

CROSSING-OVER or Recombinations

The process of mutual exchange of genetic material or fragment of two non-sister chromatids of a homologous pair of chromosome by breakage and reunion of the fragment during meiosis is called crossing-over.

- ⇒ It takes place during pachytene sub-stage of Prophase I of meiosis, but visible at diplotene sub-stage.
- ⇒ The term crossing-over was coined by T.H. Morgan. Rare occurrence of crossing over in somatic cells during mitosis has been reported in Drosophila by Stern in 1936.

Steps of Crossing over

Steps in crossing-over

1) Synapsis - The pairing phenomenon of homologous chromosomes in presence of synaptonemal complex (DAA & protein).

The lengthwise pairing of homologous chromosomes occur due to force of mutual attraction in zygote.

The pairing starts at one or more points and proceeds along the whole length in a zipper fashion.

Paired homologous chromosomes are called bivalent. Synaptonemal complex aligns the DNA molecule of two homologous chromosomes side by side and they contain same genes in same sequence.

Synapsis may be terminal, procentric or random.

⇒ Precocity theory of C.D. Darlington advocates that chromosomes pair due to singleness or to satisfy the pairing need.

⇒ Retardation theory proposed by Sax and others, suggests that pairing occur due to retardation of metabolic activity of the cell.

2) Duplication of chromosomes - Synapsis is followed by the duplication of chromosomes which changes the bivalent nature of chromosome to four-stranded stage or tetravalent. The two sister chromatids are attached with unsplit centromeres.

3) Crossing over - In this stage, exchange of segment between the non-sister chromatids of homologous chromosome occurs at tetrad stage.

⇒ It can be divided into three major steps:-

- i) Breakage of chromatid segments
- ii) their transposition (movement to the respective site).
- iii) fusion or joining.

4) Terminalisation - After crossing over the non-sister chromatids start to repel each other.

Chiasma itself moves in a zipper fashion towards the end of tetrad. This movement of chiasma is known as terminalisation.

* Crossing over and chiasma formation.

There are two theories regarding relationship between crossing-over and chiasma formation-

A) Classical theory or Two plane theory -

This theory is proposed by L.W. Sharp in 1934.

A/c to this theory, formation of chiasmata precedes the act of genetic crossing over, so that chiasmata are not the result but the cause of crossing over. This adjacent loops are organised at ~~pachytene~~ and ~~by~~ right angle to each other and hence it is called two plane theory. Chiasmata are

organised at pachytene and crossing-over takes place at diplotene stage. This theory has been considered to be tenable and hence rejected.

B) Chiasma type or one plane theory.

A/c to this theory, the act of crossing-over is followed by chiasma formation. Here the chiasma formation is the consequence of crossing over. This view states that adjacent loops are organised in one plane and hence it is called one-plane theory. A/c to this theory crossing-over takes place at pachytene stage and chiasma appear at diplotene.

KINDS OF CROSSING OVER

Depending upon the no. of chiasmata appeared, crossing over is of three kinds.

1. Single cross-over -

In this case, only one chiasma is formed which leads to formation of single cross-over gametes. It is most common type of cross-over.

ii) Double cross-over - or

In double cross-over, two chiasmata develop. These chiasmata may appear betn the chromatids or between different chromatids. This type of crossing over form double crossing-over gametes.

iii) Multiple cross-over -

Here, more than two chiasmata are constituted. It may be further classified into triple

Mechanism of crossing over

There are different views put forward to explain the mechanism of crossing over. -

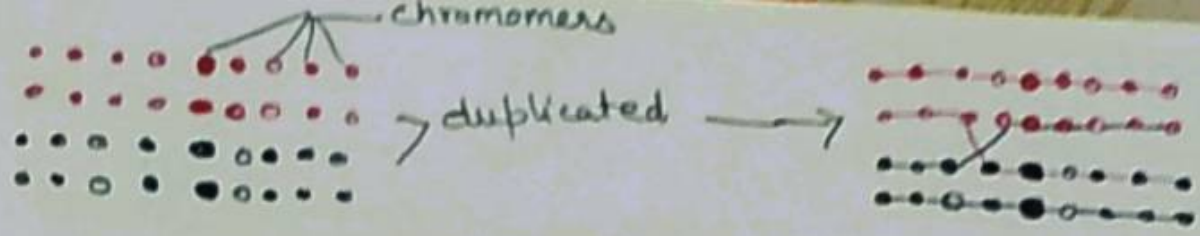
A) Precocity theory - A/c to Darlington, the pairing of homologues occurs to avoid singleness of a chromosome. The pairing need of a chromosome could be nothing less than the replication of DNA. The crossing over takes place due to torsion on chromosome created by coiling of two homologues around each other.

B) Belling's Hypothesis and copy choice model -

In 1931, a cytologist named J. Belling proposed "the copy choice theory". A/c to this theory, the paired chromosome in first meiotic prophase duplicates their genes before the fibres that join them in tandem are developed.

During the process, if the chromosome are twisted around each other, the connecting fibres may connect genes of one chromosome at some points and adjacent genes produced by other chromosome at other.

In brief, the theory assumes the crossing over is the direct result of the new chromatid copying partly from one strand and partly from other homologous strand.

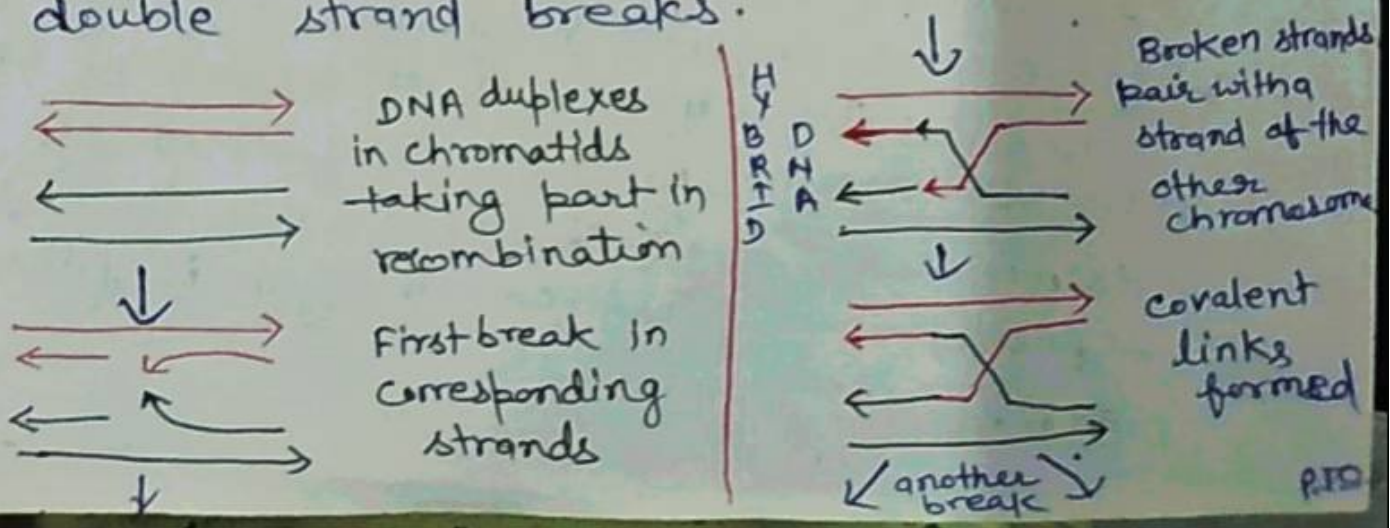


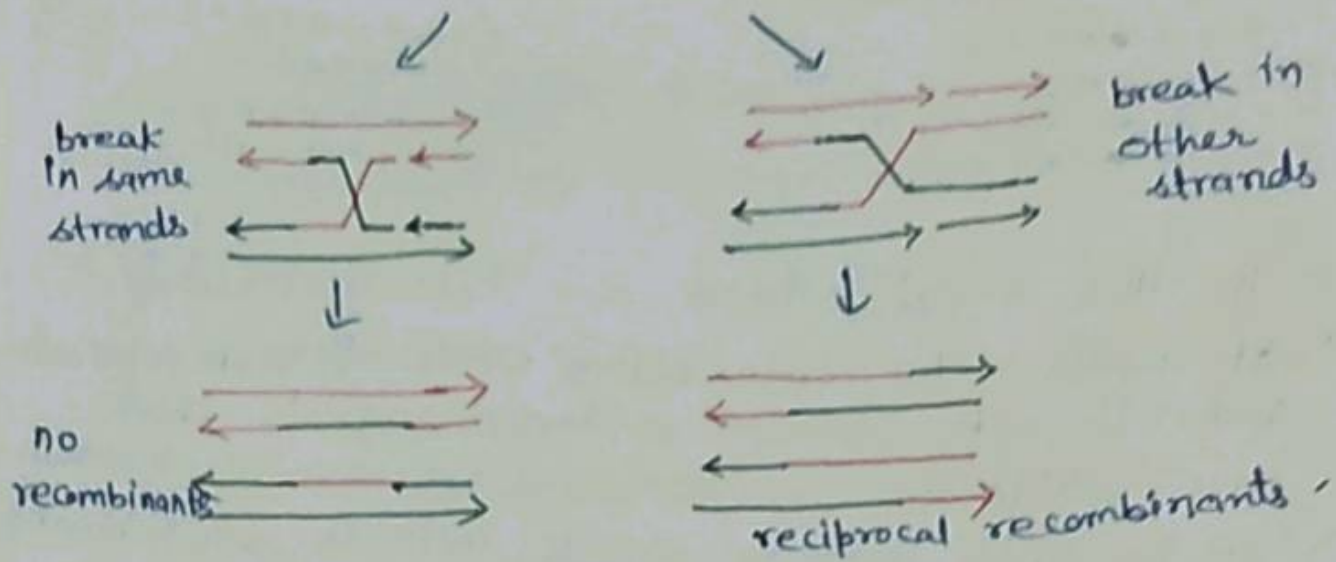
⇒ In this model, there are two main defects—

- i) It assumes the conservative mode of DNA replication but all experimental evidence suggests that DNA replicates in a semi-conservative manner.
- ii) It predicts that in every meiosis, when multiple cross-overs occur, only two of the four chromatids would be involved. The experimental evidence suggests that three strands or four strands may actually be involved in multiple cross-overs.

c) Hybrid DNA models. During 1960s, Hybrid DNA models had become very popular. ~~since these~~ In this models, only one strand in each of the two DNA duplexes, belonging to non-sister chromatids breaks. The single strands released from these breaks then pair crosswise with unbroken strands by complementary base pairing. This results in the formation of hybrid DNA segments.

R. Holliday in 1964 proposed that breaks would occur in single strand having same polarity. There are also hybrid DNA model assuming double strand breaks.





* characteristics of crossing over

- occur at two levels, at gross chromosomal level and at DNA level.
- Occurs between non-sister chromatids of homologous chromosomes.
- Exchange is normally reciprocal but sometimes unequal.
- Frequency of crossing over is closely related to physical distance between genes located on chromosomes.
- Crossing over is a crucial process that generates genetic difference with a population.

* The enzymes involved in crossing over.

- 1) Recombinase is the major enzyme regulating recombination event.
- 2) Endonuclease is responsible for breakage of 2 non-sister chromatids at corresponding sites.
- 3) Ligase enzyme - Breakage is followed by exchange of segments and finally the exchanged segments are joined or the gap is filled by ligase enz.

Factors affecting crossing over

1) Distance between genes: The frequency of crossing over between the two genes is positively associated with the distance between their location in the chromosome.

$$\boxed{\text{cross over} \propto \text{distance betn genes.}}$$

2) Sex. There is a tendency of reduction of crossing over in male mammals.

3) Mutation.

Mutation reduces crossing over.

4) Temperature - high and low temperature variations increase the percentage of crossing over in certain parts of chromosome.

5) X-ray effect -

X-ray irradiations increase crossing over in centromere.

6) Age - As the age advances, the frequency of crossing over decreases.

Significance of crossing over

- Provides strong proof in favour of linear arrangement of genes on the chromosomes.
- New gene recombinations are produced which change genetic pool by changing of gene frequency and this provide a way of evolution.
- generates genetic difference within a population.
- Linkage map and genetic maps are constructed on the basis of crossing over.