Linkage and crossing over

INTRODUCTION

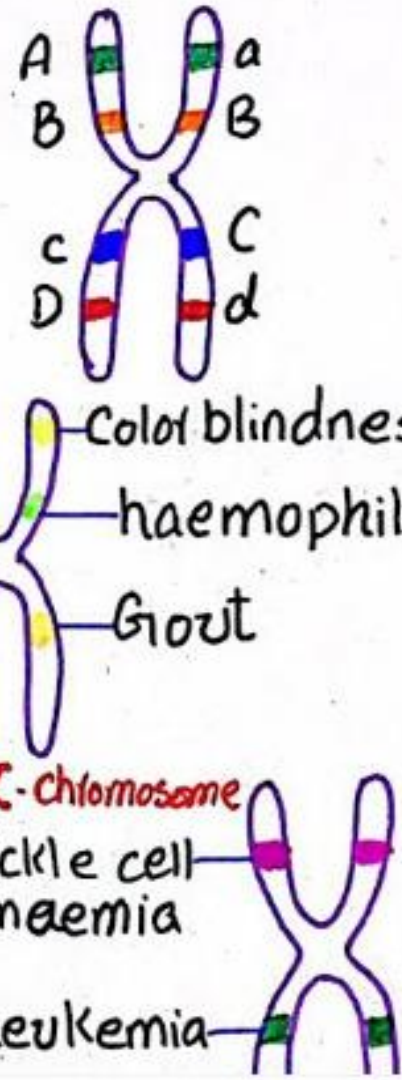
- Eukaryotic genomes contain hundreds to thousands of genes
  - Yet most species have fewer than 50 chromosomes in a haploid set
    - Humans have only 23 chromosomes per haploid set but have ~25,000 genes
- Therefore, each chromosome carries hundreds or even thousands of different genes
  - The transmission of such genes may go against Mendel's law of independent assortment

Gene Linkage

- Every organism → numerous characters
- controlled by thousands of Genes.
- But number of chromosomes is limited
- Each chromosome → Many Genes
- All the genes of same chromosome
  ↳ Linked to each other

→ Phenomenon of staying together of all genes of a chromosome is called **linkage**

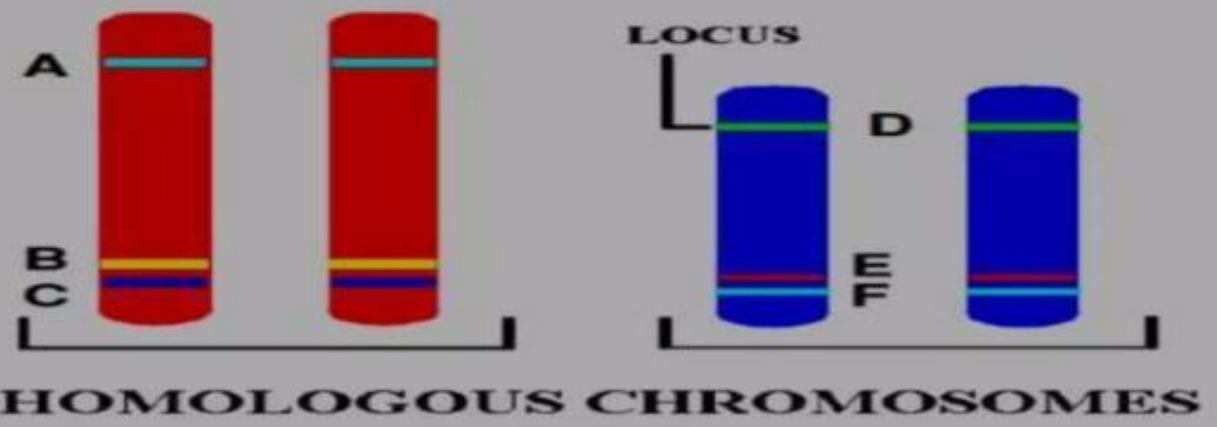
- Gene linkage is physical relationship between genes.



- Number of linkage group
  ↳ Number of homologous Pairs
- Man 23 linkage groups
- Linked genes whose loci are closed
- Do not obey "Mendel's Law of independent Assort-ment" because they
- Cannot assort independently
- Gene linkage minimize the chances of
- genetic recombination

Introduction

- The phenomenon of linkage was first reported by Bateson and Punnet in 1906, during investigation of flower colour and pollen shape in sweet pea
- Independent assortment : During gamete formation, the two alleles for one gene segregate or assort independently of the alleles for other genes.
- Genes whose loci are nearer to each other are less likely to be separated on to different chromatids during chromosomal crossover, and are therefore said to be genetically ***linked***.



LINKED GENES

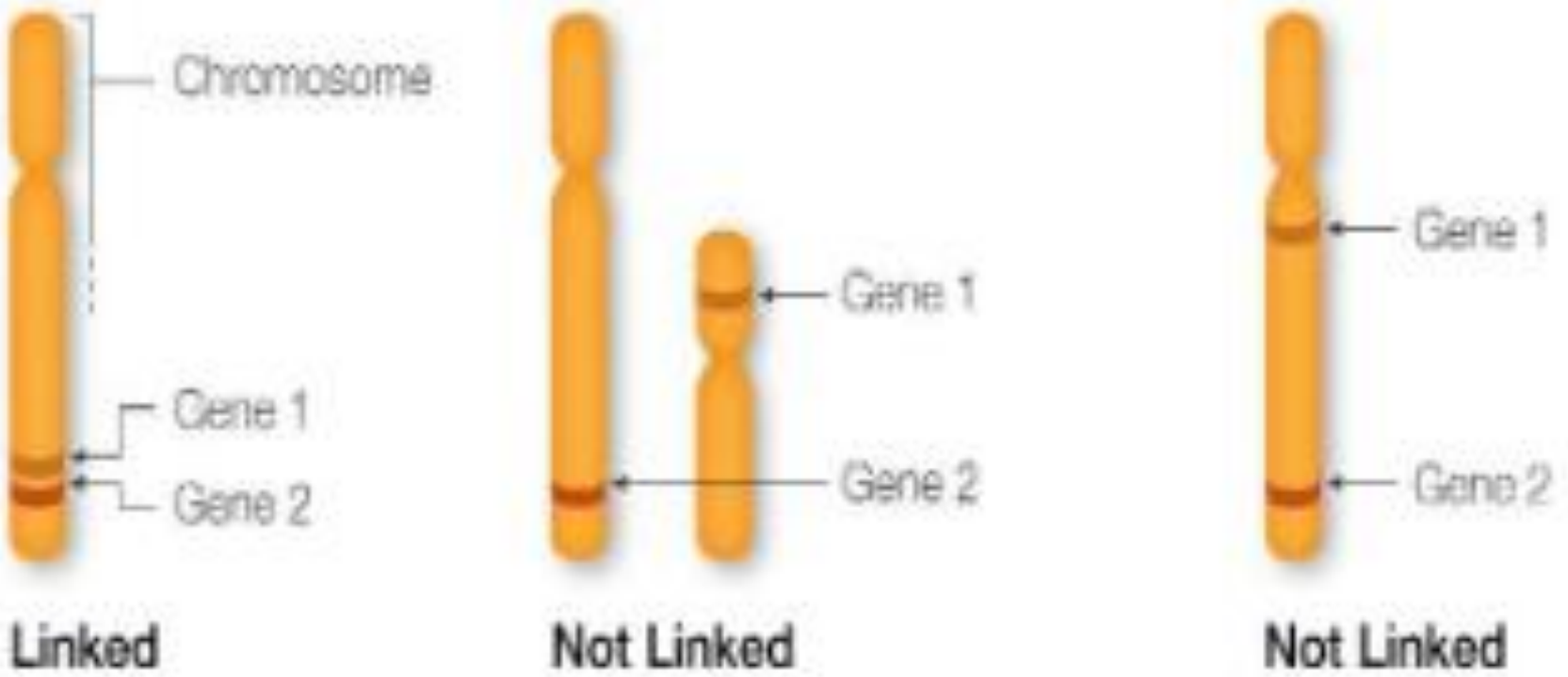
- Genes present at the same locus have the tendency to be linked together from one generation to the other and are not disturbed by the meiotic recombination.
- Linkage is defined as "**the tendency of genes to remain together during the process of inheritance**".
- When two loci were linked genetically on the same chromosome they did not segregate.
- Extent of linkage - closer the genes, stronger the linkage and vice versa.
- Linkage of genes is in the linear fashion in the chromosomes.

LINKAGE

- The genes that show linkage are located on the same chromosome.
- A linkage group is formed by all the linked genes in a chromosome.
- The strength of linkage between two genes is directly proportional to the distance between them.

Genetic linkage is the tendency of genes that are located close to each other on a chromosome to be inherited together during meiosis.

Genes whose loci are nearer to each other are less likely to be separated onto different chromatids during chromosomal crossover, and are therefore said to be genetically linked.


Chromosome
Gene 1
Gene 2
Linked
Gene 1
Gene 2
Not Linked
Gene 1
Gene 2
Not Linked

Linkage types

❑ **Types of Linkage:** It is classified on the basis of three criteria viz.,

(i) Based on crossing over

(ii) Based on genes involved

(iii) Chromosomes involved

(i) Based on crossing over :

(a) Complete linkage:

➢ It is known in case of males of *Drosophila* and females of silkworms, where there is complete absence of recombinant types due to absence of crossing over.

(a) Incomplete / partial linkage:

➢ If some frequency of crossing over also occurs between the linked genes, it is known as incomplete linkage. Observed in maize, pea, *Drosophila* etc.

(ii) Based on genes involved : Depending on whether all dominant or some dominant and some recessive alleles are linked together, linkage can be categorized into

(a) Coupling phase: All dominant alleles are present on the same chromosome or all recessive alleles are present on same chromosome.

(b) Repulsion phase: Dominant alleles of some genes are linked with recessive alleles of other genes on same chromosome.

Example : Let (T & t) and (R & r) are alleles of two different genes.

TR or tr alleles on same chromosome	Coupling phase
Tr or tR alleles on same chromosome	Repulsion phase

(iii) Based on chromosomes involved :

a) Autosomal linkage: It refers to linkage of those genes which are located in autosomes (other than sex chromosomes).

b) X-chromosomal linkage / allosomal linkage / sex linkage: It refers to linkage of genes which are located in sex chromosomes .

Characteristic features of Linkage

1. Linkage involves **two or more genes which are located in same chromosome** in a linear fashion.
2. Linkage reduces variability.
3. Linkage may involve either dominant or recessive alleles (**coupling phase**) or some dominant and some recessive alleles (**repulsion phase**).
4. It may involve either all desirable traits or all undesirable traits or some desirable and some undesirable traits.
5. It is observed for **oligogenic traits** as well as **polygenic traits**.
6. Linkage usually involves those genes which are located close to each other.
7. The **strength of linkage** depends on the distance between the linked

Characteristic features of Linkage

8. Presence of linkage leads to **higher frequency of parental types** than recombinants in test cross.
9. When two genes are linked the segregation ratio of dihybrid test cross progeny deviates significantly from 1:1:1:1 ratio.
10. Linkage can be determined from **test cross progeny data.**
11. **Maximum number of linkage groups** possible in an organism is equal to the haploid chromosome number. Onion 2n = 16 and n = 8 maximum linkage groups possible = 8
12. Linkage can be **broken by repeated intermating** of randomly selected plants in segregating population for several generations **or by mutagenic treatment.**
13. Besides pleiotropy, linkage is an important **cause of genetic correlation** between various plant characters.

(Pleiotropy refers to the control of two or more characters by a single gene.)

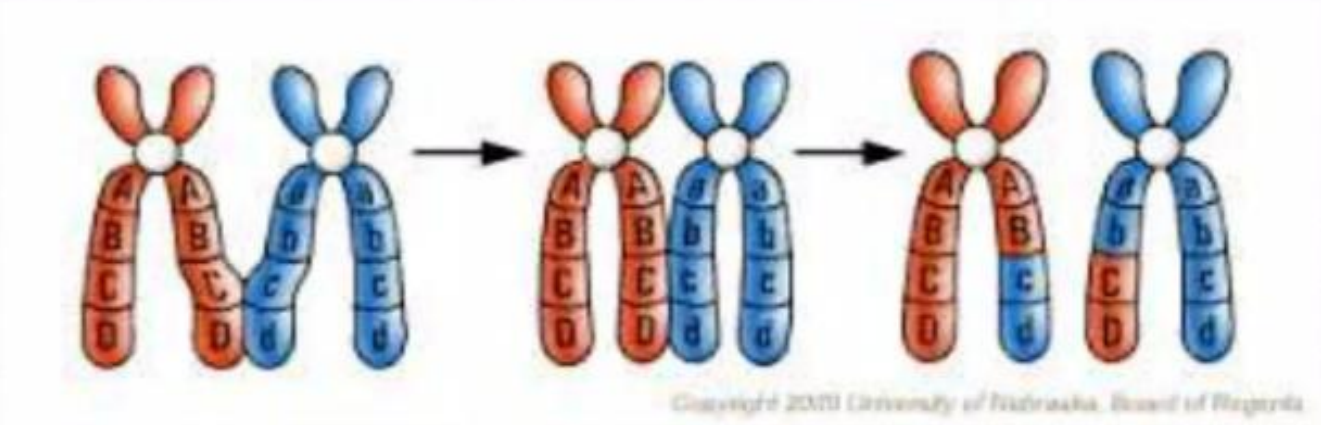
Significance of Linkage in Plant Breeding

- Linkage **limits the variability** among the individuals.
- Linkage between two or more loci controlling different **desirable characters is advantageous for a plant breeder.**
- A linkage between genes controlling two different desirable characters will help in simultaneous improvement of both the characters.
- Linkage is undesirable when desirable and undesirable genes are linked together.
- The estimates of **genetic variances** for quantitative characters are greatly influenced by the presence of linkage

(RECOMBINATION)

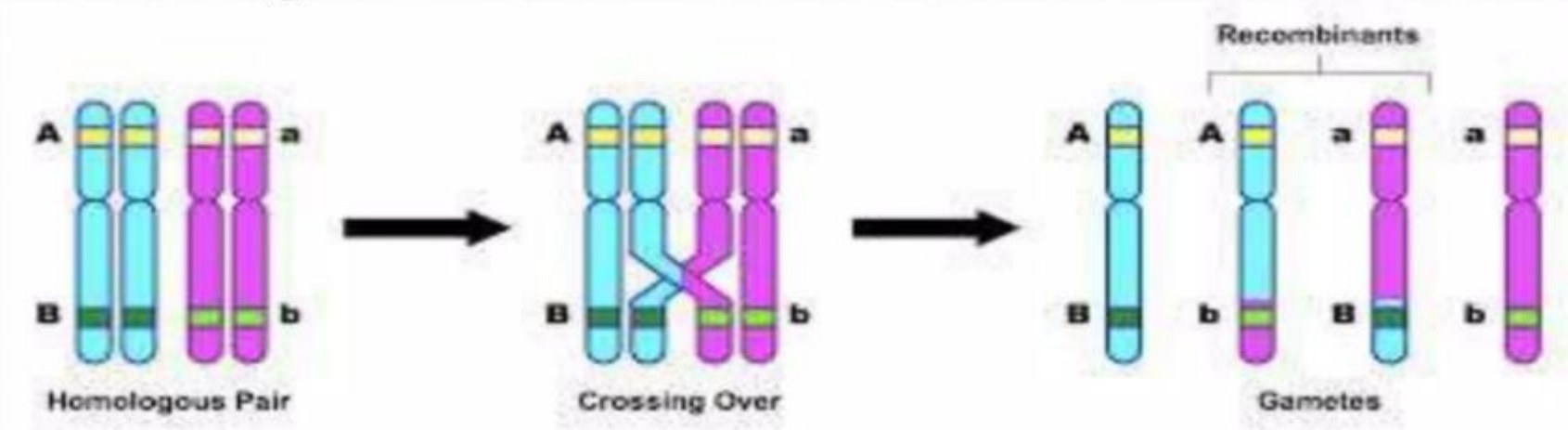
CROSSING OVER :-

- The word **CROSSING OVER** (or) **CHROMOSOMAL CROSSOVER** means the exchange of GENETIC materials between **HOMOLOGOUS** chromosomes that results in the MIXTURE of PARENTAL characteristics in **OFFSPRING.**

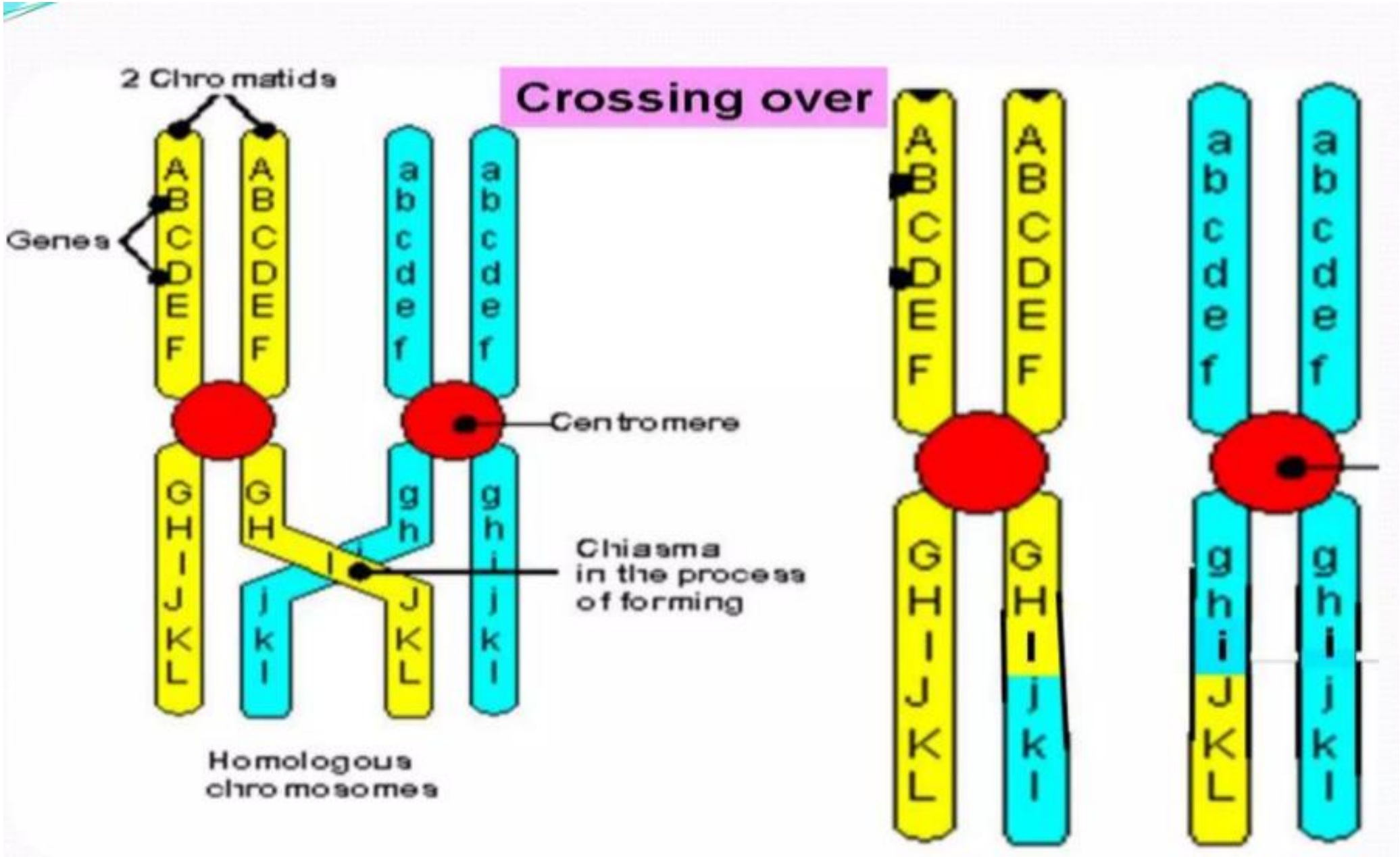


DISCOVERED :-

- Crossing over was first discovered by **THOMAS HUNT MORGAN**.
- When the genes are located closely the chance for crossing over is **LESSER**.
- When the genes are located distantly the chance for crossing over is **HIGHER**.



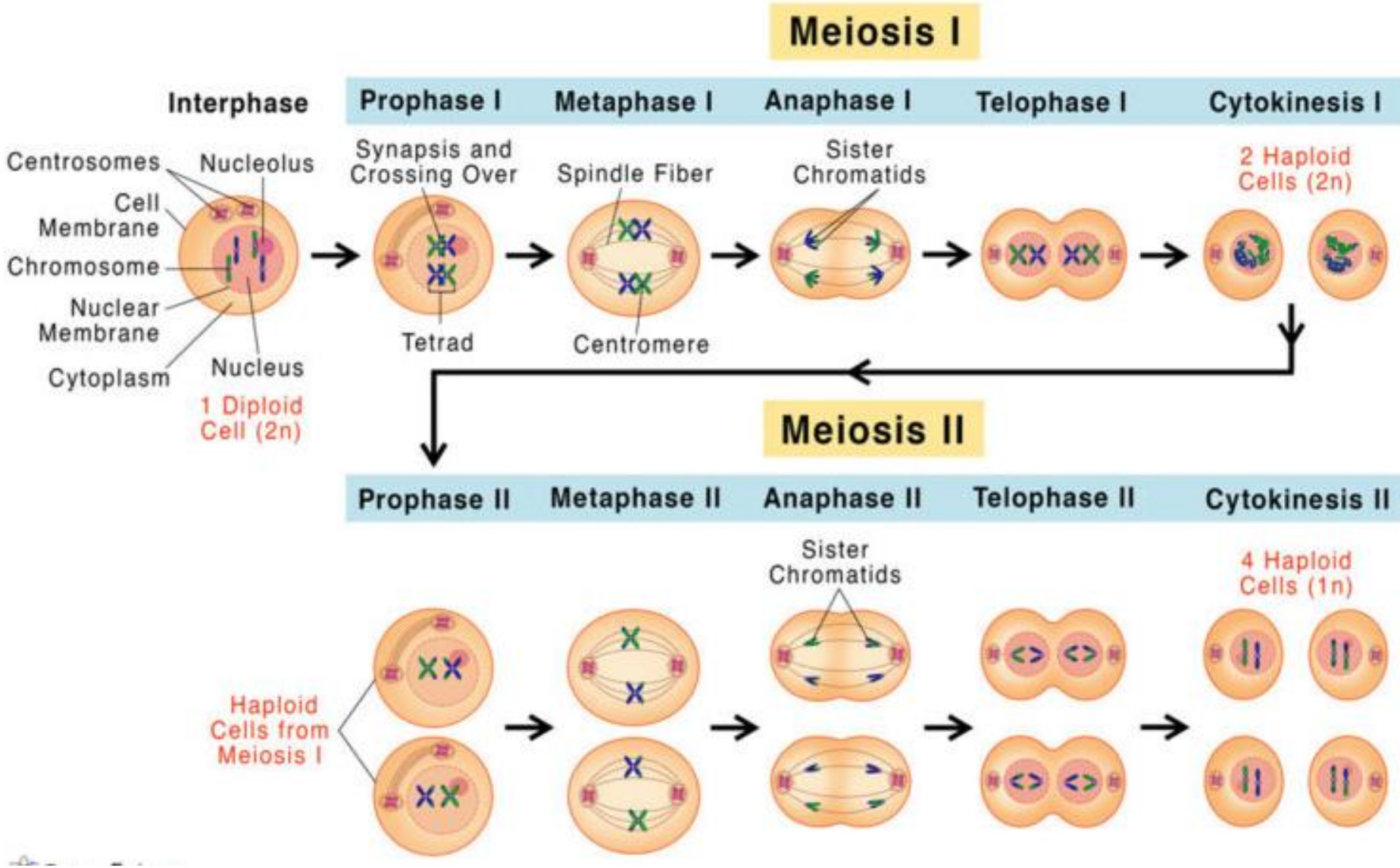
- Crossing over, as related to genetics and genomics, refers to the exchange of DNA between paired homologous chromosomes (one from each parent) that occurs during the development of egg and sperm cells (meiosis). This process results in new combinations of alleles in the gametes (egg or sperm) formed, which ensures genomic variation in any offspring produced.
- Usually crossing over occurs in germinal cells during gametogenesis. It is called meiotic or germinal crossing over.
- The two chromosomes contain the same genes, but may have different forms of the genes. The mother's form of a gene, let's say, could be moved to the father's chromosome, and vice versa. This is a very interesting and important biological activity; different combinations of different gene forms are then potentially passed down to offspring.
- This genetic variation helps to increase the diversity of a species. And diversity strengthens a species' ability to respond to changing environments over time, and therefore evolve.

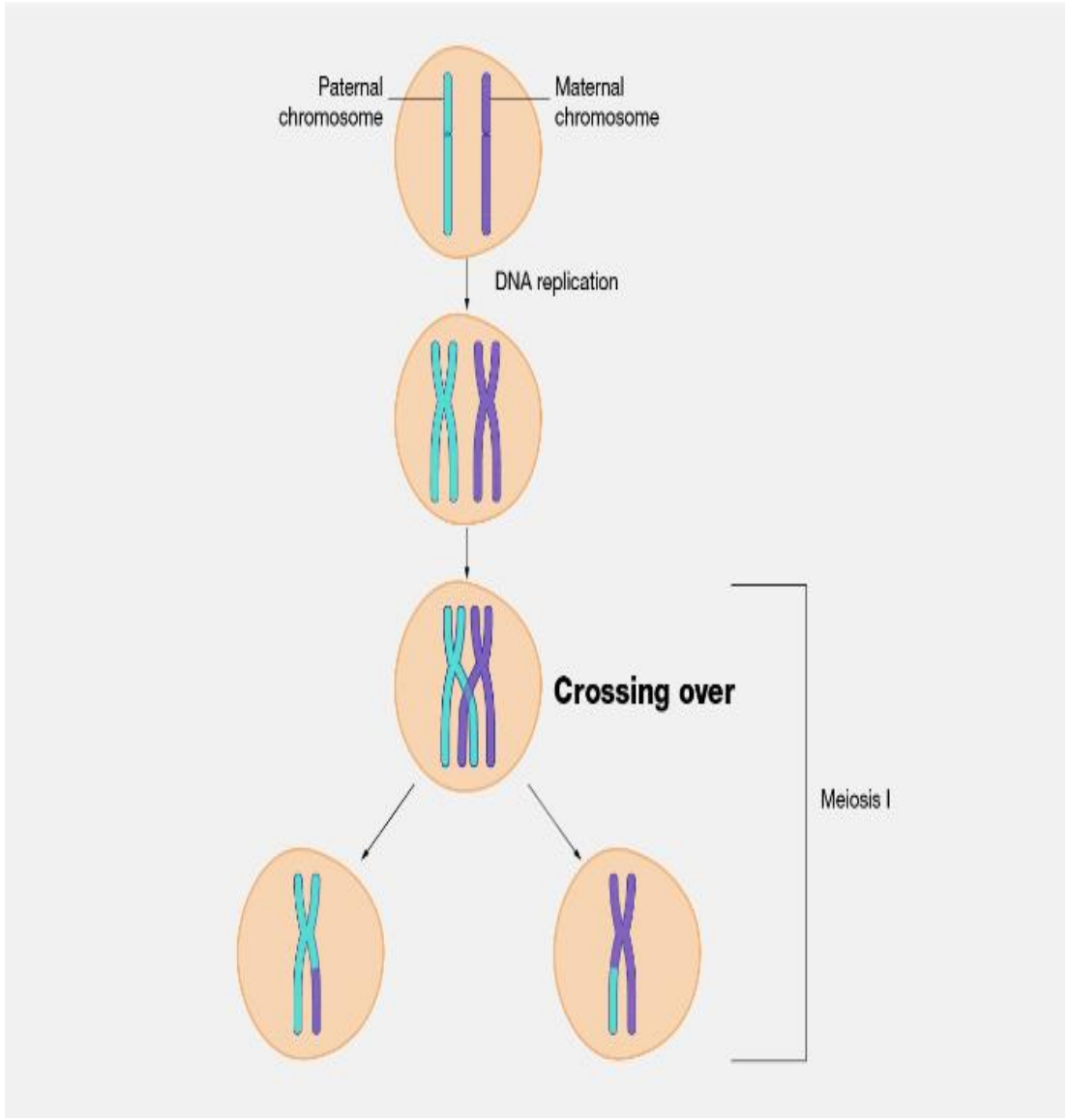

Crossing over
2 Chromatids
Genes
A B C D E F
a b c d e f
G H I J K L
g h i j k l
Centromere
Chiasma
in the process
of forming
Homologous
chromosomes

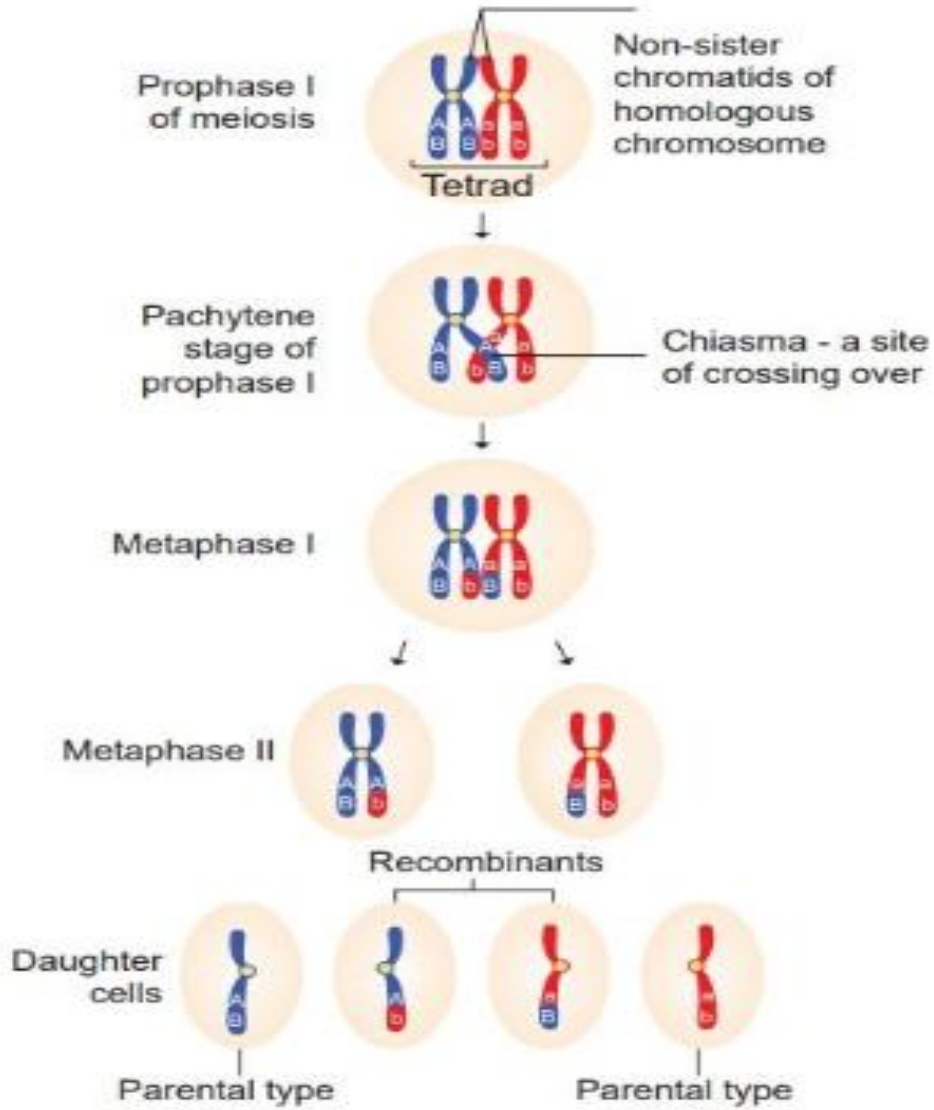
Crossing-over

- Crossing-over takes place during pachytene sub-stage of **prophase I of meiosis,**but visible at diplotene sub-stage .
- The term crossing over was coined by **Morgan**.
- It is another name for recombination or physical exchange of equal pieces of adjacent non-sister chromatids.
- During the process of crossing-over one of the paired chromosome arms exchanged physically at one or more locations.
- The two homologous chromosomes are connected at a certain point called **chiasma. When crossing-over occurs** chromatids break at chiasma and reattached to a different homologous chromosome .
- The chromatids resulting from the interchange of segments are known as the **cross over recombinants** and the chromatids that remain intact are called **noncrossover parental chromatids.**

Meiosis


Meiosis I
Interphase
Prophase I
Metaphase I
Anaphase I
Telophase I
Cytokinesis I
Centrosomes
Nucleolus
Cell Membrane
Chromosome
Nuclear Membrane
Cytoplasm
Nucleus
1 Diploid Cell (2n)
Synapsis and Crossing Over
Tetrad
Spindle Fiber
Centromere
Sister Chromatids
2 Haploid Cells (2n)
Meiosis II
Prophase II
Metaphase II
Anaphase II
Telophase II
Cytokinesis II
Haploid Cells from Meiosis I
Sister Chromatids
4 Haploid Cells (1n)


Paternal chromosome
Maternal chromosome
DNA replication
Crossing over
Meiosis I


Prophase I of meiosis
Non-sister chromatids of homologous chromosome
Tetrad
Pachytene stage of prophase I
Chiasma - a site of crossing over
Metaphase I
Metaphase II
Recombinants
Daughter cells
Parental type
Parental type

The major steps in meiotic crossing over

- 1) **Synapsis**-The pairing phenomenon of homologous chromosomes in presence of syneptonemal complex(DNA and Protein).
- 2) **Duplication of chromosome**-Homologous chromosome gets duplicated to form chromatid.
- 3) **Crossing over** –The exchange of chromosomal segments between two non-sister chromatids
- 4) **Terminalisation**-Sepration of non homologous chromosomes after crossing over

a. Synapsis:

During zygote stage of prophase I of meiosis occurring in the developing sex-cells, the homozygous chromosomes come close to each other and pairing or synopsis between the homozygous chromosomes takes place at synaptotene or zygotene substage.

b. Duplicationg of chromosomes:

During the pachytene stage of prophase I of meiosis, duplication of chromosomes took place. During this stage, each homologous chromosome of a bivalent split longitudinally into two sister chomatids. Thus the bivalent now consists of four chromatids and is known as tetrad.

c. Crossing over:

The crossing over occurs in the homologous only during the four stranded of tetrad stage. During the process of crossinover, two non-sister chromatids first break at the corresponding points due to the activity of a nuclear enzyme called *endonuclease*.

After this, a segment of one side of each connect with as segment of the opposite side of the break, so that the two non-sister chromatids cross each other at a point of break and exchange. The fusion of the chromosomal segments with that of opposite one take place due to the action of an enzyme called, *Ligase*. The crossing of the two chromatids is called chiasma formation and the resultant cross as Chiasma or Chiasmata.

Mechanism of crossing over

- Crossing over, leading to recombination of linked genes, is due to interchange of sections of homologous chromosomes.
- At meiosis, the homologous chromosomes come together and pair, or synapse, during prophase.
- The pairing is remarkably precise and is evidently brought about by mutual attraction of the parts of the chromosomes that are similar or homologous because they contain allellic genes.

Types of crossing over

1. Somatic crossing over-

Pairing of homologous chromosomes occurs in germinal cells but some times in somatic cells. Somatic crossing over is reported in **Drosophila** by **Curt Stern (1935).**somatic crossing over occurs rarely.

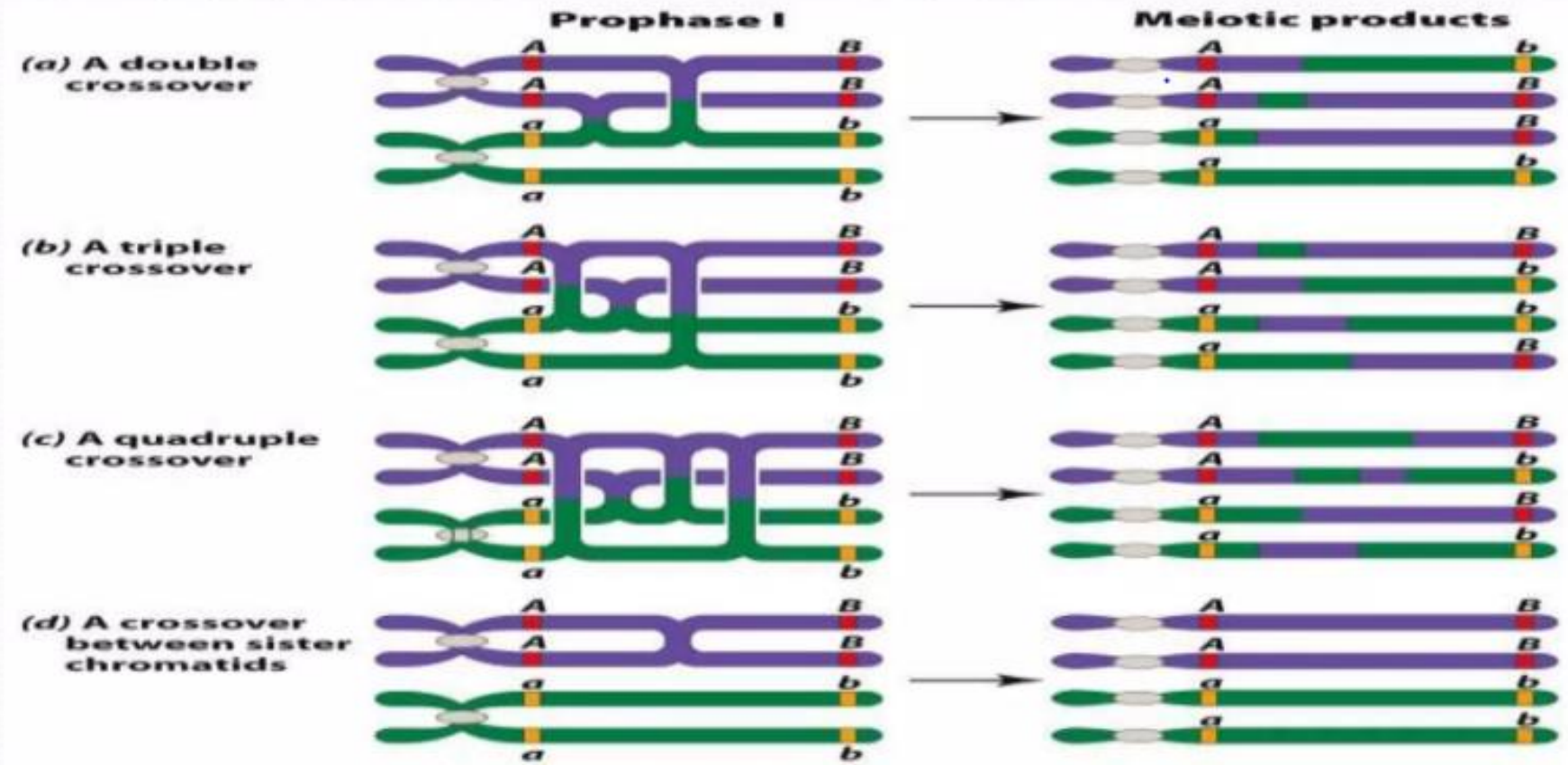
2.Meiotic crossing over or germinal crossing over-

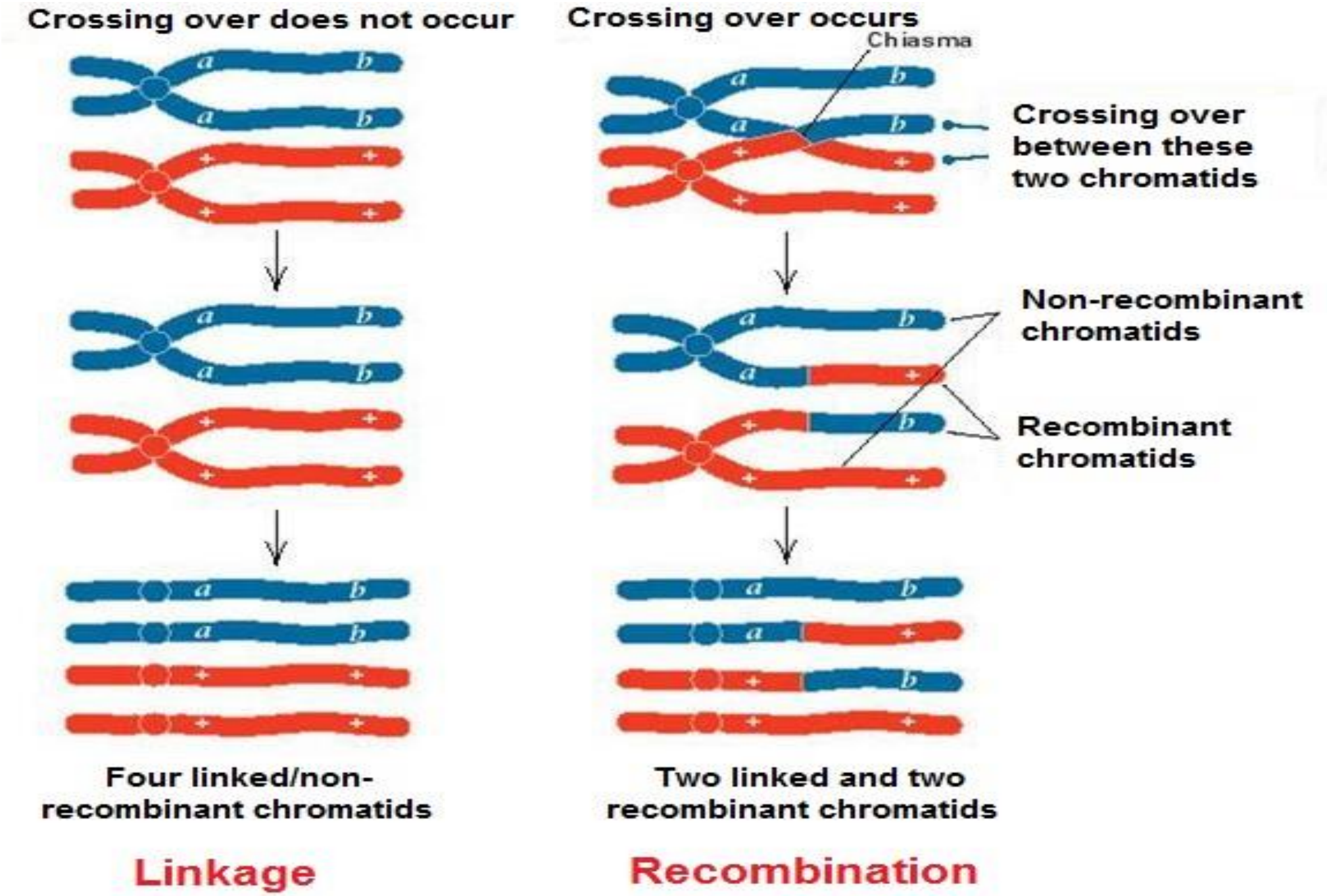
- This type of crossing over takes place in germinal cells during gametogenesis.

- **Kinds of Crossing Over**
- Single crossing over (only one chiasmata is form)
- Double crossing over (two chiasmata are form)
- Multiple crossing over . (more than two chiasmata are formed)

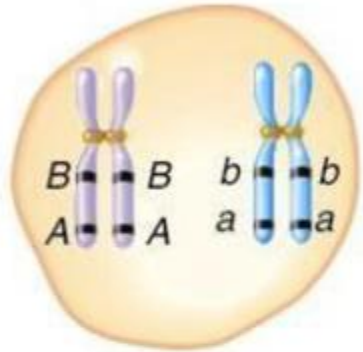
MULTIPLE CROSSING OVER :-

- When there are **many** crossing over in a homologous chromosomes then it is called as **MULTIPLE CROSSING OVER.**



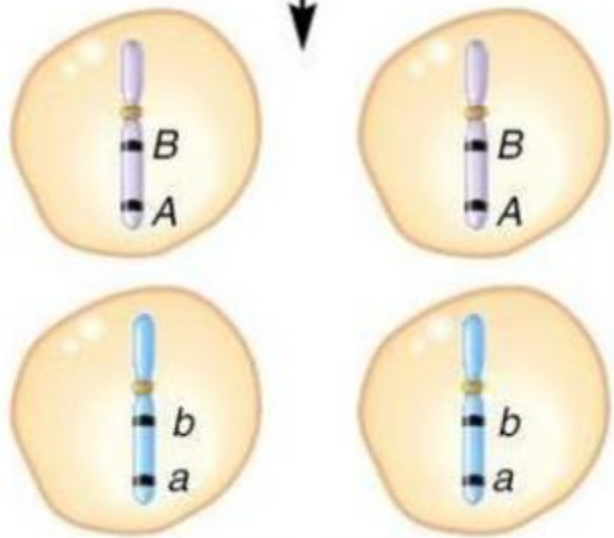

Crossing over does not occur
Crossing over occurs
Chiasma
Crossing over between these two chromatids
Non-recombinant chromatids
Recombinant chromatids
Four linked/non-recombinant chromatids
Two linked and two recombinant chromatids
Linkage
Recombination

IF NO CROSSING OVER IN REGION BETWEEN THE TWO GENES
= 100% Non-Recombinants



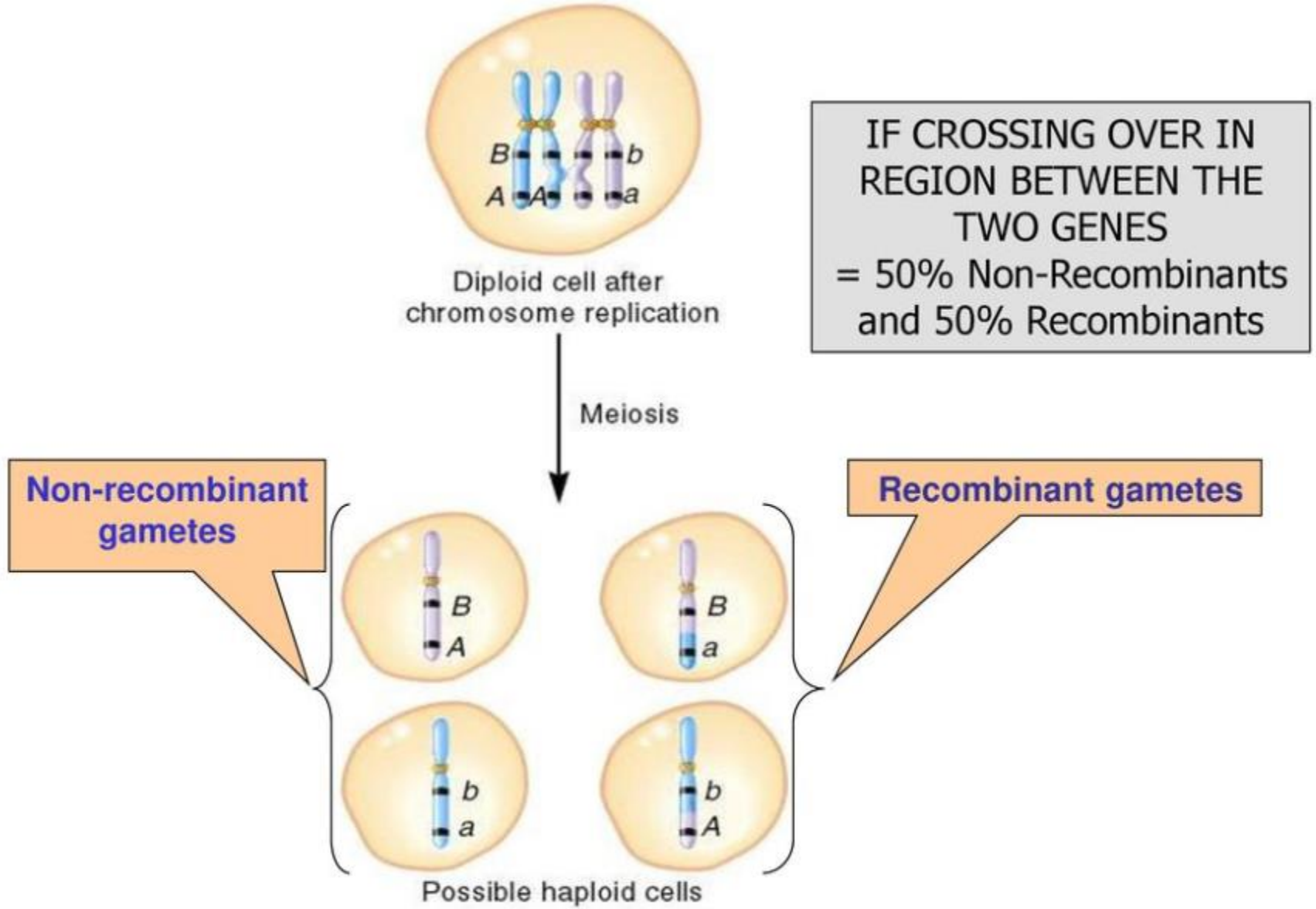
Diploid cell after chromosome replication

Meiosis



Possible haploid cells

The arrangement of linked alleles has not been altered



IF CROSSING OVER IN REGION BETWEEN THE TWO GENES
= 50% Non-Recombinants and 50% Recombinants

(b) Crossing over can reassort linked alleles.

Recombination Frequency

- Recombination fraction or frequency is a measure of the distance between two loci.
- Two loci that show 1% recombination are defined as being 1 **centimorgan** (**cM**) apart on a genetic map.
- 1 map unit = 1 cM (centimorgan)

- Two genes that carry out independent assortment have recombination frequency of 50 percent and are located on nonhomologous chromosomes or far apart on the same chromosome = un-linked

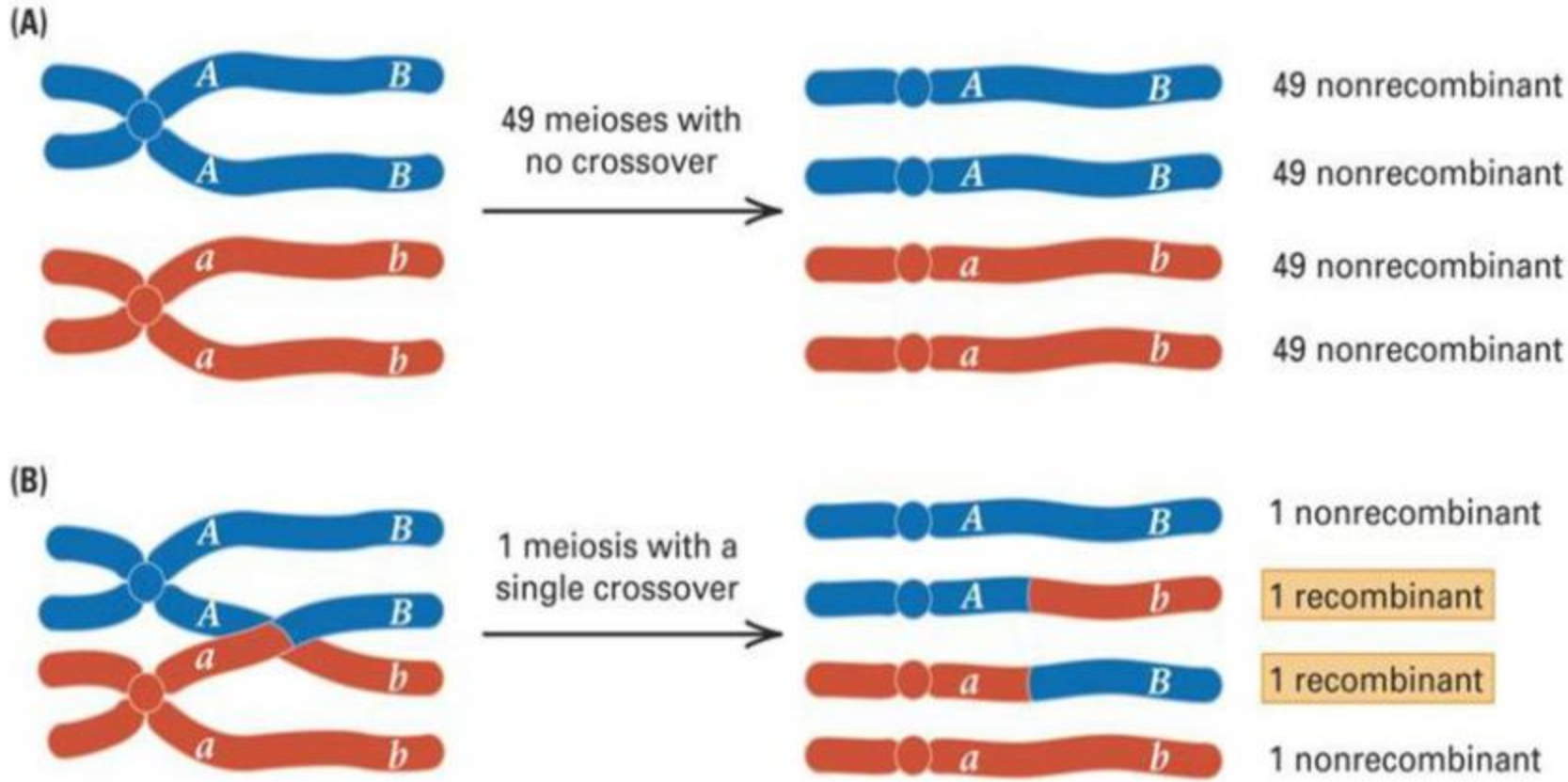
- Genes with recombination frequencies less than 50 percent are on the same chromosome = linked

Calculation of Recombination Frequency

- The percentage of recombinant progeny (off-springs) produced in a cross is called the recombination frequency, which is calculated as follows:

$$\text{Recombinant frequency} = \frac{\text{Number of recombinant offspring}}{\text{Total number of offspring}} \text{ X } 100$$

Recombination Frequency



(C) Frequency of recombination: $r = \frac{1 + 1}{49 + 49 + 49 + 49 + 1 + 1 + 1 + 1} = \frac{2}{200}$

= 1 percent = 1 map unit = 1 cM

PERCENTAGE OF CROSSING OVER :-

- The percentage of crossing over is **directly** proportional to the distance between two genes.

- Crossover = $\frac{\text{\% of total no. of off springs in F2}}{\text{Total no. of recombinants.}}$ **x 100**

- Percentage of recombinant is also called as **FREQUENCY** of crossing over.

- **% of cross over = frequency of cross over = % of recombinants.**

Significance of crossing over

- Crossing over provides a strong proof in favour of linear arrangement of genes on the chromosomes.
- Recombinations or new gene combinations are produced due to crossing over,which change genetic pool by changing of gene frequency and this provide a way of evolution(micro evolution)
- Crossing over generates genetic difference within a population .
- Linkage map and genetic maps are constructed on the basis of crossing over

- So when the chromosomes go on to **MEIOSIS-II** and separate.
- Some of the daughter cells receive daughter chromosomes with **RECOMBINED ALLELES**.
- Due to this **GENETIC RECOMBINATION** the offspring have a different set of alleles and genes than their **PARENTS** do.