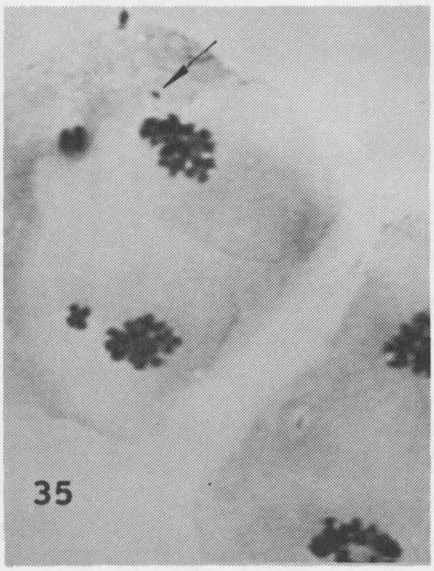


Fig. 29. Bridge only showing in anaphase II
Fig. 30. Sticky bridge in anaphase II
Fig. 31. A bridge in one of the dyads while the fragment in the other at later anaphase II
Fig. 32. A bridge and a free fragment both showing in one of the dyads in later anaphase II







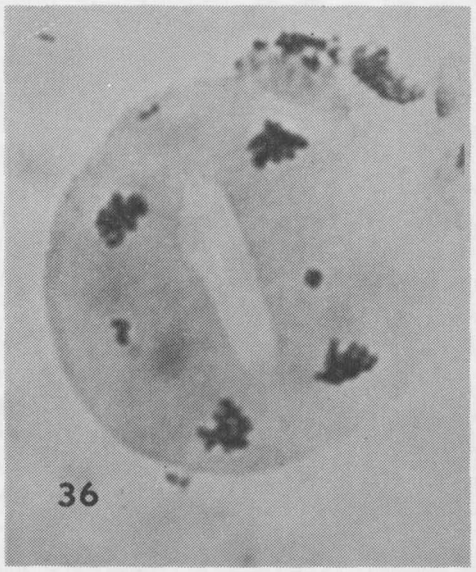
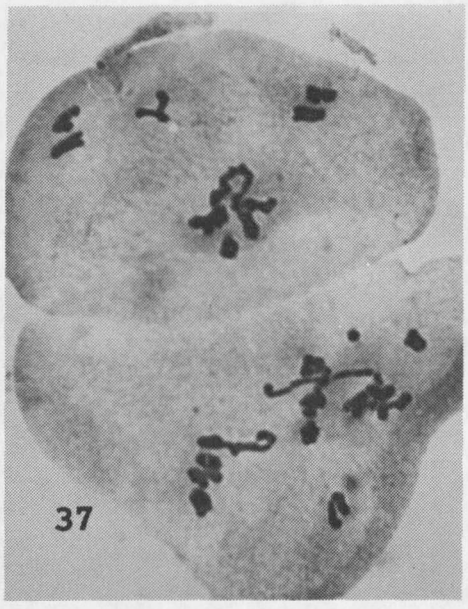


Fig. 33. A complete bridge and a free fragment showing at late telophase II

Fig. 34. Lagging chromosome showing in both cells of the dyads at anaphase II

Fig. 35. Lagging chromosome showing in both ends of one of the dyads in telophase

Fig. 36. Lagging chromosome staying at the center of both cells of the dyads in telophase II



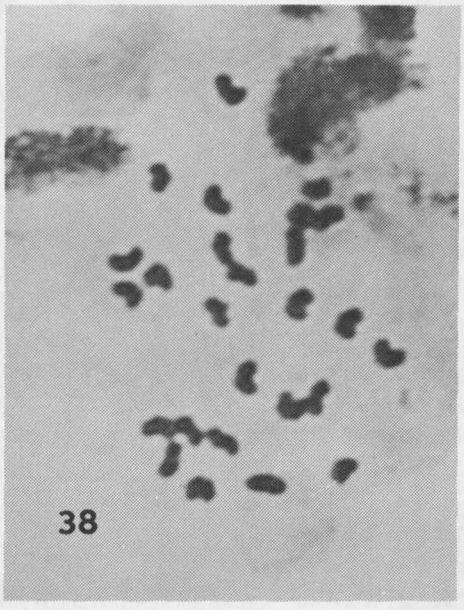


Fig. 37. Bridge like chromosomes and free fragment in anaphase II
Fig. 38. Numerous univalent chromosomes in PMC

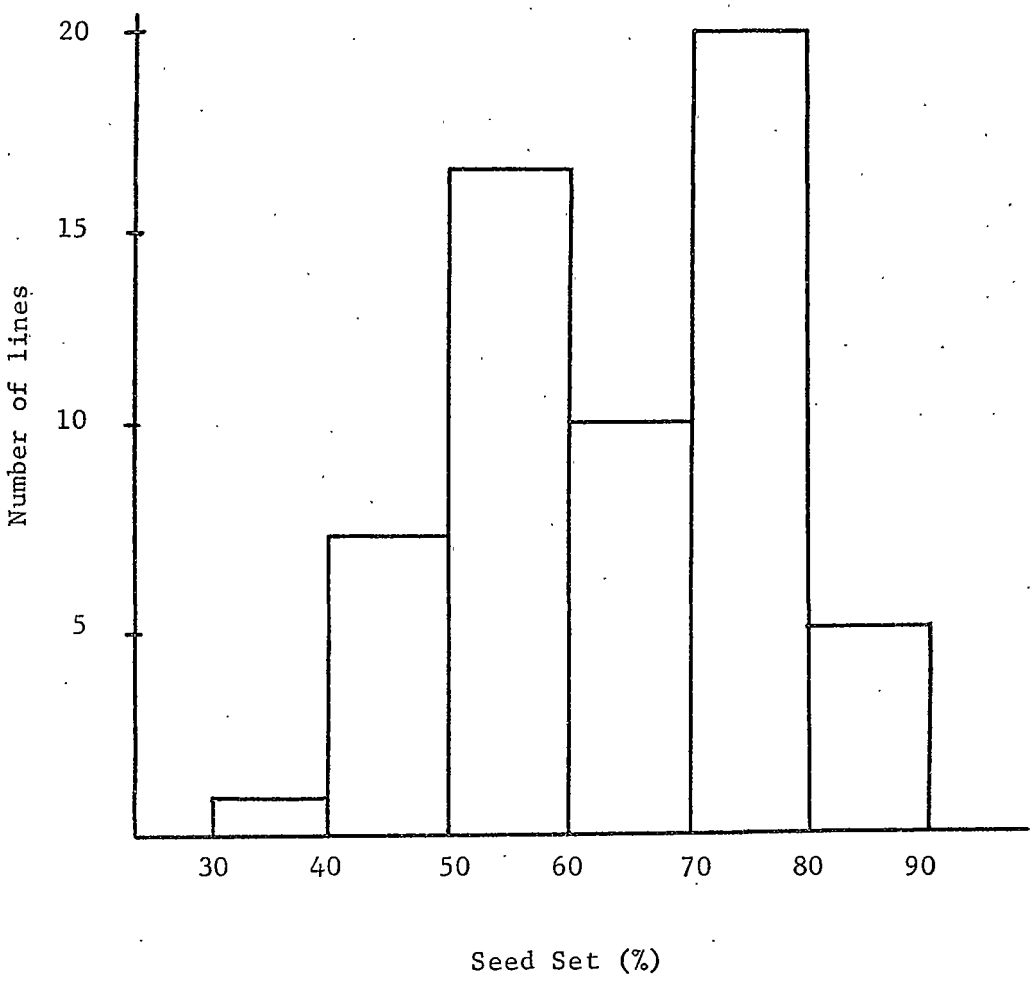


Fig. 39. Frequency distribution for seed set in the offspring of the partially sterile plants from the 60 lines.

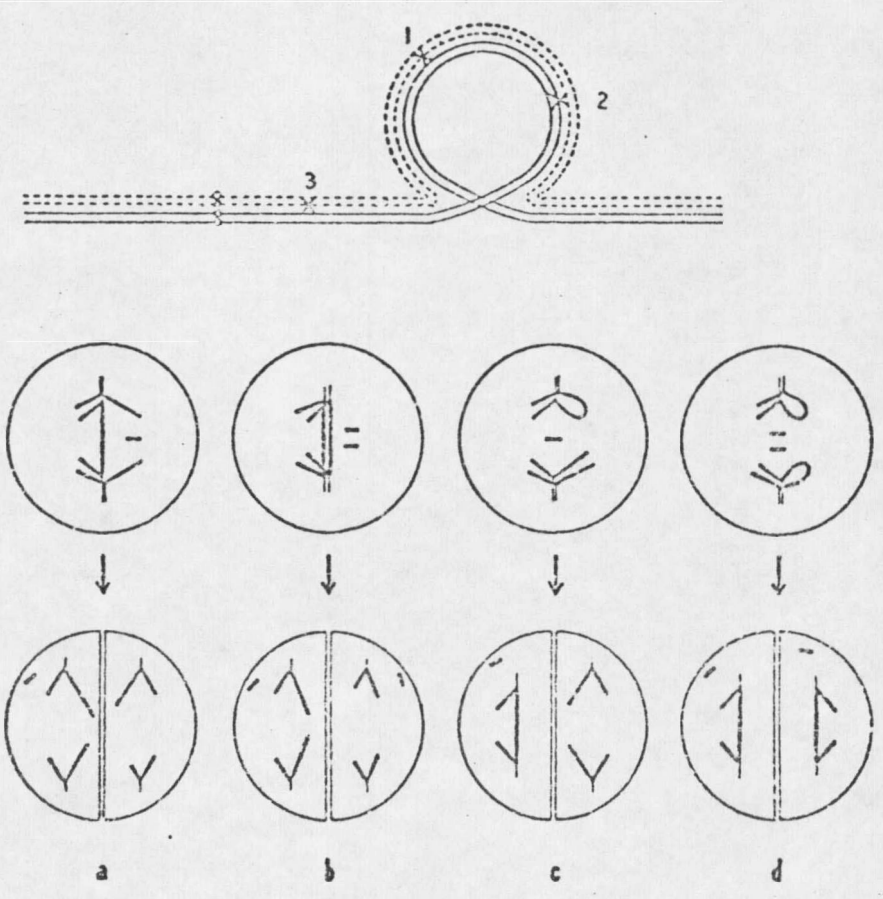


Fig. 40. Anaphase I and Anaphase II configurations resulting from various combinations of crossovers within a paracentric inversion. a, a single crossover at position 1 or 2 within the inversion loop; b, a four-strand double crossing over at position 1 and 2; c, two crossovers within and outside of the inversion loop at positions 2 and 3; d, a triple crossover at positions 1, 2 and 3 (McClintock, 1938).

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