**Linkage**

**T**he hereditary units or genes which determine the characters of an individual are carried in the chromosomes and an individual usually has many genes for the determination of various different characters. As there are more genes than the chromosomes, it can be expected that each chromosome contains more than one gene. The genes for different characters may be either situated in the same chromosome or in different chromosomes. When the genes are situated in different chromosomes, the characters they control appear in the next generation either together or apart, depending on the chance alone. They have assorted independently according to Mendel’s law of independent assortment.

But if the genes are situated in the same chromosome and are fairly close to each other, they tend to be inherited together. **This type of coexistence of two or more genes in the same chromosome is known as linkage.**

The difference between independent assortment and linkage can be understood by the following two examples :

**P1 :** AA BB × aa bb

**P1 gametes :** (AB) ↓ (ab)

**F1 :** Aa Bb

**Test cross :** Aa Bb × aa bb

**Gametes :**  (AB) (Ab) (aB) (ab) (ab)

**F2** : ¼ Aa Bb : ¼ Aa bb : ¼ aa Bb : ¼ aa bb

or 1 : 1 : 1 : 1

**Example 2.** Linked genes do not assort independently, but tend to stay together in the same combination as they were in the parents. In the following figure, the genes to the left of the slash line (/) are on one chromosome and those on the right are on the homologous chromosome.

P1 : AB/AB × ab/ab

P1 gametes : (AB) ↓ (ab(

F1 : AB/ab

**Test cross** : AB/ab × ab/ab

Gametes : (AB) (ab) (ab)

F2 : ½ AB/ab : ½ ab/ab

Or 1 : 1.

This type of large deviation of F2 results of example 2 from a 1 : 1 : 1 : 1 ratio in the test cross progeny of dihybrid is an evidence for linkage.

**Chromosome Theory of Linkage**

**Morgan** along with **Castle** formulated the chromosome theory of linkage which is as follows:

1. The genes which show the phenomenon of linkage are situated in the same chromosomes and these linked genes usually remain bounded by the chromosomal material so that they cannot be separated during the process of inheritance.

2. The distance between the linked genes determines the strength of linkage. The closely located genes show strong linkage than the widely located genes which show the weak linkage.

3. The genes are arranged in linear fashion in the chromosomes

* **KINDS OF LINKAGE**:- T.H. Morgan and his co-workers by their investigation on the Drosophila and other organisms have found two types of linkage, viz., complete linkage and incomplete linkage.

1**- Complete Linkage** The complete linkage is the phenomenon in which parental combinations of characters appear together for two or more generations in a continuous and regular fashion. In this type of linkage genes. are closely associated and tend to transmit together.

**Example**. The genes for bent wings (bt) and shaven bristles (svn) of the fourth chromosome mutant of Drosophila melanogaster exhibit complete linkage.

* **Complete linkage in male Drosophila**. In most of the organisms crossing-over takes place both in males and females. But in male Drosophila and female silkworm, crossing-over takes place either very rarely or not at all. This becomes clear from Morgan’s(1957) experimental results from Drosophila. In 1919, T.H. Morgan mated gray bodied and vestigial winged(b+vg/b+vg) fruit flies with black bodies and normal long wings (bvg+/bvg+).

gray bodied and vestigial winged black bodies and normal long wings

b+vg/b+vg x bvg+/bvg+

F1 b+vg/bvg+

progeny had gray bodies and normal long wings indicating thereby that these characters are dominant.

**Test cross** : F1 male Gray, Long × Female Black, Vestigial

b+vg/bvg+ bvg/bvg

Gametes : (b+vg) (bvg+) (bvg)

* only two types of gametes due to complete linkage and lack of crossing over in male Drosophila

b+vg/bvg bvg+/bvg

: ½ Gray, Vestigial : ½ Black, Long

1: 1

When F1 males (b+vg/bvg+), were backcrossed (i.e., test crossed) to double recessive females (bvg/bvg or black vestigial), only two types of progeny (one with gray bodies and vestigial wings, b+vg/bvg and the other with black bodies and normal wings, to bvg+/bvg instead of four types of phenotypes were obtained. Here, the use of the testcross is very important. Because one parent (the tester) contributes gametes carrying only recessive alleles, the phenotypes of the offspring represent the gametic contribution of the other double heterozygote parent. So the genetical analyst can concentrate on one meiosis and forget the other. This is in contrast to the situation in an F1 where there are two sets of meiotic divisions to consider one for the F1 male parental gametes and one for the F1 female.

2**. Incomplete Linkage** The linked genes do not always stay together because homologous non-sister chromatids may exchange segments of varying length with one another during meiotic prophase. This sort of exchange of chromosomal segments in between homologous chromosomes is known as **crossing over** The linked genes which are widely located in chromosomes and have chances of separation by crossing over are called incompletely linked genes and the phenomenon of their inheritance is called incomplete linkage.

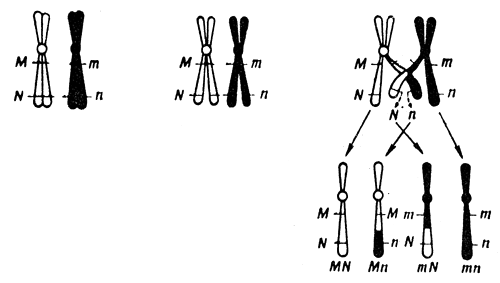


Fig 1: Crossover between chromatids of a pair of homologous chromosomes

* **Incomplete linkage in female Drosophila**. When F1 females of the Morgan’s classical cross in Drosophila between gray, vestigial (b+vg/b+vg) and black, normal or long (bvg+/bvg+) were testcrossed to double-recessive (bvg/bvg) males, all four types of progeny were obtained in following ratio, showing the occurrence of crossing-over:

Parents : Gray, Vestigial × Black, Long

b+vg/b+vg bvg+/bvg+

Gametes : (b+vg) (bvg+)

F1 **: b+vg/bvg+**

**Gray, Long**

**Test cross** : F1 Female Gray, Long × Male Black, Vestigial

b+vg/bvg+ bvg/bvg

↓ ↓

**Gametes** : (b+vg) (bvg+) = Non-cross overs (bvg)

(b+vg+) (bvg) = Recombinants

Test cross ratio :

1- Gray, Vestigial; b+vg/bvg = 41.5% 83% parental combination

2- Black, Long; bvg+/bvg = 41.5% showing linkage

3- Gray, Long ; b+vg+/bvg = 8.5% 17% recombinants due to

4- Black, Vestigial; bvg/bvg = 8.5% crossing over

**LINKAGE GROUPS** All the linked genes of a chromosome form a linkage group. Because, all the genes of a chromosome have their identical genes (alleomorphs) on the homologous chromosome, therefore linkage groups of a homologous pair of chromosome is considered as one. The number of linkage group of a species, thus, corresponds with ha ploid chromosome number of that species.

Example. 1. Drosophila has 4 pairs of chromosomes and 4 linkage groups.

2- Man has 23 pairs of chromosomes and 23 linkage groups.

3-. Corn (Zea mays) has 10 pairs of chromosomes and 10 linkage groups.

However, in organisms the female or male sex having dissimilar sex chromosomes (e.g., human beings, Drosophila, fowl, etc.), one more linkage group occur than the haploid number

* Example.

1. Female human beings = 22 pairs of autosomes or non-sex chromosomes + 1 pair of : homomorphic X chromosomes

= 22 autosomal linkage groups + 1 X chromosomal linkage group

23= linkage groups.

2-Male human beings : = 22 pairs of autosomes + 2 heteromorphic sex chromosomes,

= 22autosomal linkage group + 1 X chromosomal linkage group + 1 Y chromosomal linkage group = 24 linkage groups.

**SIGNIFICANCE OF LINKAGE**

The phenomenon of linkage has one of the great significance for the living organisms that it reduces the possibility of variability in gametes unless crossing over occurs.

**Q-How many linkage groups are there in the (a) human male, (b) human female, (c) female grasshopper and (d) male grasshopper.**

1. **24; (b) 23 (c) 12; (d) 12.**