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Linkage

- Tendency of two or more genes to remain together in the original combination in the same chromosome during the process of inheritance for a number of generations
- T. H. Morgan
- Principles
  - A chromosomes contains Many genes
  - Genes are arranged in linear fashion
  - The genes present in the chromosomes are Linked
  - Linked genes are Inherited together from parents to offsprings.

- Bateson and Punnet studied linkage in sweet pea (*Lathyrus odoratus*). In sweet pea blue flower BB is Dominant over Red flower bb. Long pollen grain is dominant LL over Round pollen grain ll.

LINKAGE

Morgan (1910) noted similar behaviour in *Drosophila melanogaster* (Fig. 8.2) and recorded that coupling and repulsion are two aspects of a single phenomenon called *linkage*. Morgan was the first to relate linkage to the segregation of homologous chromosomes and the occurrence of crossing over between homologous chromosomes during meiosis. His group noted numerous hereditary characteristics which were associated together in groups. It was suggested that the tendency of linked genes to remain in original combinations was due to their occurrence in the same chromosome. The strength of linkage can be determined by the distance between two genes, i.e. greater the distance, lower will be linkage strength. The linkage is broken down by the process of *crossing over* occurring during meiosis.

Incomplete

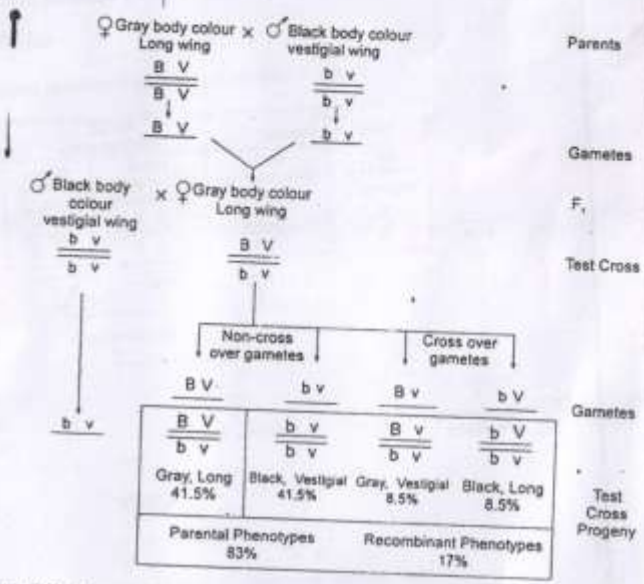

Fig. 8.2 Diagram illustrating linkage (incomplete) in *Drosophila*.

Morgan's Conclusions : Morgan concluded that—

1. genes located in the same chromosome tend to stay together during inheritance; this tendency is called linkage;
2. genes are arranged in a linear fashion in the chromosomes;

Gray Longwing Black vestigial wing

B V b V

3. the linkage is broken down by the process of crossing over occurring during meiosis;
4. the intensity of linkage between two genes is inversely related to the distance between them in the chromosome;
5. coupling and repulsion phases are two aspects of linkage.

Linkage groups : The genes of a species may be divided into linkage groups. The members of a linkage group show linkage to each other. In genetically well studied species, the number of linkage groups is equal to the number of chromosome pairs (the haploid number of chromosome) which the species possess. In an organism the nuclear linkage groups have not been shown to exceed the haploid number. Although in organisms where genetic data are more difficult to obtain, the number of presently known linkage group is less than the haploid number of chromosomes.

Complete Linkage: When genes are so closely associated that they are always transmitted together, do not undergo crossing over, linkage between them is considered *complete*. For example, the genes for bent wings and shaven bristles of the IVth chromosome of *Drosophila* exhibit complete linkage (Fig. 8.3). The almost complete absence of independent assortment between these two gene pairs is evidence of very strong linkage between them.

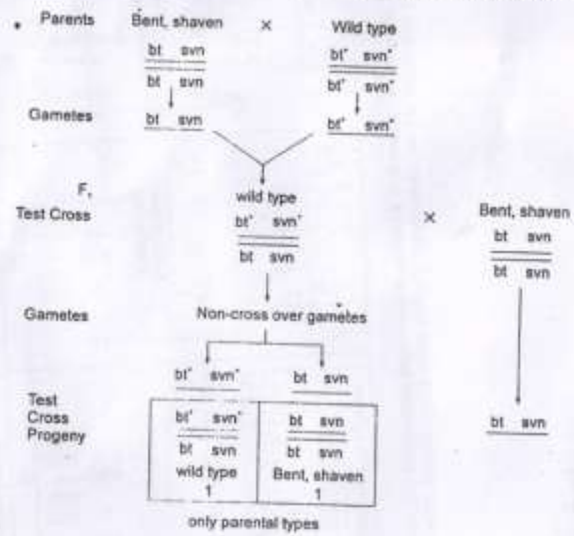

Fig. 8.3 Diagram illustrating linkage (Complete) in *Drosophila*.

bt

Incomplete linkage: Complete linkage between genes on the same chromosome, is rare. As a rule, linkage is not complete, and the gene pairs in most linkage groups, assort at least partially independently of each other. Linkage is a physical relationship between genes and can be modified by a physical crossing over during meiosis between gene pairs on homologous chromosomes. This phenomenon of *incomplete linkage* has been found in female *Drosophila* and various other animals as well as in maize (Fig. 8.4), tomato and large number of crop species. Thus the result of independent assortment, complete linkage and incomplete linkage are different (Fig. 8.5).

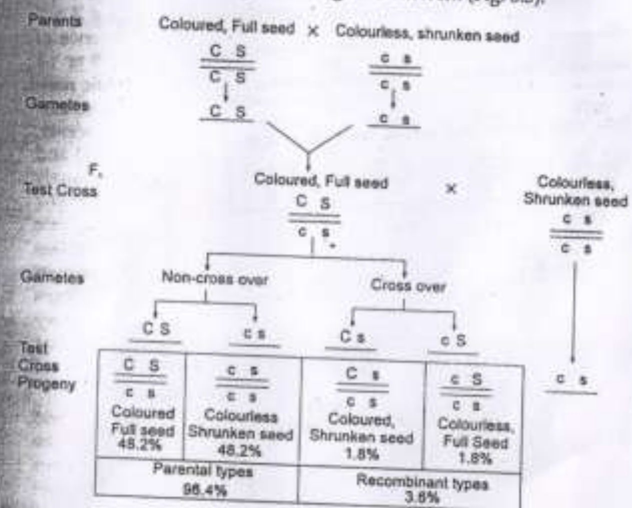

Fig. 8.4 Diagram illustrating linkage (incomplete) in maize.

CROSSING OVER

Recombination of genes on the same chromosome is accomplished by *crossing over*, a process by which parts of homologous chromosomes are interchanged. Crossing over is important in evolution because it generates variation in a species. Crossing over and independent assortment are mechanisms that produce new combination of genes.

The *important features* of the concept of crossing over are:—

(i) The loci of the genes on a chromosome are arranged in a linear sequence.

(ii) The two alleles of a gene in a heterozygote occupy corresponding positions in the homologous chromosomes, that is, allele A occupies the same position in homologue 1 that allele a occupies in homologue 2.

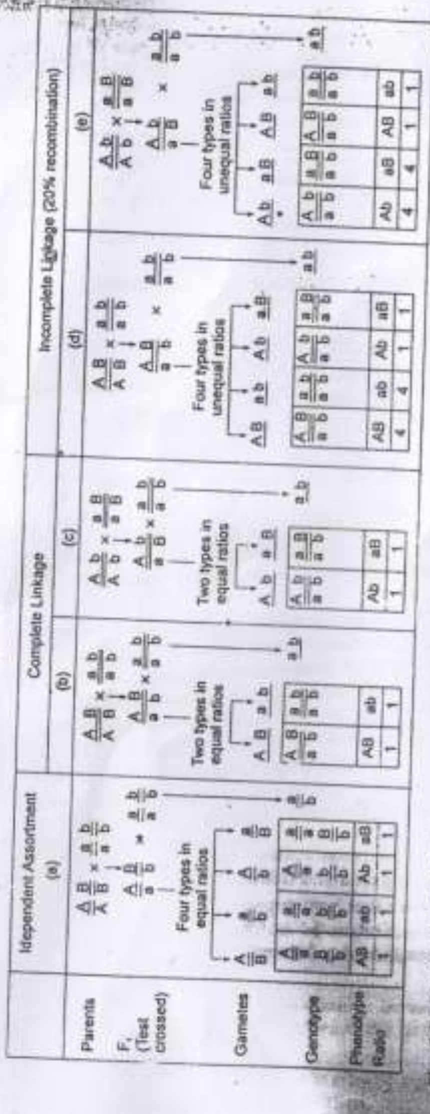

Fig. 8.5 Diagram illustrating the consequences of two pairs of genes, A, a and B, b following independent assortment (a), complete linkage (b, c) and incomplete linkage (d, e). Note F1 genotypes are all identical, but the test cross progenies are different in their types and ratios) in all the cases.

Linkage in sweat peas

Blue long Red Round

Parents B B b b

L L × l l

F1 B b

L l Blue long

F1 Test crossed B b b b

Blue long L l × l l

B b

L l crossing over

Blue Long	Blue Round	Red long	Red round
B b	**B b**	**b b**	**b b**
L l	**l l**	**L l**	**l l**
7	**1**	**1**	**7**

7 : 1 : 1 : 7

- The strength of the linkage depends on the distance between the linked genes
- Closely located genes show strong linkage.
- Distantly located genes show weak linkage.

Linkage arrangements- Two types

1. Cis arrangement : when dominant genes are located on one homologous chromosomes and the recessive genes on other homologous chromosome.

2. Trans arrangement : Dominant and recessive genes are arranged in one chromosome.

Linkage Groups

- All the linked genes of a homologous pair of chromosome constitute one group are called linkage groups.
- Example : Drosophila has 4 linkage groups and 4 pairs of chromosomes.

- Types of Groups : two types

1. Complete linkage: Chromosome do not break and linked genes inherited together for many generations.

   Eg. F1 Male Drosophilla

2. Incomplete linkage: chromosomes break occasionally and linked genes separate due to crossing over

   Eg. F1 Female Drosophilla

Complete Linkage

- These are closely associated and tend to inherit together.
- New characters do not appear.
- F_1 Male hybrid

Complete Linkage in Drosophilla (Male)

Parents Grey Long × Black Vestigial

G G × g g
L L × l l

Gametes F1: G L and g l → G g / L l Grey long

F1: Male G g / L l Grey long × g g / l l Female Black Vestigial

Gametes: G L, g l, g l

F2: G g / L l, g g / l l

Grey long (50%) Black vestigial (50%)

Incomplete Linkage in Drosophilla (Female)

Parents	**Grey Long**			**Black Vestigial**
	G G L L	×		g g l l
Gametes F1	G L	G g L l Grey long		g l
Test Cross	G g L l			g g l l
	G G g g L l L l	Crossing over		
Gametes	G G L l	g L	g l	g l
F2	G g L l Grey Long (41.5%)	G g l l Grey Vestigial (8.5%)	g g L l Black Long (8.5%)	g g l l Black Vestigial (41.5%)

Coupling and Repulsion

- if dominant alleles or recessive alleles are present in the same plant, they tend to remain together resulting in increased parental forms.

- Thus, the two genes which inherit together are called linked genes. This aspect is called **coupling**.

- if dominant alleles or recessive alleles are present in the different plants, they tend to remain separate resulting in increased parental forms. This aspect is called **repulsion**.

Crossing over

- Crossing over is the interchange of chromosomal parts between non – sister chromatids of a homologous pair of chromosomes resulting in recombination of genes.
- Discovered by Morgan.
- Occurs during meiosis / gametogenesis.
- The number of crossing over depends on the length of the chromosome. The longer the length higher the percentage of crossing over.
- The percentage of crossing over is directly proportion to the distance between the two genes.
  - $$\text{Crossing over} = \frac{\text{\% total number of offsprings in F2}}{\text{total number of recombinations.}} \times 100.$$

- The percentage of crossing over is also called frequency of crossing over.
- When there is a single crossing in a homologous chromosome is called single crossing over.
- When there is a two crossing in a homologous chromosome is called double crossing over.
- When there are many crossing overs in a homologous chromosome is called as multiple crossing over.

Crossing Over in Drosophila

- The phenomenon of crossing over is well illustrated in *Drosophila melanogaster.* When grey long Drosophila is crossed with a black vestigial, the F1 hybrid is grey long.

- When female flies of F1 generation are back crossed with double recessive male, four types of offsprings are produced.

    - Among the four, two types black vestigial and grey long they just like parents are called parental combination.

    - Other two types grey vestigial and black long are different from the parents are called non parental combinations

Crossing over in Drosophila

Parents — **Grey Long** × **Black Vestigial**

Parents	G G L L	×		g g l l
Gametes F1	G L	G g L l Grey long		g l
Test Cross	G g L l			g g l l

G G g g
L l L l

Crossing over

Gametes	G L	G l	g L	g l	g l

F2	G g L l Grey Long (41.5%)	G g l l Grey Vestigial (8.5%)	g g L l Black Long (8.5%)	g g l l Black Vestigial (41.5%)

Significance of Crossing over

1. **Linear arrangement of genes:** Crossing over is clearly illustrates the linear arrangement of genes in the chromosomes.

2. Chromosome Maps: The frequency of crossing over is very useful to construct the chromosomal maps.

3. Recombination: Crossing over produces new combination of genes.

4. Variations: crossing over leads to genetic variation which is the raw material for evolution.

Mechanism of Crossing Over

- The phenomenon of pairing of homologous chromosomes is called synapsis.
- The paired homologous chromosomes are called bivalents.
- Each chromosomes splits into two chromatids.
- Four chromatids are produced from two homologous chromosomes is called tetrad. Two chromatids of a chromosome are attached by a single centromere are called sister chromatids.
- Non sister chromatids of homologous chromosomes are connected with eachother called Chiasmata (chiasma = singular).

- At the chiasma the chromatids are break by an enzyme called endonuclease. The broken segment is fused using ligase enzyme by ligation.

- The exchange of chromosomal segments between nonsister chromatids is called crossing over.

- After crossing over the nonsister chromatids repel each other and separation starts from the centromere towards ends like zip the separation is called terminalization.

Theory

- Five theories - to explain the mechanism of crossing over.

1. Chiasma type theory
2. The breakage first theory
3. The contact first theory
4. Strain or Torsion theory
5. Differential Contraction theory
   - Single crossing over
   - Double crossing overs
   - Multiple crossing over

Chiasma Type Theory

- The chromosomes of bivalent get duplicated to form a tetrad.
- Crossing over occurs between the non sister chromatids of a tetrad.
- In diplotene stage the nonsister chromatids overlap with one another and form chiasma or point of contact.
- In chiasma, chromatids break and they rejoin with the mutual exchange of segments. The other two chromatids remain intact.

Factors affecting crossing over

1. High temperature increases the frequency of crossing over.
2. X-ray increases the frequency of crossing over
3. The frequency of crossing over decreases with increasing age in female Drosophila.
4. Some genetic mutation decreases the frequency of crossing over.
5. Crossing over is less frequent near centromeres and the tips of the chromosomes.
6. Inversions of chromosome segments suppress the crossing over.
7. Chiasma formation at one point prevents the chiasma formation in the vicinity. This phenomenon is known as interference.

Cytological evidence for crossing over

- The crossing over occurs during the tetrad stage of meiosis. This is proved by cytological evidences.

1. Stern's experiment
2. Tetrad analysis
3. Creighton and Mc Clintock's experiment