6. Linkage

Linkage is defined as *the 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.* All the genes on a chromosome are said to be linked to one another.

Linkage was discovered by ***T.H. Morgan.***

Linkage was found in *Drosophila,* sweet peas, maize, man, etc.

In *Drosophila,* the genes of body colour and nature of wings are linked and located on the same chromosome.

In sweet pea, the genes of flower colour and size of pollen grains are linked.

In maize, the genes for colour and shape of seeds are linked.

In man, the genes for ***haemophilia*** and ***colour blindness*** are linked.

T.H. Morgan (1911) proposed the ***theory of linkage*** based on his experiments in *Drosophila.* The theory of linkage explains the main principles of linkage. They are the following :

1. A chromosome contains ***many genes.***
2. The genes are arranged in a ***linear fashion*** on the chromosomes.
3. The genes present in a chromosome are ***linked.***
4. The linked genes are ***inherited together*** from the parents to the offspring.
5. Linkage is a ***rare*** phenomenon when compared to crossing over.
6. The strength of linkage depends on the ***distance*** between the linked genes. Closely located genes show ***strong linkage.*** Widely located genes show ***weak linkage.***
7. ***Mendel's law*** of independent assortment is ***not universal.***
8. The linked genes do not show ***independent assortment.***

The genes located on different chromosomes only show independent assortment.

9. When dominant genes are located on one homologous chromosome and the recessive genes on the other homologous chromosome, the arrangement of linked genes is called ***cis arrangement.***

When the dominant and recessive genes are linked in one chromosome, the arrangement is called ***trans arrangement.***

10. All the linked genes of a homologous pair of chromosome constitute one group called ***linkage group.*** The number of linkage group in an organism is equal to the number of pairs of chromosomes.

Thus *Drosophila* has 4 linkage groups as it has 4 pairs of chromosomes.

Pea plant has 7 linkage groups as it has 7 pairs of chromosomes.

Man has 23 linkage groups as he has 23 pairs of chromosomes.

11. Linkage is of two types, namely ***complete linkage*** and ***incomplete linkage.*** In complete linkage, the chromosomes do not break and the linked genes inherit together for many generations.

Eg. F_1 male *Drosophila.*

In incomplete linkage, the chromosomes break occasionally and the linked genes separate due to crossing over. Eg. F_1 female *Drosophila.*

1. Linkage in Drosophila

In *Drosophila,* ***grey colour(G)*** is dominant over ***black colour (g)*** and ***long wing (L)*** is dominant over ***vestigial wing (l).*** The genes for these two characters (colour of the body and length of the wings) are linked together in the same chromosome.

The ***linked*** genotypes of the parents are written as follows:

Grey long - ***GL/GL***

Black vestigial - ***gl/gl***

When a fly with grey body and long wings ***(GGLL)*** is crossed with another fly having black body and vestigial wings ***(ggll),*** all the F_1 individuals are having grey body and long wings ***(GgLl).***

When F_1 male hybrid is ***test crossed*** with the double recessive parent, the F_2 contains only two types of individuals in equal numbers (1:1 ratio) instead of the expected 1:1:1:1 dihybrid test cross ratio.

In the F2 generation, all the flies are like their parents. There are no new combinations. This is because the gene ***G*** is linked with ***L*** in one chromosome and the genes g and l are linked in another chromo-

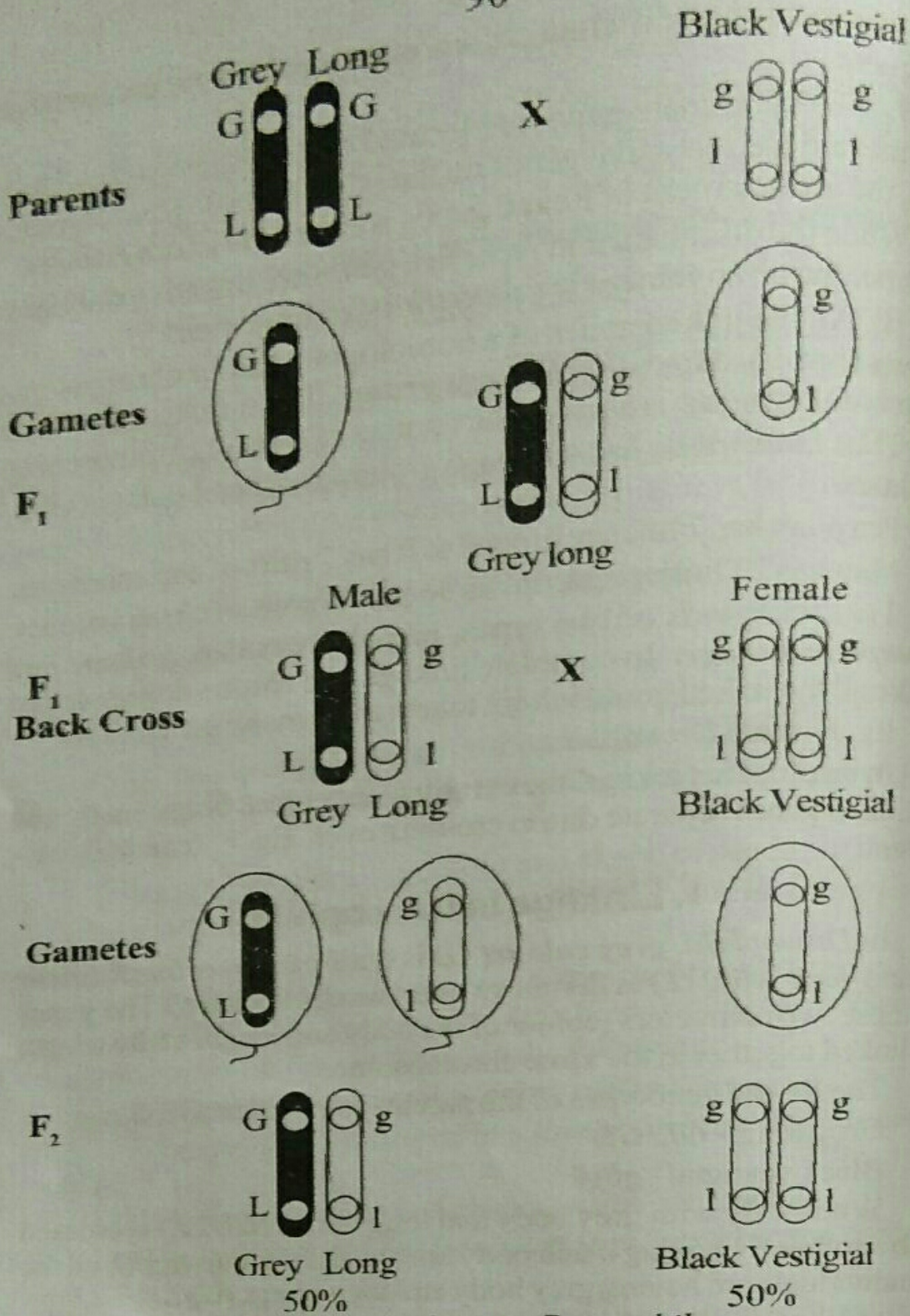


Fig.6.1: Linkage in Drosophila.

some. Hence during gamete formation, they cannot segregate independently. Hence only two types of gametes are formed resulting in the formation of two types of combinations in F2.

The resulting offspring are resembling the grand parents. This is because gene ***G*** is linked with ***L*** and the gene ***g*** is linked with ***l***.

2. Linkage in Maize

Hutchison experimentally proved the existence of linkage in maize (*Zea mays*). In maize, ***coloured*** seed (*CC*) is dominant and ***colourless*** seed is ***recessive*** (*cc*). ***Full*** seed (***endosperm***) is dominant (*FF*) and ***shrunken*** seed is recessive (*ff*).

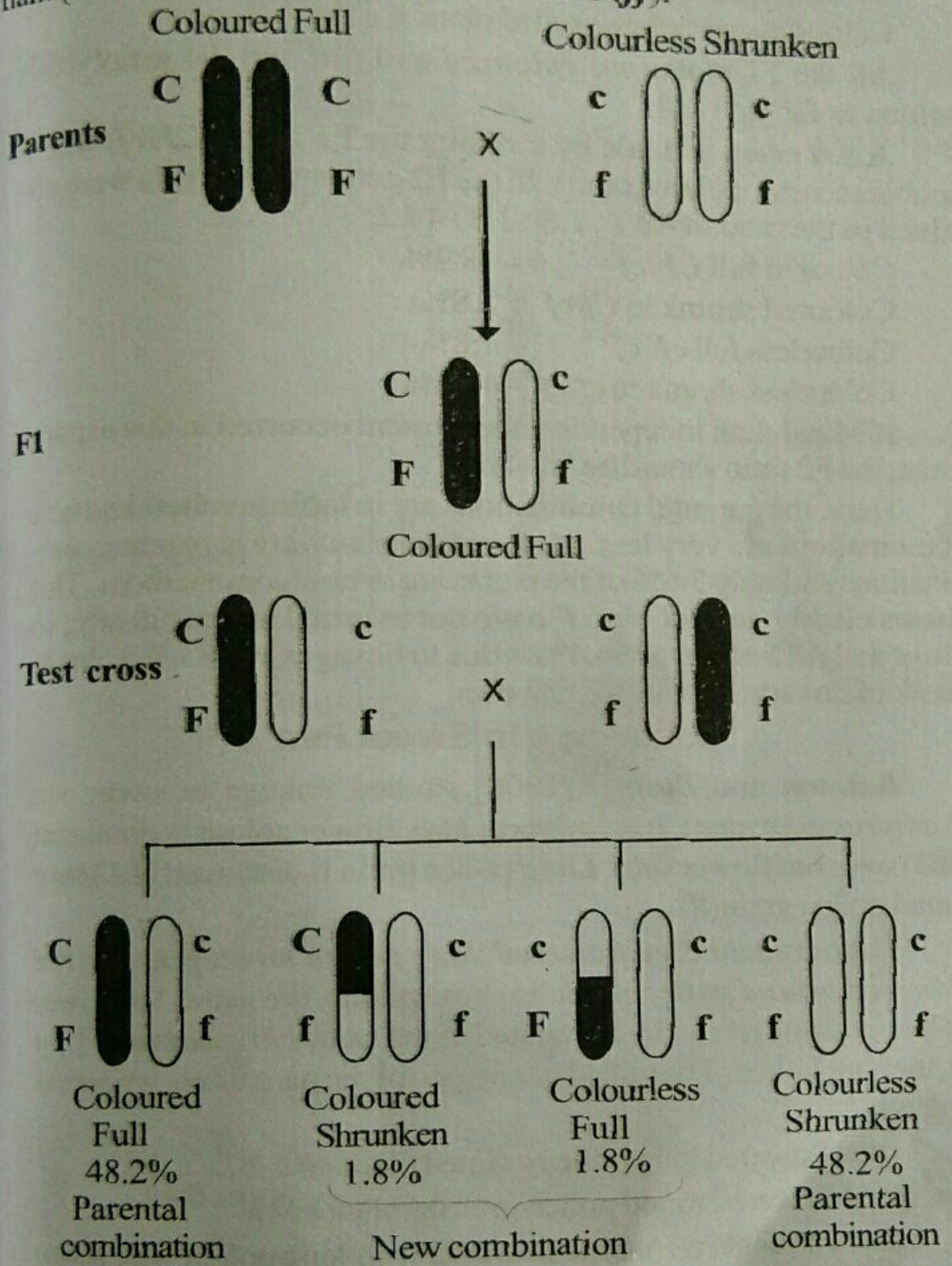


Fig.6.2: Linkage in maize.

A cross was made between ***coloured full seeded*** plant with a ***colourless shrunken*** seeded plant. The genes for seed colour and shape are ***linked***. i.e. C and F are linked; c and f are linked. The linked genotypes of the parents are written as follows.

Coloured full seeded plant - ***CF/CF***

Colourless shrunken seeded plant - ***cf/cf***

All the F1 plants are ***coloured*** and ***full*** and the genotype is written as ***CF/cf***

A ***test cross*** is made by crossing the F1 plant (***CF/cf***) with a double recessive plant (cf/cf). In the F2 generation, plants were obtained in the ratio of 48.2 : 1.8 : 1.8 : 48.2.

Coloured full ***CF/cf*** - 48.2%

Coloured shrunken ***Cf/cf*** - 1.8%

Colourless full ***cF/cf*** - 1.8%

Colourless shrunken ***cf/cf*** - 48.2%

If Mendelian independent assortment occurred in this experiment, the F2 ratio should be 1:1:1:1.

Here, the parental combinations are in large numbers and new combinations are very less. 96.4% of the plants are in parental combinations and only 3.6% of the plants are in new combinations. This shows clearly genes ***C*** and ***F*** have not assorted independently; so also ***c*** and ***f***. That means 96.4% is due to linkages and 3.6% is due to break of linkage; that is crossing over.

3. Linkage in Sweet Pea

Bateson and ***Punnet*** (1906) studied linkage in sweet pea (*Lathyrus odoratus*). In sweet pea, ***blue*** flower colour is dominant (BB) over ***red*** flower (***bb***). ***Long*** pollen grain is dominant (***LL***) over round pollen grain(***ll***).

They crossed ***blue flowered, long pollen*** sweet pea with ***red flowered, round pollen*** plant. In these plants, the genes for flower colour and pollen shape are located in the same ***chromosome***. That is, they are linked. The linked genotypes of the parents are written as follows:

Blue flowered long pollen grained plant - ***BL/BL***

Red flowered round pollen grained plant - ***bl/bl***

The F1 plants were blue flowered with long pollen. The genotype is written as ***BL/bl***.

The F1 plant (***BbLl***) was test crossed with double recessive plant (***bl/bl***). In the F2 generation, the plants appeared in the ratio 7:1:1:7 instead of the Mendelian test cross ratio 1:1:1:1.

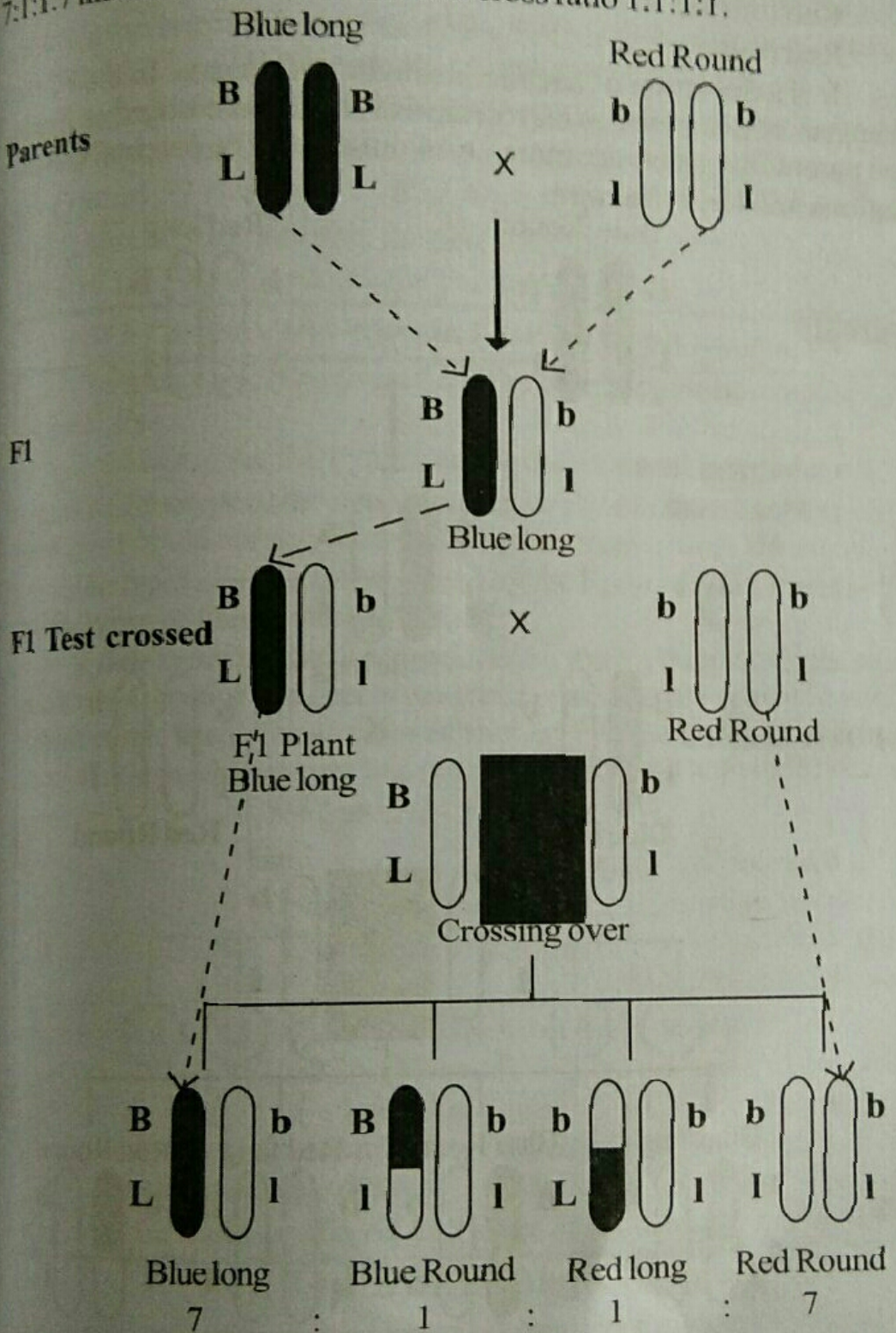


Fig.6.3: Linkage in Sweet pea.

Blue long - 7
Blue round - 1
Red long - 1
Red round - 7

It is a deviation of Mendel's dihybrid test cross. In the F2 the dominant alleles as well as the recessive alleles inherited together. Hence the parent like plants are more i.e 14 out of 16. The parental combinations are due to ***linkage.***

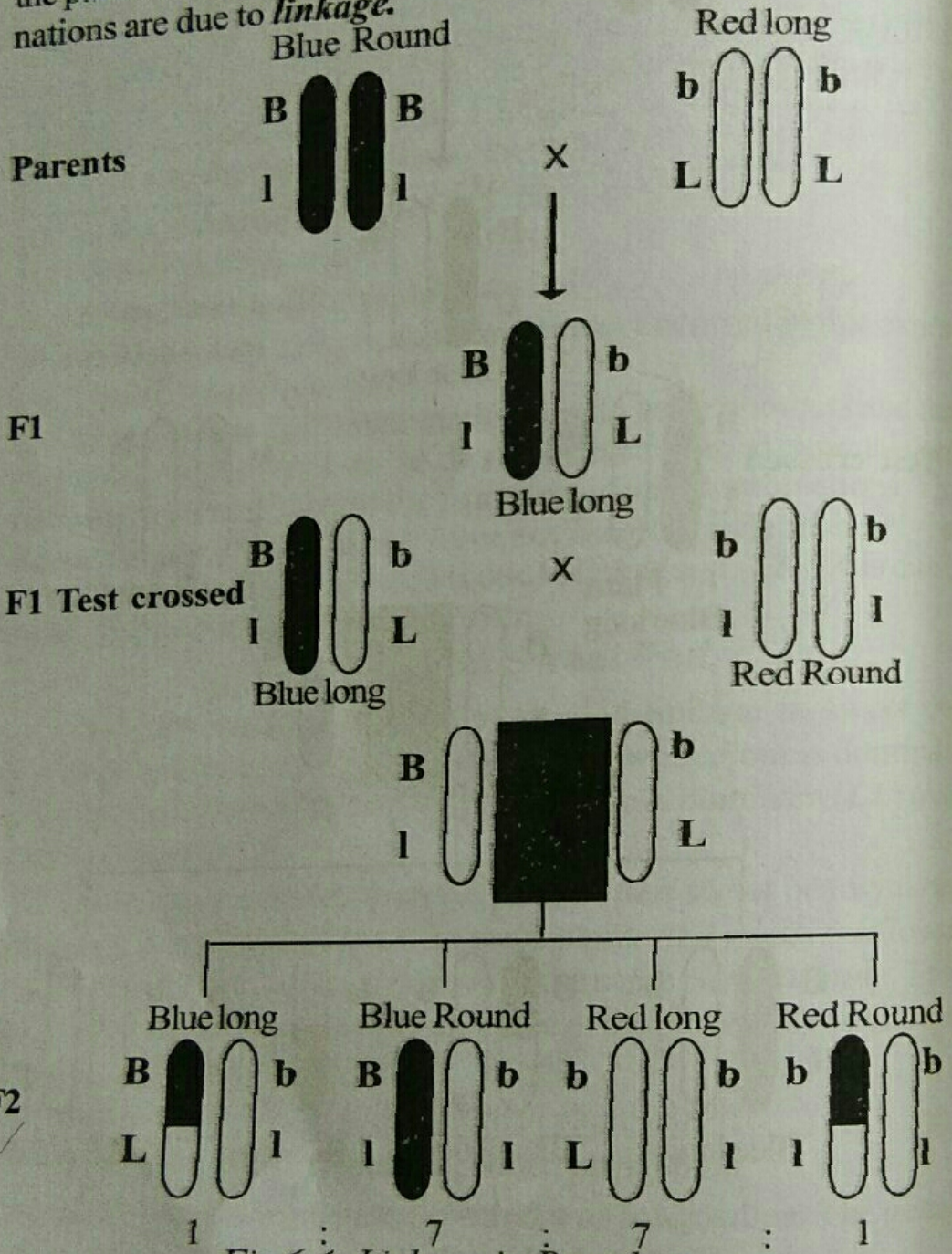


Fig.6.4: Linkage in Pea plant.

The new combinations are less just 2 out of 16. The new combinations are due to ***crossing over***.

In the same sweet pea plant, ***Bateson*** and ***Punnet*** conducted another experiment. They crossed ***blue*** flowered ***round*** pollen grained pea plant with ***red*** flowered ***long*** pollen grained plants were ***blue long***. When they are test crossed with ***red round***, in the F2, the pea plants appeared in the ratio of 1 ***Blue long*** : 7 ***Blue round*** : 7 ***Red long*** : 1 ***Red round.***

In this experiment also, the parental combinations are more. ie, 14 out of 16. This means that the parental genes are linked together.

Why is there test cross in Linkage Experiments?

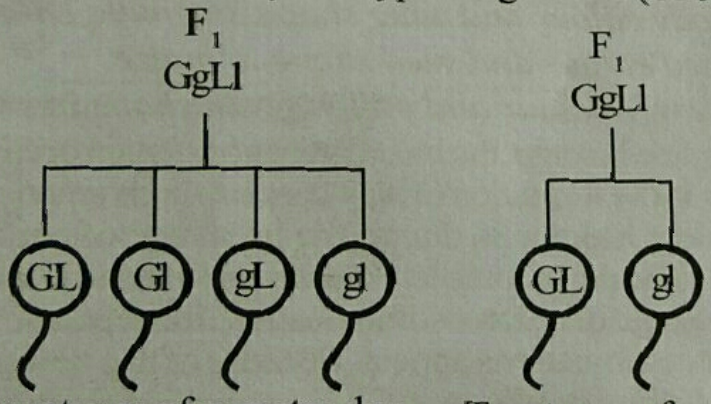
The test cross helps to find out the types of gametes produced by the F_1 fly.

In the test cross, the F_1 fly is crossed with a double recessive fly.

The genotype of the double recessive fly is known. i.e. Here it is *ggll*. So it produces only one type of gamete ***gl***.

The types of gametes produced by the F_1 fly can be understood by the types of flies produced in the F_2.

If ***four*** types of flies are produced in the F_2, then the F_1 fly has produced 4 types of gametes (4 types of F_1 gametes X 1 type of double recessive gametes). If two types of flies are produced, then the F_1 fly should have produced only two types of gametes (2 X 1 = 2).



Four types of gametes due to independent assortment

Two types of gametes due to linkage

Fig .6.5: Gametes produced by F1 fly in test cross experiment.

Types of Linkage

Linkage is of two types, namely ***complete linkage*** and ***incomplete linkage.***

1. Complete Linkage

In complete linkage, linked genes inherit together for many generations. Here crossing over does not occur. In complete linkage the genes are closely situated.

Eg. *1. Body colour and shape of wings in male Drosophila.*
2. Bent wings and shaven bristles in the 4th chromosome of Drosophila. (Fig. 6.1)

Complete linkage is *the phenomenon in which two or more genes or characters are inherited together for a number of generations*. In this, genes are closely associated and tend to inherit together. Complete linkage is due to the fact that there occurs no break in the chromosomes. As a result of complete linkage, the young ones inherit only the parental characters. New characters do not appear among the youngones. So complete linkage produces only parental combination; new combinations do not arise. This phenomenon is very rare. It is found only in male *Drosophila*. The F_1 male hybrid is back crossed with recessive female parent. The F_1 male hybrid produces only two types of gametes in which the linked genes (***G*** and ***L*** or ***g*** and ***l***) are inherited together. So only two types of offspring are produced in the F_2 generation in equal numbers.

2. Incomplete Linkage

The separation of linked genes during inheritance is called *incomplete linkage*. The linked genes are separated due to crossing over, chromosomal breaks, etc.

Eg. *1. Body colour and wing shape in female Drosophila.*
2. Seed colour and seed shape in maize.
3. Flower colour and pollen grain shape in sweet pea.

In incomplete linkage, the linked genes on certain occasions separate. This leads to the formation of new combinations among the young ones. Incomplete linkage is due to the breakage of chromosomes during gametogenesis. Incomplete linkage is found in ***female*** *Drosophila*. This breakage of chromosomes leads to the separation of linked genes and new combinations appear. Because of this new genic combination the offspring produced in the F_2 generation are different from their parent in their phenotype and genotype. So the incomplete linkage involves the accidental breakage of chromosomal segments or linked genes, resulting in new combination of genes.

In the below experiment, the F_1 female hybrid produces four types of gametes. Among four types, two types of gametes carry new combinations due to the separation of linked genes. The gene ***G*** is separated

from *L* and joins with *l*. In the same way the *L* joins with *g*. These combinations are different from the original combination. This type of inheritance is different from the ***independent assortment***. If the genes are assorted independently the four types of offspring produced in the F2 generation of the above experiment should be in the 1:1:1:1 ratio.

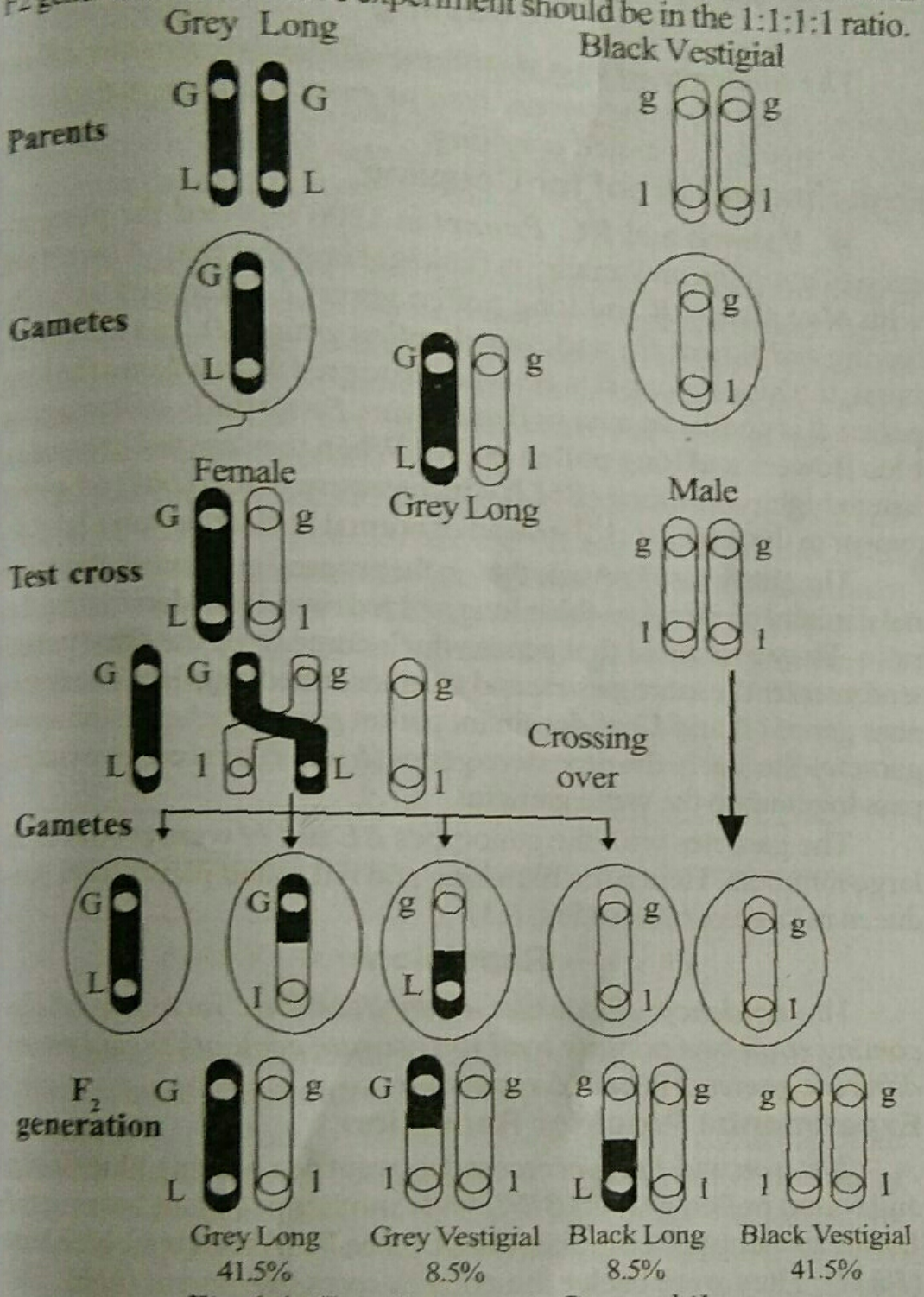


Fig.6.6: Crossing over in Drosophila.

Coupling and Repulsion

Bateson and ***Punnet*** in 1906 proposed the hypothesis of coupling and repulsion to explain the later proposed ***linkage***.

Coupling

The tendency of two dominant alleles or recessive alleles coming from the same parent tend to enter the same gamete and inherit together is called ***coupling***.

Experimental Proof for Coupling

W. Bateson and ***RC. Punnet*** in 1906 reported the phenomenon of coupling and repulsion (linkage) in sweet peas. A sweet pea with ***blue flower B*** and long pollen grains ***L*** is crossed with one having ***red flower (b)*** and ***round pollen*** grains (***l***). In this experiment, the blue colour ***B*** is dominant over red colour ***b*** and the long pollen ***L*** is dominant over pollen ***l*** grains. So all the F_1 offspring has blue flowers and long pollen grains. When they are test crossed (a heterozygous blue long (***BbLl***) with recessive parent (***bbll***) offspring appear in the ratio 7:1:1:7 instead of normal back cross ratio 1:1:1:1.

The above result reveals that, in the progeny generation; the original parental phenotypes (blue long and red round) are dominating the ratio. They explained that genes which come from the same parent tend to enter the same gamete and are transmitted together. The dominant genes (***B*** and ***L***) of dominant parent pass together to the same gamete. Similarly the recessive genes (***b*** and ***l***) of recessive parent pass together to the same gamete.

The gametes with the genotypes ***BL*** and ***bl*** were produced in large numbers. Hence the blue long and red round plants were produced in large numbers.(Fig. 6.3).

Repulsion

The tendency of two dominant alleles or recessive alleles coming from two parents tend to separate each other and enters different gametes is called ***repulsion***.

Experimental Proof for Repulsion

Bateson and ***Punnet*** crossed a sweet pea bearing blue flower and round pollen grains (***BBll***) with another pea plant bearing red flower and long pollen grains. (***bbLL***). The F1 hybrids were blue long (***BbLl***). They were back crossed with recessive parent (***bbll***). The back cross ratio was 1:7:7:1 instead of normal 1:1:1:1 ratio.

Here the two dominant alleles (***B*** and ***L***) or recessive alleles (***b*** and ***l***) repelled each other because they came from different parents. The gametes with genotypes ***Bl*** or ***bL*** were formed in more numbers, Hence the blue round and red long plants were produced in more numbers. (Fig.6.4).

Arrangement of Linked Genes

Sturtevant in 1913 found out that the genes are arranged in the chromosome in a ***linear manner***. Based upon the arrangement of the genes in the chromosome the linkage can be classified into two types.

1. ***Cis arrangement :*** In cis arrangement, the two dominant genes (***B*** and ***L***) are located on one member of the chromosome pair; the two recessive genes (***b*** and ***l***) are located on the other. This type of arrangement, with two dominants on same chromosome is called ***cis arrangement***. The heterozygotes with such arrangement are known as ***cis heterozygotes***.

2. ***Trans arrangement :*** In this type, the dominant gene of one pair and the recessive gene of other pair. (***B*** and ***l***) are located on one chromosome and the recessive gene of the first pair and dominant gene of the second pair (***b*** and ***L***) are located in the second chromosome. The heterozygotes with such arrangement are known as ***transheterozygotes***.

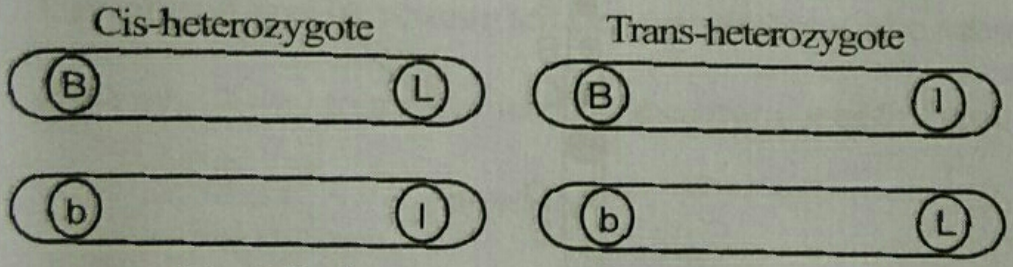


Fig.6.7: Arrangement of linked genes.

Theories of Linkage

There are two theories on linkage. They are the following:

Differential Multiplication Theory

Bateson (1930) assumed that linkage is due to the ***differential multiplication of cells containing different combinations of genes.*** After the segregation of genes during gamete formation, the set of gametes possessing parental combinations multiplies rapidly than the set having non-parental combination. This theory was disproved because after segregation of genes, there is only one division.

Chromosome Theory of Linkage

Morgan and ***Castle*** proposed the chromosomal theory of linkage. The main features of the chromosomal theory of linkage are the following:

1. The genes are arranged in a linear fashion on the chromosomes.
2. The genes on a chromosome are linked
3. Genes showing linkage are located on the same chromosome.
4. Linked genes will remain together during inheritance.
5. The distance between the genes will determine the strength of linkage. The closely located genes show strong linkage. Distantly located genes show weak linkage.

Importance of Linkage

1. Linkage presents variation in evolution.
2. Linked genes of desired traits help the plant and animal breeders in hybridization programs.

Linkage Groups

All the linked genes of a homologous pair of chromosomes form one group called ***linkage group.***

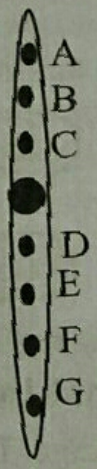


Fig. 6.8: A linkage group.

In *Drosophila,* there are four linkage groups corresponding to the four pairs of chromosomes.

The garden pea plant has seven pairs of chromosomes and has 7 linkage groups.

Man has 23 linkage groups corresponding to 23 pairs of chromosomes.

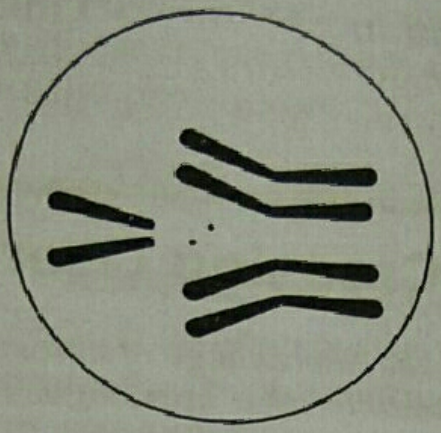


Fig.6.9: Four linkage groups of Drosophila.

Each linkage group has a particular number of genes. The number of genes is proportional to the length of the chromosomes.

In *Drosophila,* the smallest chromosome has the smallest linkage group of 12 linked genes. The largest chromosome has the largest linkage group of 150 linked genes.

Factors Affecting Linkage

Linkage is affected by the following factors:

1. Distance: Closely located genes show strong linkage while genes widely located show weak linkage.

2. Age: With increasing age the strength of linkage decreases.

3. Temperature: Increasing temperature decreases the strength of linkage.

4. X-rays: X-ray treatment reduces the strength of linkage.

7. 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.*

Crossing over was discovered by ***Morgan.***

Crossing over is the interchange of chromosomal segments between the homologous chromosomes.

It occurs during ***meiosis*** or ***gametogenesis.***

The crossing over occurs only between ***non-sister chromatids*** of the homologous chromosomes.

The number of crossing over depends upon the ***length*** of the chromosome. *The longer the length, the higher the percentage of crossing over.*

When the genes are located distantly, the chance for crossing over is higher. When the genes are closely located the chance for crossing over is lesser.

The number of crossing over between two genes is represented by ***percentage of crossing over.***

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

The percentage of crossing over is the expression of the number of recombinations in percentage to the total number of offspring.

$$\textbf{Crossing over} = \frac{\text{Percentage of total number of offspring in } F_2}{\text{Total number of recombinations}} \times 100$$

The percentage of crossing over is also called ***frequency of crossing over.***

Thus percentage of crossing over = Frequency of crossing over = Percentage of recombination.

Generally crossing over is less frequent near the centromere and the tip of the chromosome.

Crossing over at one point prevents another crossing over nearby.

When there is a single crossing over in a homologous chromosome, it is called ***single crossing over.***

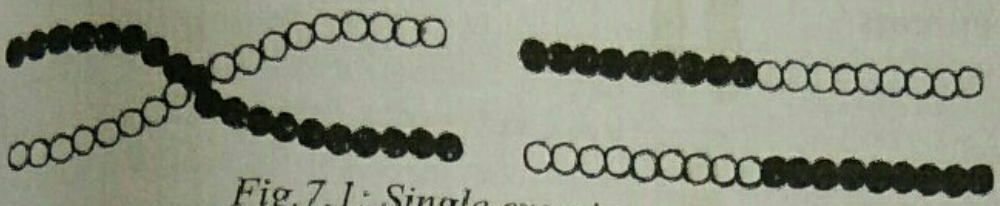


Fig.7.1: Single crossing over.

When there are two cross overs in a homologous chromosome, it is called ***double crossing over.***

When there are many cross overs in a homologous chromosome, it is called ***multiple crossing over.***

The crossing over may be formed between two strands or 3 strands or 4 strands. It is always formed between non-sister chromatids.

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 F_1 hybrid is ***grey long.***

When ***female*** flies of F_1 generation are back crossed with double recessive male, four types of offspring are produced.

Among the four types of offspring, two types - black vestigial and grey long - are just like the parents and they are known as ***parental combinations.*** Among the F_1, about 41.5% of flies are like the dominant parent and another 41.5% are like the recessive parent.

The other two types grey vestigial and black long are different from their parents genotypically and phenotypically, and they are known as ***non-parental combinations.*** The non-parental combinations of F_1 flies include 8.5% grey vestigial and 8.5% black long.

The F_1 female hybrid produces four towards each other and come to lie side-by-side. This phenomenon of pairing of homologous chromosomes is 4 kinds of eggs. Two types of eggs carry the linked genes in original combination. But the other two types of eggs carry the genes in a new combination. If the law of independent assortment of genes takes place in the above cross, all the F_2 offspring are in equal numbers (1:1:1:1) as a result of back cross.

The actual results of the above cross indicates that the law of independent assortment is not operating in these crosses.

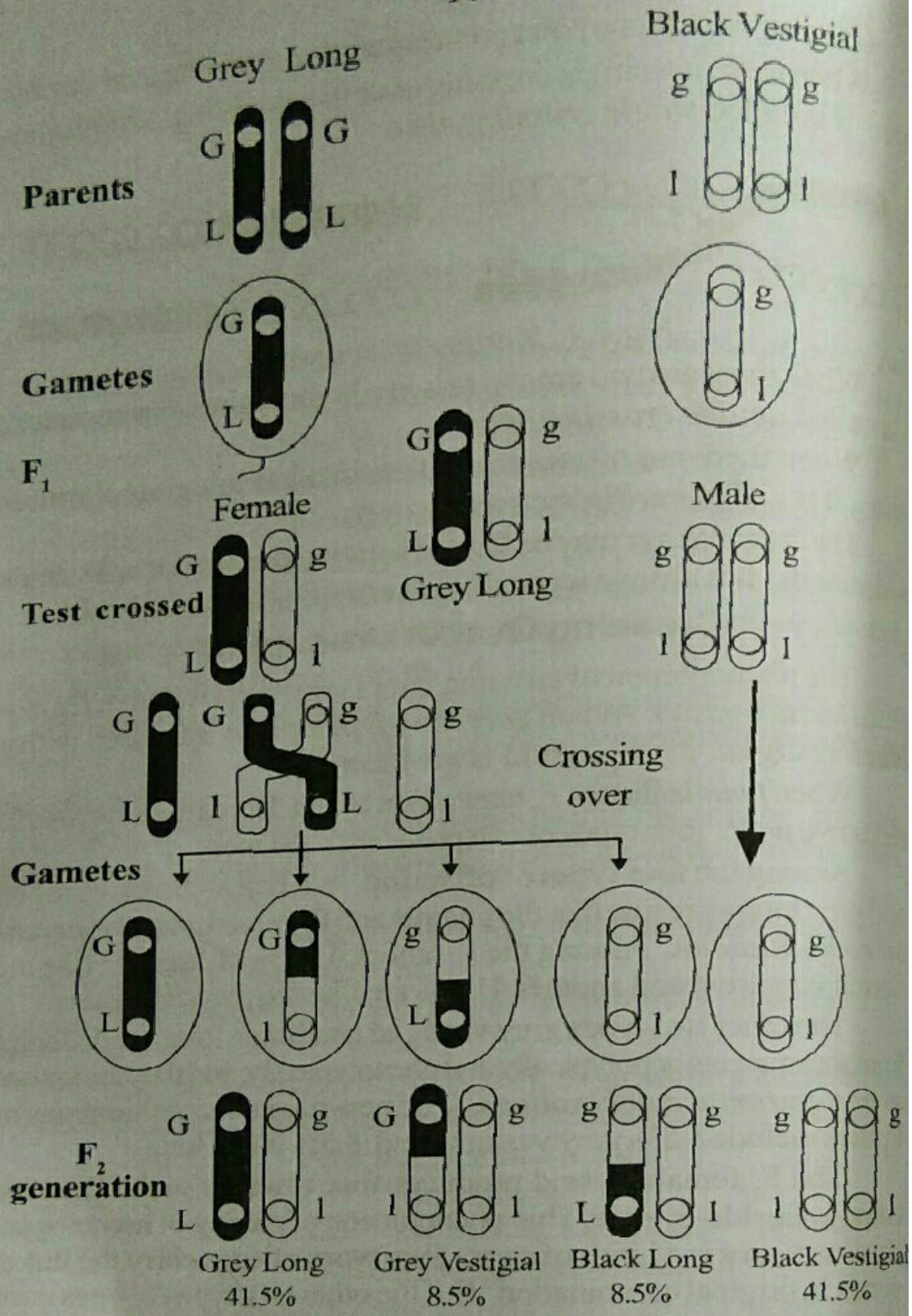


Fig.7.2: Crossing over in Drosophila.

When F1 ***female*** is test crossed with double recessive fly. In the F2, 4 types of offspring are produced in the ratio 41.5% : 8.5% : 8.5% : 41.5%

Grey long GL/gl - 41.5%

Grey Vestigial Gl/gl - 8.5%
Black Long gL/gl - 8.5%
Black vestigial gl/gl - 41.5%

Here the ***parental combinations*** grey long and black vestigial are very large (83%). They are due to ***linkage***. The new combinations are less (17%). They are due to crossing over in the F1 female fly.

In *Drosophila*, F1 ***male***, there is no crossing over as far as these two characters are concerned. So here the ***linkage*** is ***complete***.

In F1 ***female***, there is linkage as well as crossing over. This is called ***incomplete linkage***.

Significance of Crossing Over

Crossing over is of great significance.

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

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

Crossing over is *the interchange of chromosomal segments between non-sister chromatids.*

Crossing over occurs during ***meiosis*** of ***gametogenesis.*** The homologous chromosomes move towards each other and come to lie side by side. *This phenomenon of pairing of homologous chromosomes* is called ***synapsis***. The paired homologous chromosomes are called ***bivalents.***

The homologous chromosomes split longitudinally. Each chromosome splits into two ***chromatids.*** Hence four chromatids are produced from two homologous chromosomes. This stage is called ***tetrad stage.*** The two chromatids of a chromosome are attached by a single centromere. These are called ***sister chromatids.***

The ***non-sister chromatids*** of homologous chromosomes twist over each other. At certain points, the non-sister chromatids are connected with each other. *The points of contact between non-sister chromatids* are called ***chiasmata (chiasma***=singular*)*. Chiasma means a ***cross***.

At the chiasma the chromatids ***break***. This is brought about by an enzyme called ***endonuclease***. The broken segment of one chromatid is fused with the other chromatid and vice versa. This fusion is brought about by another enzyme called ***ligase.*** The process of fusion is called ***ligation.*** The exchange of chromosomal segments between non-sister chromatids is called ***crossing over.***

After crossing over, the non-sister chromatids repel each other. They separate from each other from twisting. The separation starts from the centromere towards the ends like a zip. This separation is called ***terminalization.*** This leads to the separation of homologous chromosomes.

There are many theories to explain the mechanism of crossing over.

1. Chiasma Type Theory

This theory was proposed by ***Janssens.*** This theory suggests that prior to crossing over, the chromosomes of each bivalent get duplicated to form a ***tetrad.*** Crossing over occurs only between the non-sister chromatids of a tetrad. In the ***diplotene stage,*** the non-sister chromatids overlap with one another and form ***chiasma*** or ***point of contact***. In the chiasma, the chromatids break and they rejoin

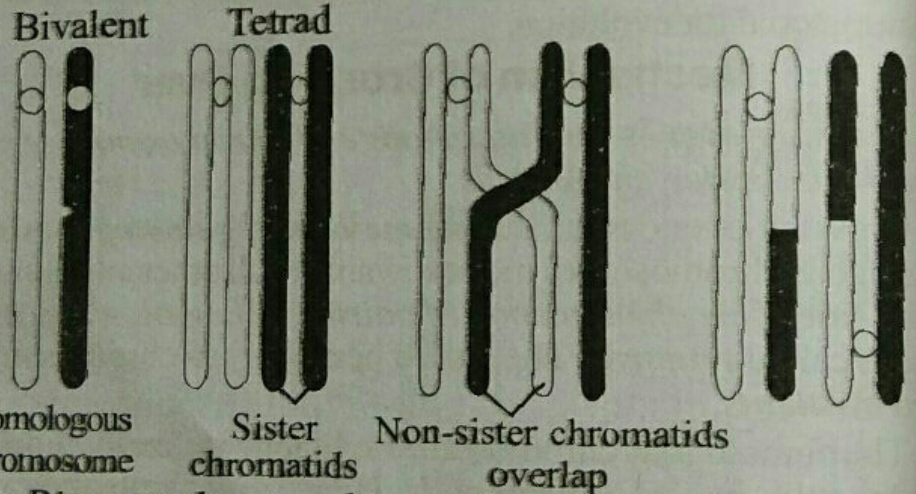


Fig.7.3: Diagram showing chiasma formation and crossing over.

with the mutual exchange of segments. The other two chromatids remain intact. This theory is known as ***chiasma type theory.***

2. The Breakage First Theory

This theory was proposed by ***Muller.*** According to this theory, the non-sister chromatids of homologous chromosomes first break off without crossing over. The broken segments rejoin to form new combinations.

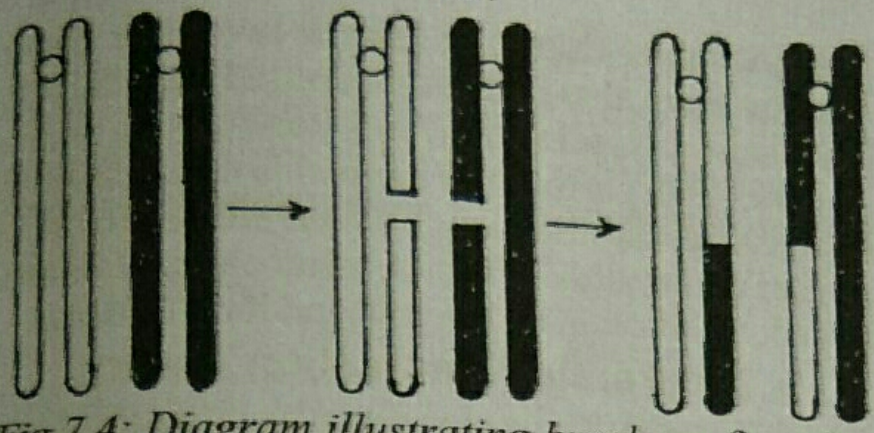


Fig.7.4: Diagram illustrating breakage first theory.

3. The Contact First Theory

This theory was proposed by ***Serebrovsky.*** According to this theory, the non-sister chromatids first touch and cross each other. The breakage occurs at the points of contact of the chromatids. The broken segments rejoin to form new combinations.

4. Strain or Torsion Theory

This theory was proposed by ***Darlington.*** According to this theory, the homologous chromosomes (bivalent) are relationally coiled around each other in a specific fashion.

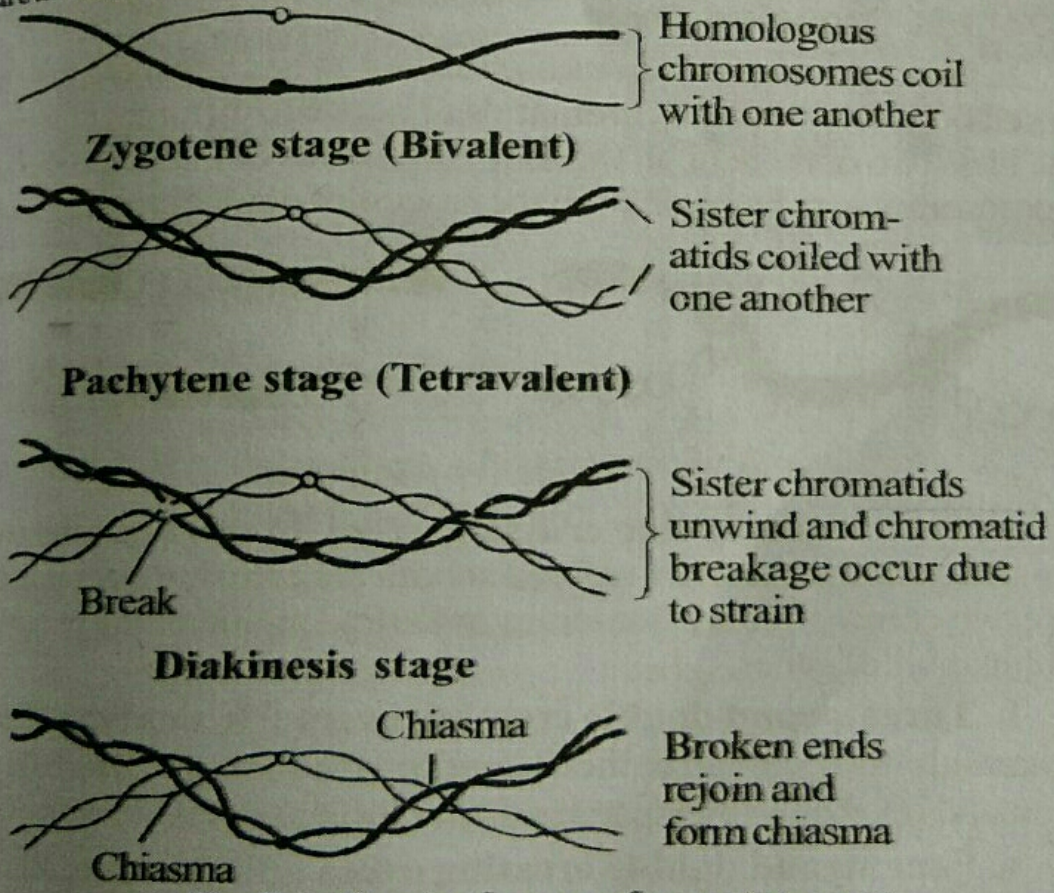


Fig.7.5: Strain theory of crossing over.

The chromosomes duplicate and the two sister chromatids in each chromosome are also coiled one around the other. When the chromosomes start separating their relational coiling unravel in one direction and the sister chromatids unravel in the opposite direction. The repulsion causes torsion, which exerts pressure or strain on the weak non-sister chromatids. The non-sister chromatids break at the point of contact and broken ends rejoin and form chiasma.

5. Differential Contraction Theory

Huskin suggested that tension set up by differential contraction after pairing may cause breaks at overlap. Separation starts from the centromere towards the ends like a zip. This separation is called ***terminalization***. This leads to the separation of homologous chromosomes.

Based upon the number of chiasmata formed, crossing over may be classified into three types. They are as follows:

1. Single Crossing Over

In this type, only one chiasma is formed. Only one chromatid of each chromosome is involved in single crossing over.

2. Double Crossing Over

In this type, two chiasmata are formed. The chiasmata may be formed between the same chromatids or between different chromatids. Thus two or three or all the four chromatids of the homologous chromosomes may be involved in the process of double crossing over.

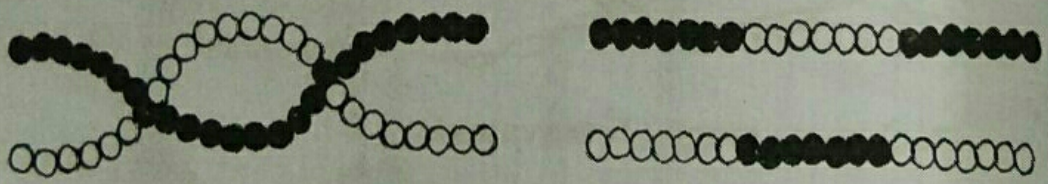


Fig. 7.6: Double crossing over.

a. Two strand double crossing over: In this type, the two non-sister chromatids are involved at both the crossing over points. Here two chromatids are non-cross overs and maintain the parental combination of genes.

b. Three strand double crossing overs : In this type, three chromatids are involved in the formation of chiasmata. Here three chromatids exchange their parts and one chromatid is non-cross over.

c. Four strand double crossing overs : In this type, all the four chromatids are involved in the formation of chiasmata.

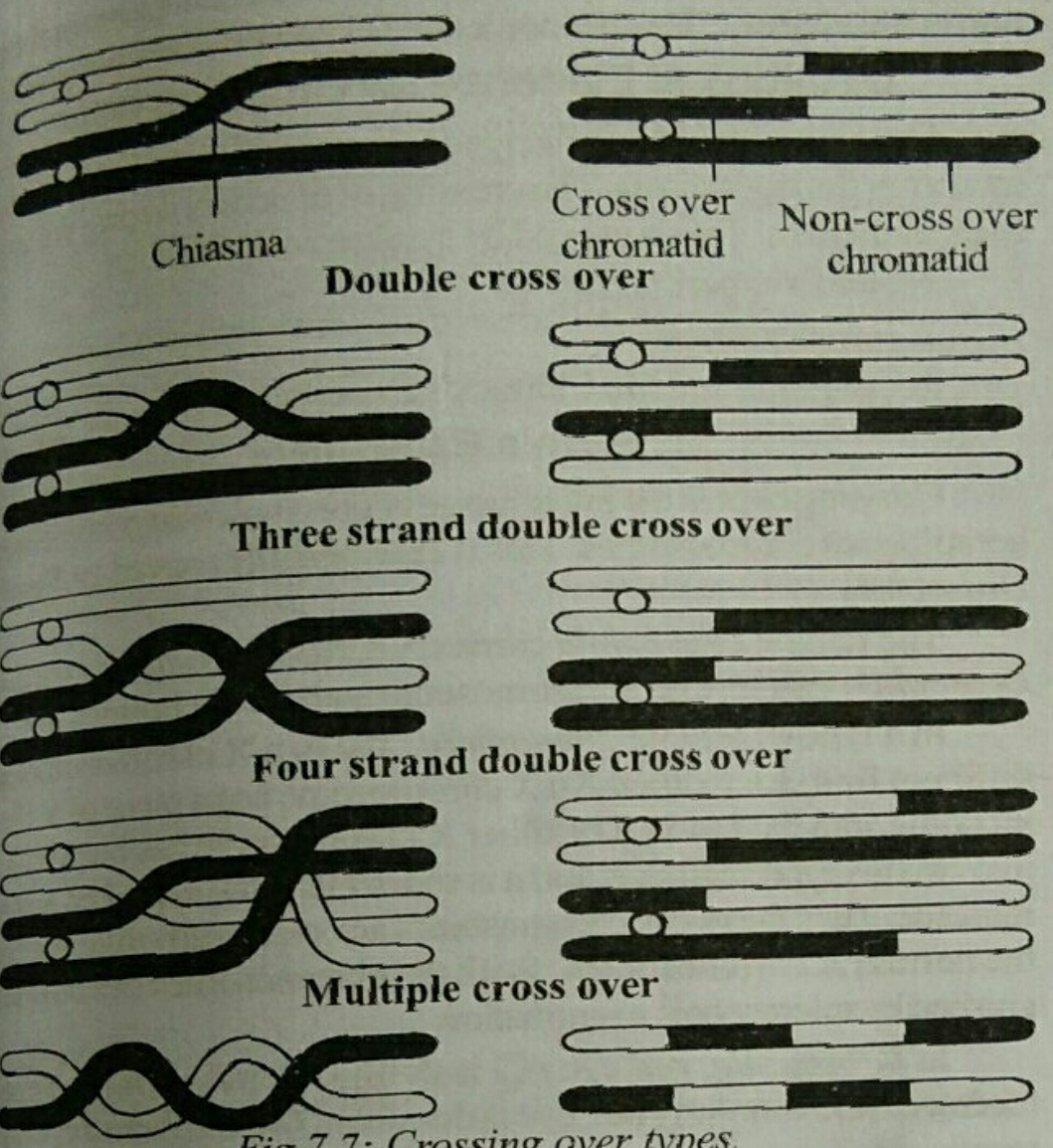


Fig. 7.7: Crossing over types.

3. Multiple Crossing Over

In this type, more than two chiasmata are formed. Multiple crossing over is very rare because of interference in crossing over.

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 genic mutation decreases the frequency of crossing over.
5. Crossing over is less frequent near centromeres and the tips of the chromosomes.
6. Inversion 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

Crossing over is the exchange of chromatid blocks between chromosomes during meiosis. 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

1. Stern's Experiment

Crossing over is the interchange of chromosomal parts between homologous chromosomes. This is ***cytologically*** proved by ***Stern*** in *Drosophila.*

The female *Drosophila* carries XX chromosome and the male *Drosophila* carries one X chromosome and one Y chromosome.

In a type of female *Drosophila*, the two X chromosomes are different from each other. An X chromosome has a piece of Y chromosome attached to it. The other X chromosome has been broken into two unequal segments and it is shorter than the unbroken X chromosome. Thus the two X chromosomes are structurally different from the normal X chromosomes. Both the chromosomes can be distinguished by microscopic examination.

In *Drosophila*, ***red*** eye ***(C)*** is dominant and ***carnation*** eye is recessive ***(c)***. Similarly ***bar*** eye is dominant ***(B)*** and ***round*** eye ***(b)*** is recessive.

The broken X chromosome contains a recessive gene ***(c)*** for carnation eye colour and a dominant gene ***(B)*** for ***bar*** eyes, while its homologue contains ***C*** and ***b.***

This female having ***red bar*** eyes is crossed with a double recessive male having carnation round eyes.

In the absence of crossing over, only two types of female gametes are produced; one type having broken X containing c and B genes; the other type having the X with a piece of Y attached containing C and b.

But if crossing over occurs, two more types of gametes are produced; one type having c and b in a normal size X and the other type having C and B on a broken X with a piece of Y chromosome. These

four types of gametes, after fertilization will produce four types of offspring and they are-

1. *Carnation bar*
2. *Red round*
3. *Carnation round* and
4. *Red bar*

The X chromosome of these four types are then identified. Each offspring has the expected chromosomal configuration.

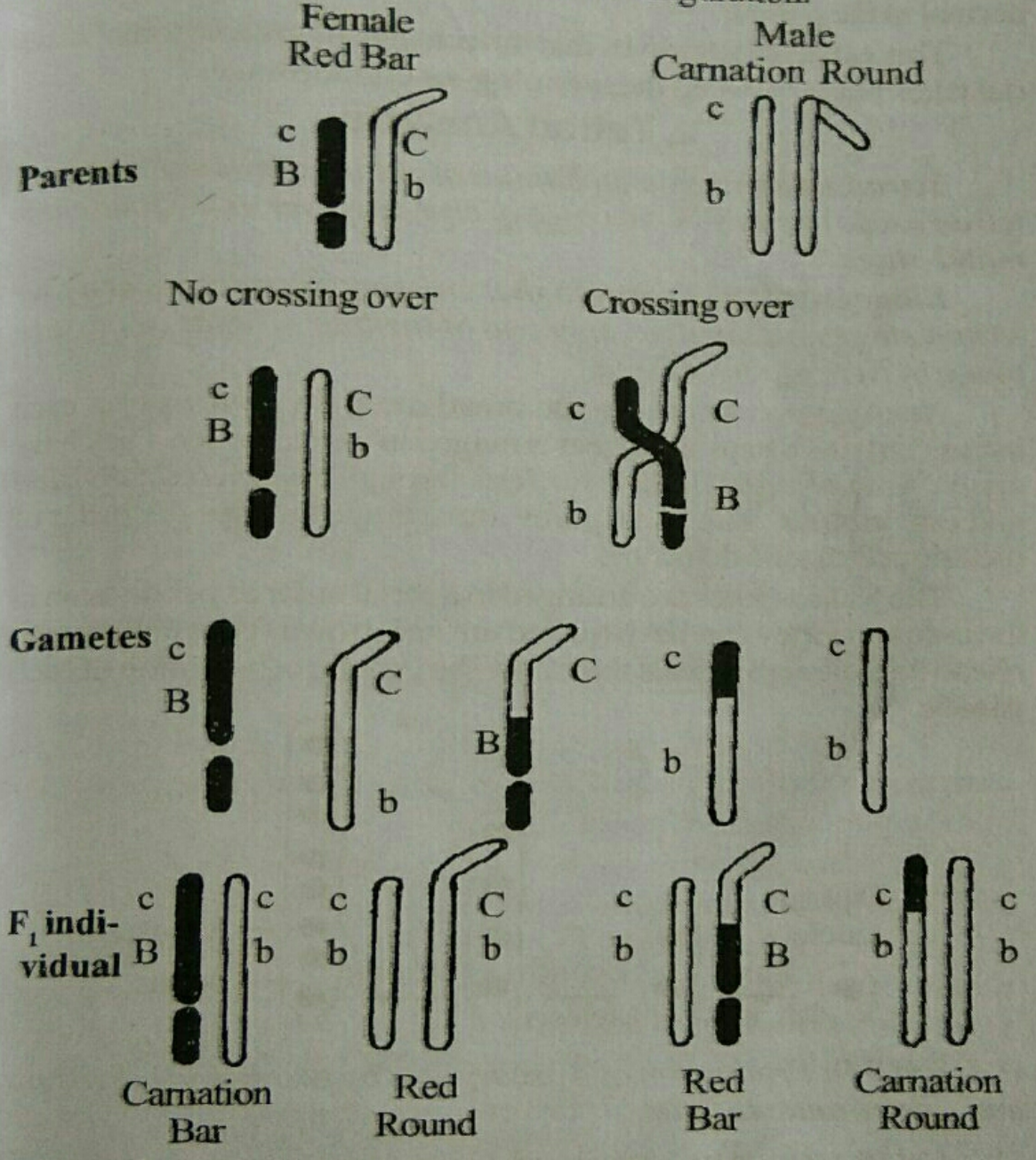


Fig. 7.8: Cytological proof for crossing over.

Phenotypically the red bar eye fly is a product of crossing over. The crossing over is also evident by the cytological observation of this fly. The fragment of Y chromosome, which was attached to the normal size X chromosome in the parent, is now attached to the short, broken X chromosome in the red bar eye fly of F1.

Similarly, phenotypically the carnation round eye fly is a product of crossing over. The crossing over is also evident by the cytological observation of this fly. It has a normal chromosome, which was abnormal in the parent.

This experiment proves that interchange of chromosomal material takes place between the homologous chromosomes.

2. Tetrad Analysis

Tetrad analysis is a *technique of using individual spores of tetrad ascus to study occurrence of crossing over at the four chromatid stage.*

Lindegren (1933) *proved that crossing over occurs at a four strand stage and involves only two of the four strands at any one place in Neurospora crassa.*

Neurospora crassa is a red bread mold. In *Neurospora*, each ***ascus*** contains 8 haploid ***spores*** arranged in a serial order. They have arisen from a single diploid nucleus through ***two meiotic division*** and one ***mitosis***. The ascospores are arranged as per the order of meiotic and mitotic divisions.

The 8 ascospores are arranged in a serial order as per division in the ascus and they can be dissected out and grown separately, giving rise to haploid individuals that show the genetic constitution of each gamete.

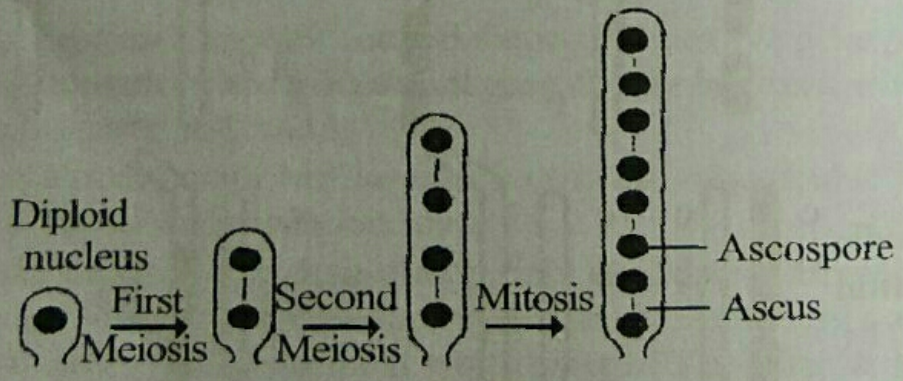


Fig. 7.9: Production of 8 ascospores by two meiotic divisions and one mitotic division.

Let us assume two strains of *Neurospora*, one with ***AA*** genotype and another with ***aa*** genotype. They are crossed.

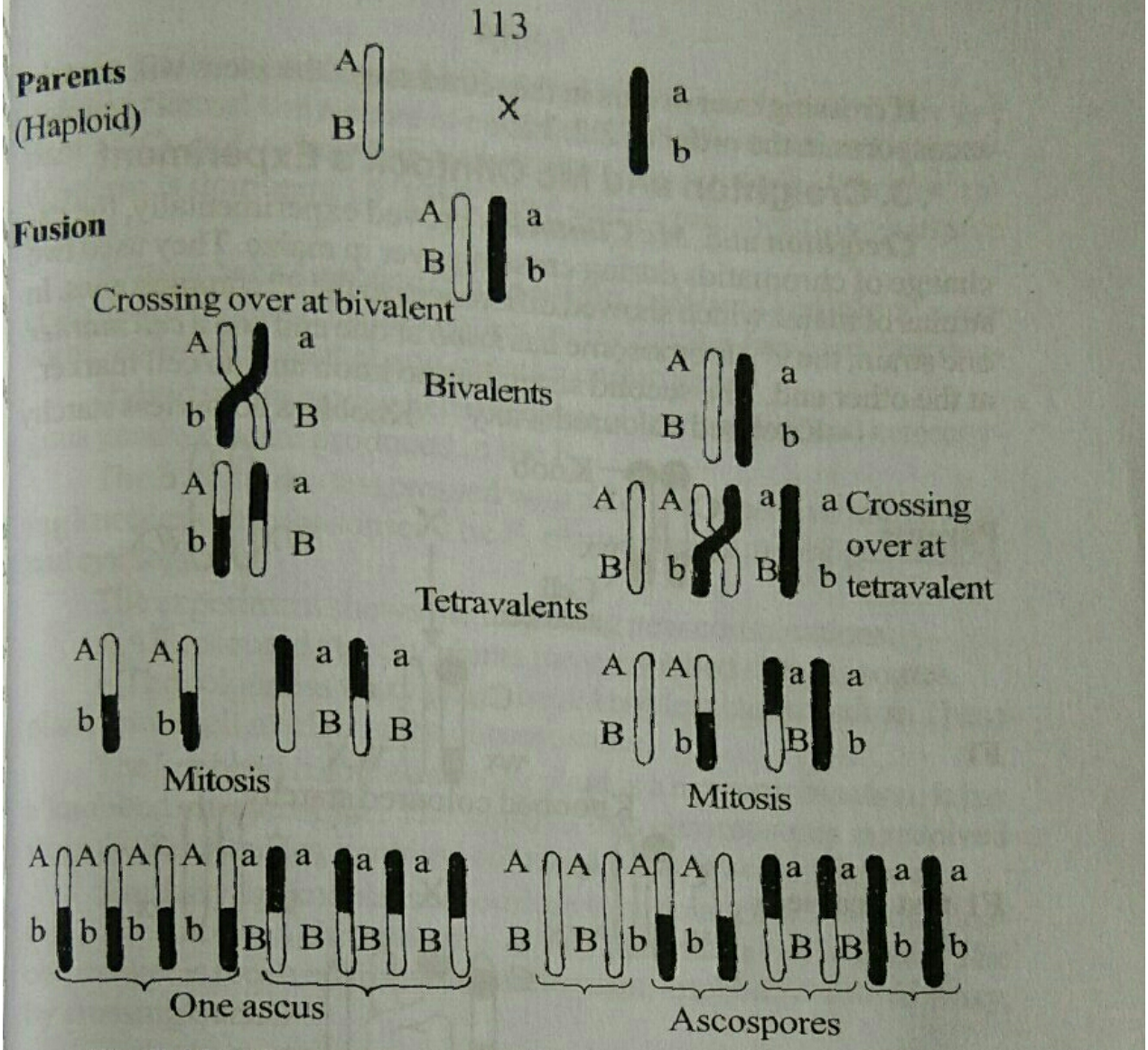


Fig.7.10 : Crossing over in Neurospora in bivalent and tetravalent stages.

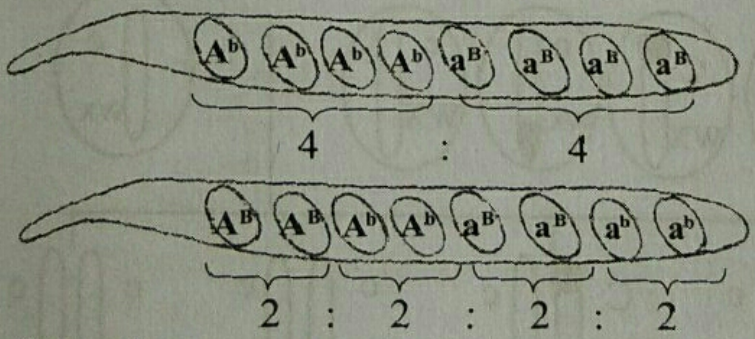


Fig.7.11: Crossing over in Neurospora in bivalent and tetravalent stages.

If crossing over occurs in the bivalent stage, the ascus will contain ascospores in the order of ***4:4***.

If crossing over occurs in the tetrad stage, the ascus will contain ascospores in the order of 2:2:2:2.

3. Creighton and Mc Clintock's Experiment

Creighton and ***Mc Clintock***'s proved experimentally, the exchange of chromatids during crossing over in maize. They used two strains of maize which showed differences in the 9th chromosomes. In one strain, the 9th chromosome has ***knob*** at one end and a ***cell marker*** at the other end. The second strain has no knob and no cell marker.

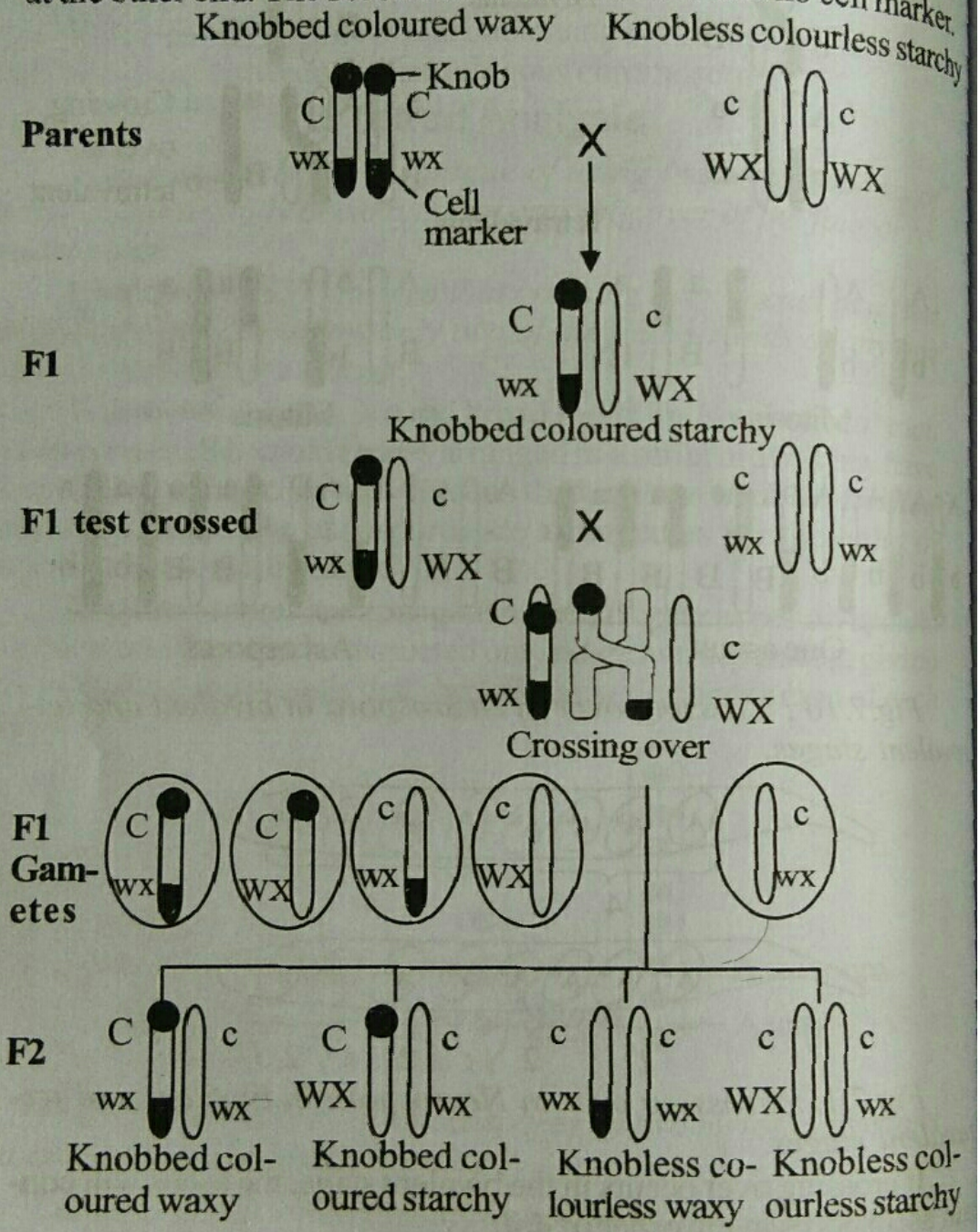


Fig.7.12: Cytological evidence for crossing over in maize.

In addition, two genetical characters are selected. They are *colour* of kernel and ***nature*** of endosperm. ***Coloured*** kernel is dominant (***CC***) and ***colourless*** kernel is recessive (***cc***). ***Starchy*** endosperm is dominant (***WXWX***) and ***waxy*** endosperm is recessive (***wxwx***).

A maize with ***knobbed*** chromosome, ***coloured*** kernel and ***waxy*** endosperm is crossed with another maize having ***knobless*** chromosome, ***colourless*** kernel and ***starchy*** endosperm.

Hybrid maize having heterozygous chromosomes and heterozygous genotypes are produced in the F_1.

The F_1 hybrid is test crossed with a double recessive maize having knobless chromosome. The F_2 plants are examined genetically and cytologically.

The experiment shows the following new combinations.

- All coloured starchy plants have knobbed chromosomes.
- The colourless waxy plants have knobless chromosome. These plants have cell marker in the chromosome.

The knobbed coloured starchy plant is a new combination. It has a knobbed chromosome. The knob of this chromosome is received from the parent plant, knobbed coloured waxy, by crossing over.

Similarly the knobless colourless waxy plant is a new combination. The knobless chromosome of this plant has a ***cell marker.*** The cell marker is received from the parent plant, knobbed coloured waxy, by crossing over.

8. Chromosome Map

The ***chromosome map*** may be defined as *a line, on which the genes are represented by points, separated by distances proportional to the amount of crossing over.*

The chromosome maps are also referred to as ***cross over maps*** since they are sketched by the amount of crossing over.

The percentage of crossing over is directly proportional to the distance of the alleles showing crossing over in the chromosome.

The chromosome maps are *the graphic representation of the genes in a chromosome.*

The percentage of crossing over is calculated by test crosses. In mapping the genes, a unit of distance is used and it is called as ***map unit*** or ***Morgan unit.***

The first chromosome map was made in 1911 by ***Sturtevant*** and soon after additional maps were made by ***Bridges*** and others.

Drosophila is the earliest material used by the scientists, for constructing maps.

Procedure for the Chromosome Mapping

In fact, genes are plotted on the chromosome on the basis of crossing over results between different pairs of linked genes. *The actual distance between two genes is said to be equivalent to the percentage of crossing over between these genes.*

When the % of crossing over between two genes is 5, then the distance is 5 units. For example, five genes ***A, B, C, D*** and ***E*** are to be plotted on a chromosome. If cross over results indicate that genes A and E have the highest percentage of crossing over, it means that these should be placed at the maximum distance.

In this example, the gene ***A*** can be taken as a starting point in the chromosome and can be represented by ***O.***

Now if the gene ***A*** and ***B*** exhibit 7% crossing over, the gene ***B*** can be placed on the chromosome at a distance of 7 units.

If the gene ***C*** shows 8% crossing over with gene ***B*** and about 15% crossing over with gene ***A***, it can be plotted on the chromosome at a distance of 15 units from gene ***A***.

Similarly if gene ***A*** and ***E*** exhibit 20% and 30% crossing over with gene ***D*** and 5% and 10% with gene ***C*** these, are located on the chromosome 5 and 10 units away from the gene ***C*** respectively.

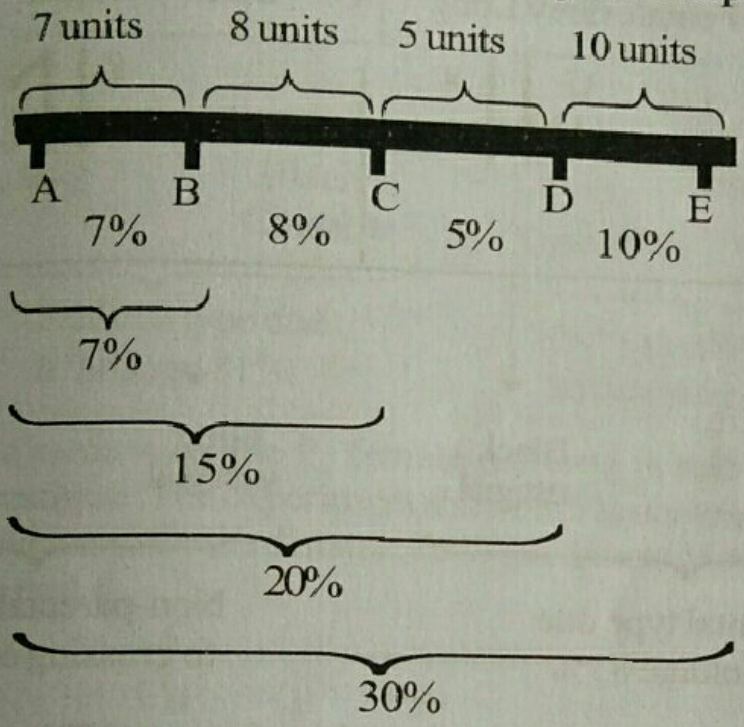
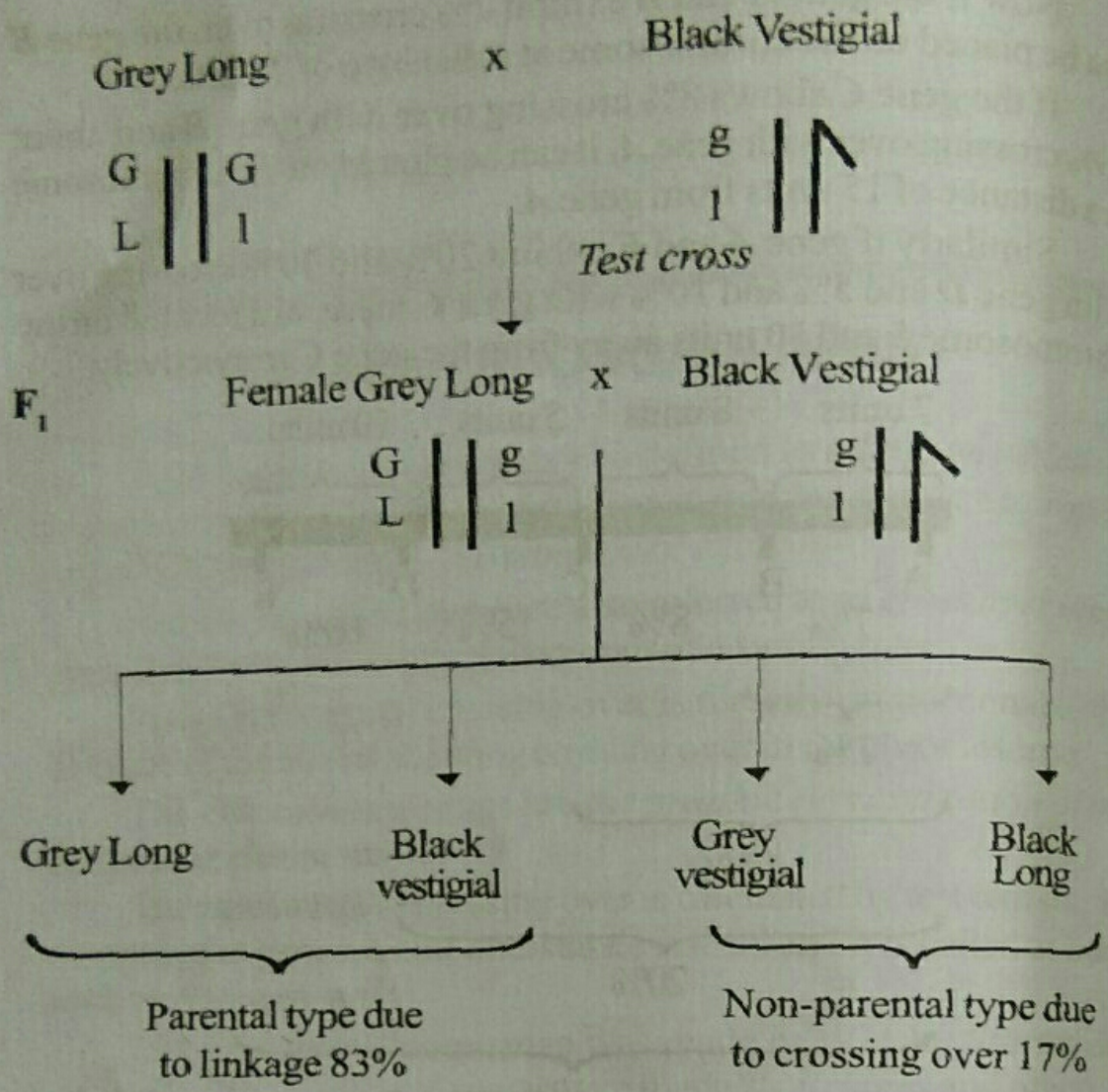


Fig.8.1: Diagrammatic representation of the method of locating genes on a chromosome on the basis of % of crossing over.

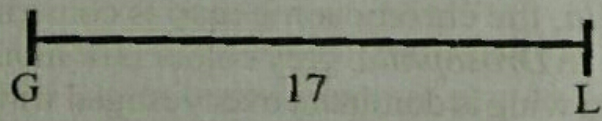
Construction of Chromosome Map in Drosophila

In *Drosophila*, the chromosome map is constructed with the help of test cross. In *Drosophila,* grey colour is dominant over black colour and the long wing is dominant over vestigial wing.

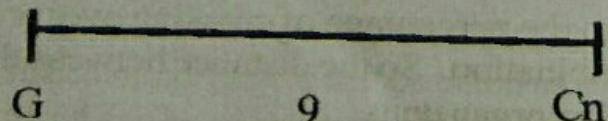
The F_1 female hybrid is ***test crossed.*** Four types of individuals are formed. Out of four types, two types are parental type (G:L & B:V) and other two are non-parental type (G:V & B:L) due to crossing over. Non-parental type is 17%. So the percentage of crossing over is equivalent to 17%. The distance between the two genes (G-L) is equivalent to the percentage of crossing over or percentage of non-parental combination. So the distance between the gene G & L is equivalent to 17 morgan units.

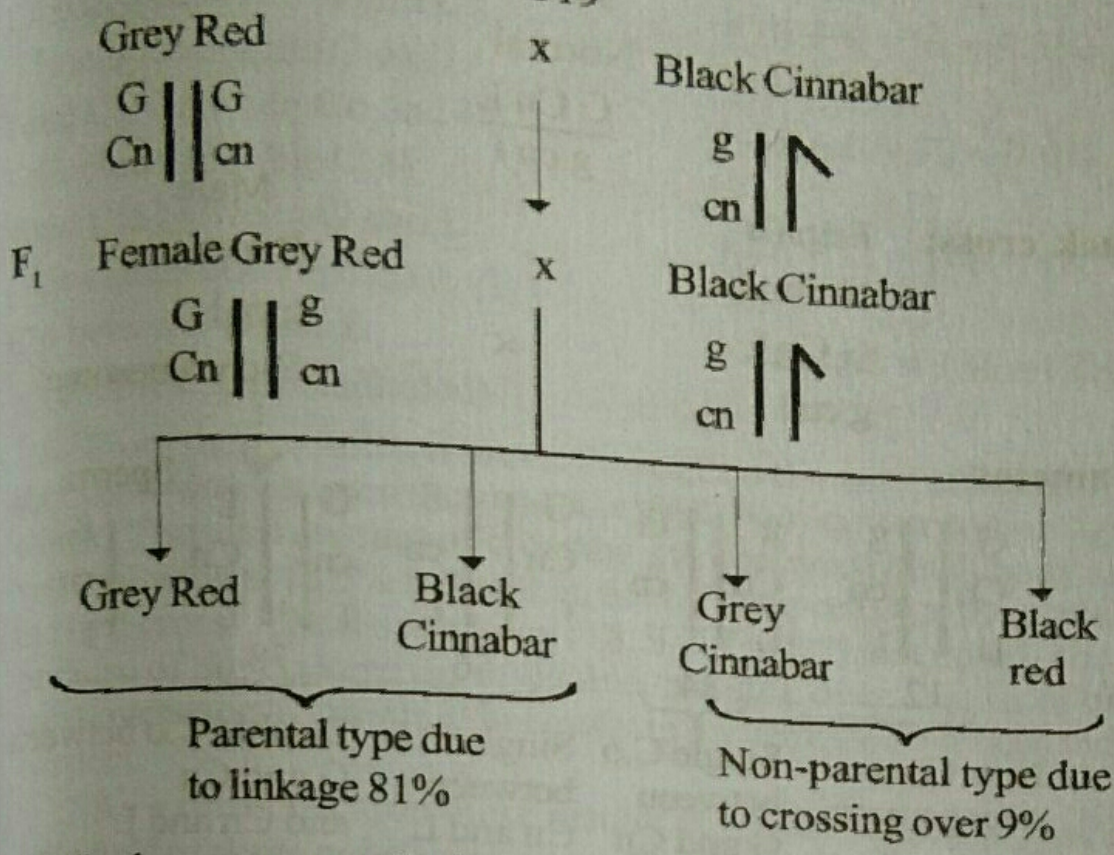


Percentage of non-parental combination = 17%
So the percentage of crossing over = 17
So the distance between the gene G & L = 17 map unit

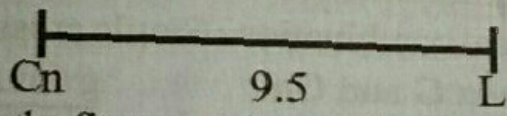


In another experiment, the F_1 female grey red is test crossed with black cinnabar. The experiment shows 9% non-parental combination individuals. So the distance between the gene G & Cn is equivalent to 9 map unit.





In the same way, the F_1 female red long is test crossed with cinnabar vestigial. The experiment shows 9.5% non-parental combination individuals. So the distance between the gene Cn is equivalent to 9.5 map unit.



According to the first experiment, the distance between G & L is equivalent to 17 map unit. But the second and third experiment show 18.5 map units between the two genes. To find out the actual reason for this difference in the distance, conduct a 3 point cross.

Three Point Cross

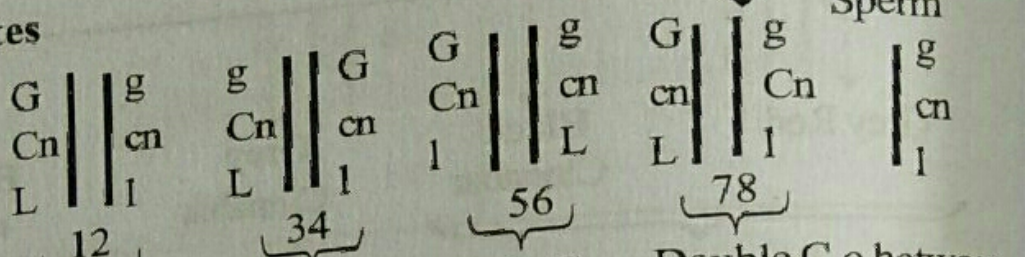
In the three point cross, all the three pairs of genes are considered in the experiment. The F_1 hybrid female is test crossed. They produce 8 different types of individuals. Out of 8 types, two types are parental. Remaining six are non-parental.

	Male		Female
Parent:	Grey Red Long		Black Cinnabar Vestigial
	$\frac{\text{G Cn L}}{\text{Y-chromosome}}$	x	$\frac{\text{g cn l}}{\text{g cn l}}$

F_1 : Normal $\frac{G\ Cn\ L}{g\ cn\ l}$

Back cross: Female Normal $\frac{G\ Cn\ L}{g\ cn\ l}$ × Male Recessive $\frac{g\ cn\ l}{Y\text{-chromosome}}$

Gametes



Non Cross over gamete 82.25%

Single C.o between G and Cn 9%

Single C.o between Cn and L 9.5%

Double C.o between G and Cn and Cn and L 0.75%

F_2 Offspring

Parental combinations due to linkage = 658 = 82.25%

Non-parental combination : Single cross over:

a) Between **G** and **Cn**

1. Black red long $\frac{g\ Cn\ L}{g\ cn\ l} = 36$
2. Grey cinnabar vestigial $\frac{G\ cn\ l}{g\ cn\ l} = 34$

} = 70

b) Between **Cn** and **L**

1. Grey red vestigial $\frac{G\ Cn\ l}{g\ cn\ l} = 35$
2. Black cinnabar long $\frac{g\ cn\ L}{g\ cn\ l} = 31$

} = 66

Double cross over

1. Grey cinnabar long $\frac{G\ cn\ L}{g\ cn\ l} = 4$
2. Black red vestigial $\frac{g\ Cn\ l}{g\ cn\ l} = 2$

} = 6

Total C.o between **G** and **Cn** (includes double C.o) = 70 + 6 =76 = 9.5%

Total C.o between **Cn** and **L** (includes double C.o) = 66 + 6 = 72 = 9.0%

Total C.o between **G** and **L** (includes double C.o) = 76 +72 = 148 = 18.5%

C.o between **G** and **L** (double C.o not included) = 70 + 66 = 136 =17%

From these results, it is concluded that the gene cinnabar lies about half-way between the genes for black body colour and vestigial wings. The total amount of crossing over between black body and vestigial wing is 18.5% rather than the 17% expected on the basis of the first cross. The discrepancy (18.5 - 17 = 1.5) just noted, arises because of the occurrence of double crossing over, that is, of two cross overs occurring simultaneously in the same cell between these two loci.

As a final check on these results, it would be well to make a ***trihybrid*** or ***three point cross*** using all three pairs of genes at once. When pure recessive flies are crossed with normal flies, all the F_1 flies are normal phenotypically. When the F_1 females are back crossed to triple recessive males, eight ***phenotypes*** are obtained.

From the data obtained the relative position of the genes can be calculated. The distance between ***G*** and ***Cn*** is 9 units, the distance between ***Cn*** and ***L*** is 9.5 units; the L gene could be to the right of ***Gn*** locus or to the left. If the first order ***(CnL)*** is correct, then the distance between ***G*** and ***L*** is 17 units. This small discrepancy is due to double crossing over. Based upon the above data, the three genes can be mapped as follows:

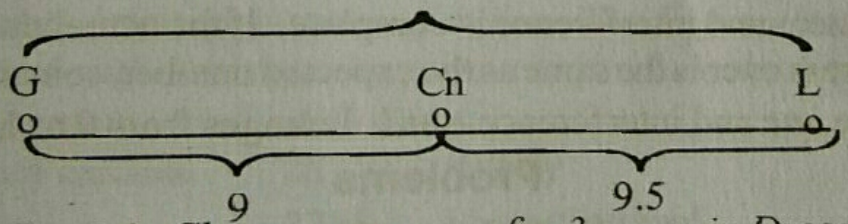


Fig.8.2: Chromosome map for 3 genes in Drosophila.

Chromosome Maps of Drosophila

The chromosome maps of *Drosophila* include four linkage groups corresponding to four chromosome pairs. The genes present in the ***X*** chromosome constitute the first linkage group, those present in 2nd

and 3rd chromosome constitute 2nd and 3rd linkage groups and those on the fourth chromosome form ***fourth linkage group***. The fourth linkage group is the smallest of all.

Chromosome Maps of Maize

Chromosome maps of maize have been drawn by ***R.A. Emerson***. As there are 10 pairs of chromosome 10 chromosome maps are seen.

Factors Affecting the Mapping

Chromosome map can be constructed only with the help of crossing over percentage. The crossing over percentage is highly modified by the ***interference*** and ***coincidence.***

Interference

Normally the double crossing over frequency is very low. Because the crossing over and chiasma formation in the homologous non-sister chromatids interferes with the crossing over and chiasma formation at other points nearby. This is called as ***interference.*** This was discovered by ***Muller*** (1911). The interference is ***inversely proportional to the crossing over percentage***. The interference is maximum over a short distance and decreases as the distance increases.

Coincidence

The ***coincidence*** is *an inverse measure of interference.* It is ***measured*** as a ratio between actual number of double cross overs and the expected number of double cross overs.

$$\textbf{Coincidence} = \frac{\text{Actual number of double cross overs}}{\text{Expected number of double cross overs.}}$$

If the actual number of double cross overs is zero, then coincidence is zero and interference is complete. If the actual number of double cross over is the same as the expected number, coincidence is said to be ***one*** and interference is ***nil.*** It ranges from 0 to 1.

Problems

1. In corn, white endosperm (p) is recessive to purple (P) and shrunken (f) is recessive to full (F). A pure purple shrunken is crossed to a pure white full. The F_1 is then crossed to a white shrunken and the offsprings are as follows:

Purple shrunken - 1575 White shrunken - 58

Purple full - 60 White full - 1667

Calculate the distance between white and shrunken.

Total number of individuals = 3360

No. and % of parental combination individuals due to linkage:

Purple shrunken	= 1575	=	46.9%
White full	= 1667	=	49.6%

No. and % of non-parental combination individuals due to crossing over.

Purple full	= 60	=	1.78%
White shrunken	= 58	=	1.72%

Total % of individuals produced by crossing over =3.5%

So cross over value between the gene P and F	=	3.5 %
So the distance between the gene P and F	=	3.5 unit distance

Answer: The distance between white and shrunken is = 3.5 unit.

F ——— 3.5 ——— P

2. In Drosophila, a ***kidney bean shaped*** *eye is produced by a recessive gene* ***k.*** ***Cardinal*** *eye colour is produced by another recessive gene* ***cd*** *on the same chromosome. Between these two loci is a third locus with a recessive allele* ***e*** *producing* ***ebony*** *body colour. Homozygous kidney, cardinal normal body colour females are mated to homozygous ebony males. The F_1 females are then test crossed with the recessive parent to produce the F_2. Among 5000 F_2 progeny are the following:*

Kidney cardinal	2215	Kidney	114
Ebony	2228	Ebony Cardinal	100
Kidney-ebony	166	Kidney ebony cardinal	3
Cardinal	170	Wild type	4

Determine the map distance between the genes. (use the modern symbols).

	Female		Male
Parents:	Kidney, normal, cardinal k+cd k+cd	x	Homozygous ebony +e+ +e+

F_1 Offspring: Kidney, normal, Cardinal

k + cd

+ e+

Test cross:	F_1 Female k + cd +e+	x	Recessive Male k e cd k e cd

F_2:

1. Kidney cardinal	-	k + cd / k e cd	= 2215	Parental combination
2. Ebony	-	+ e+ / k e cd	= 2228	
3. Kidney ebony	-	k e + / k e cd	= 166	Single cross over
4. Cardinal	-	+ + cd / k e cd	= 170	
5. Kidney	-	k + + / k e cd	= 114	Single cross over
6. Ebony cardinal	-	+ e cd / k e cd	= 100	
7. Kidney ebony cardinal	-	k e cd / k e cd	= 3	Double cross over
8. Wild type	-	+ + + / + + +	= 4	

Total number of individuals = 5000

Among 8 types of individuals, the first two types are non- cross over parental types. The kidney ebony and cardinal (3 and 4) are due to a single cross over between the genes ***k*** and ***e***. The kidney and

ebony cardinal (5 and 6) are due to a single cross over between the genes *e* and *cd*. The kidney ebony cardinal and wild types (7 and 8) are due to double cross overs.

The cross over % between k and e =

$$\frac{\text{No. of S.C.O. individuals + No. of D.C. O individuals}}{\text{Total number of individuals}} \times 100$$

No. of S.C.O. individuals between k and e = 166 + 170 = 336

No. of D.C.O. individuals = 3 + 4 = 7

Total number of individuals = 5000

So the C.O% between k and e $= \frac{336 + 7}{5000} \times 100$

$= 6.86 = 7\%$

No. of S.C.O. individuals between e and cd = 114 + 100 = 214

So the C.O% between e and cd $= \frac{214 + 7}{5000} \times 100$

$= 4.42\%$

Map unit distance between two genes is = % crossing over between the two genes

So the map unit distance between the genes

k and e = 7%

e and cd = 4.42%

K ——— e ——— cd

7% 4.42%

Coefficient of Coincidence

$$\text{Coincidence} = \frac{\text{\% of actual double cross over}}{\text{\% of expected double cross over}}$$

Actual double cross over = 4+3 = 7

% of actual double cross over $= \frac{7}{5000} \times 100$

$= 0.14\%$

Expected double cross over $= \frac{7}{100} \times \frac{5}{100} \times 100$

$= 0.35\%$

So coefficient of coincidence = $\frac{\text{Observed D.C.O percentage}}{\text{Expected D.C.O percentage}}$

$= \frac{0.14}{0.35} = 0.4$

Coincidence = 0.4

3. In Drosophila, pink eyes (r) are recessive to red (R); the spineless condition (s) is recessive to the spined condition (S). Both pink and spineless are in the third chromosome. A pure red spined Drosophila is crossed to a pink spineless. Give the genotypes of the P_1 and F_1. If an F_1 female is crossed to pink spineless male, what is the genotypic nature of the offspring? What percent will each type be of the total and what will be their appearance? Tell what % the cross over are of the total offspring and tell, therefore, what the 'distance' between pink and spineless is judged to be.

4. A red spined Drosophila is crossed to a pink spineless and the F_1 female is test crossed to a pink spineless male. The number of the offspring produced by the test cross is as follows:

Red spined	- 226	Red spineless	- 25
Pink spined	- 28	Pink spineless	- 221

Calculate the distance between pink and spineless as judged by this experiment.

*5. In maize genes **P, S** and **Py** are on sixth chromosome. From the following cross and the test cross between the F_1 and full recessive, what phenotypes would be expected and in what proportions?*

P S Py x ps py
P S Py ps py

11. Sex Linked Inheritance

The transmission of body characters from parents to offspring along with a sex is called ***sex linked inheritance.*** It is also called ***sex linkage.***

The genes controlling body characters located on the sex chromosomes are called ***sex linked genes.***

The body characters (other than sex characters) controlled by genes located on the sex chromosomes are called ***sex- linked characters.***

Sex linked inheritance was discovered by ***T.H. Morgan*** in 1910.

The following are the common examples for sex-linked inheritance:

1. *Colour blindness*
2. Haemophilia
3. *Eye colour in Drosophila*
4. *Hypertrichosis (Hair in the ear pinna)*
5. *Ichthyosis hystrix.*

The sex linked genes are located on ***X*** chromosome or ***Y*** chromosome or both ***X*** and ***Y*** chromosome.

The genes, controlling body characters, located on X chromosome are called ***X-linked genes.*** The inheritance of X-linked genes is called ***X-linked inheritance.*** The characters controlled by X-linked genes are called ***X-linked characters.*** Eg. *Haemophilia, colour blindness, eye colour in Drosophila.*

The genes controlling body characters located on Y chromosome are called ***Y-linked genes.*** The inheritance of Y-linked genes is called ***Y-linked inheritance.*** The characters controlled by Y-linked genes are called ***Y-linked characters.*** Eg. *Hypertrichosis* (hair in the pinna), *Ichthyosis hystrix* (scales on the body).

The genes controlling body characters located on both X and Y chromosomes are called ***XY linked genes.*** The inheritance of XY linked genes is called ***XY linked inheritance.*** The characters con-

trolled by XY linked genes are called ***XY linked inheritance.*** Eg *Xeroderma pigmentosum, Retinitis pigmentosa, nephritis,* etc.

Most of the sex linked characters are ***recessive.*** They are more common in man than in woman.

Most of the sex linked genes follow ***criss-cross inheritance (zig-zag inheritance).*** *The inheritance of a character from the father to his grandson through his daughter is* called ***criss-cross inheritance.*** That is, the sex linked character appears only in ***alternate generations.***

1. Colour Blindness

1. Colour blindness is a ***sex linked character*** discovered by ***Wilson*** in 1911.

2. It is a ***hereditary disease*** and the affected persons cannot distinguish red colour and green colour.

3. The red blindness is called ***protonopia.*** These persons cannot see red colour. The green blindness is called ***deuteronopia.*** Such persons cannot see green colour.

4. Colour blindness is a recessive character.

5. It is caused by recessive genes represented by cc. The normal persons contain the genes ***CC*** or ***Cc*** or ***C*** alone (in man). The recessive genes prevent the proper development of colour sensitive cells in the retina.

6. The genes for colour blindness are located on the X chromosomes. Their alleles are absent from Y chromosome.

So man has only one gene. The presence of only one gene for a character is called ***hemizygous***. So man is a ***hemizygote*** for colour blindness.

7. This character is common in man but rare in woman.

8. Colour blindness follows ***criss-cross inheritance*** as this character is transmitted from the father to the grandson through the daughter. It appears only in ***alternate*** generations.

9. This character is never transmitted to the son from the father.

10. The daughter carrying one recessive gene for colour blindness is called ***carrier.*** The carriers are normal in their vision.

When a normal woman possessing the dominant gene for normal vision (CC) happens to marry a colour blind man (cY), all their daughters get one gene for colour blindness from their father. But

they receive a dominant gene C from their mother. So they are normal. But they carry the recessive gene in one of their X chromosomes. So the daughters are called ***carriers*** because they carry the gene for colour blindness. The sons never get the disease because they receive their X chromosome from the normal mother and the Y chromosome from their father, from which the allelic gene is absent.

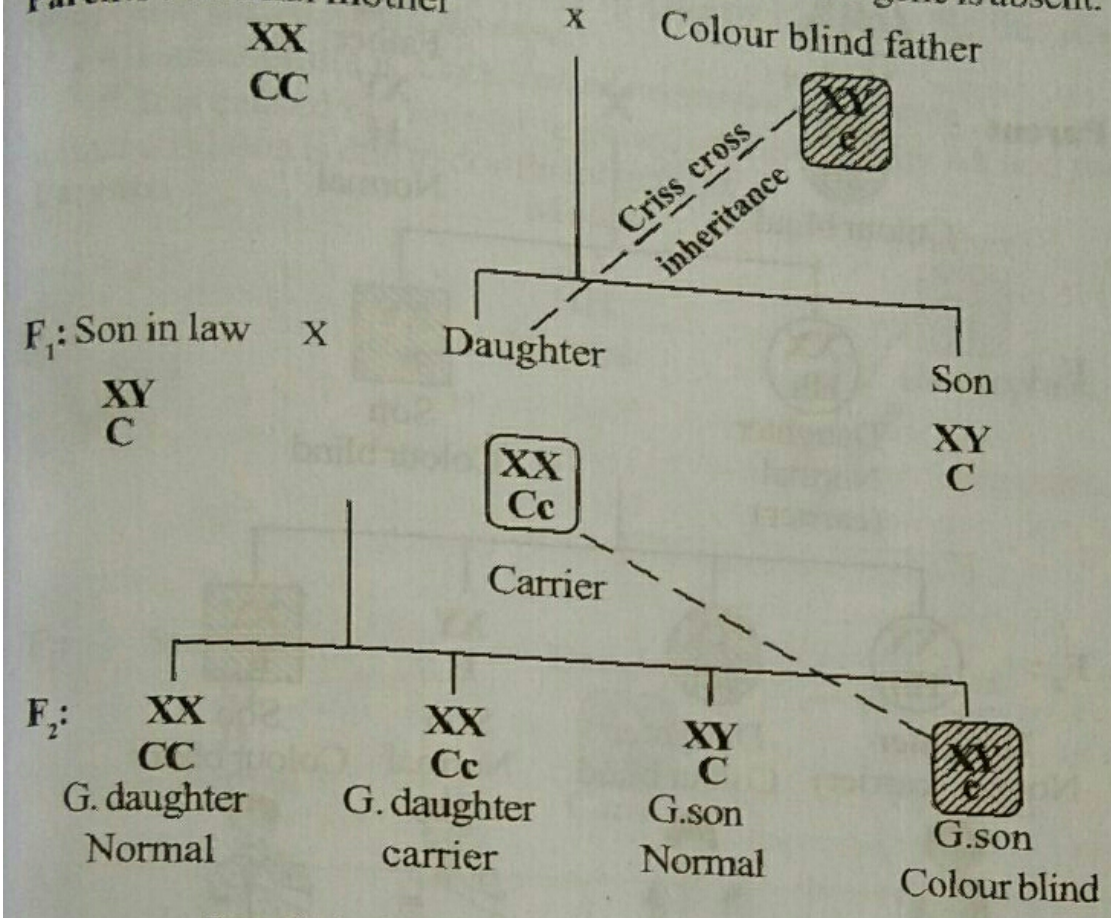


Fig.11.1: Inheritance of colour blindness.

When the daughters (carriers) are married to men with normal vision, some colour blind sons are formed. These affected sons receive their one X chromosome (in which the recessive gene is present) from their mother (carrier Cc).

If a colour blind woman is married to a normal man, all her sons are colour blind. The daughters are normal but they carry the recessive gene in one of their X chromosomes and they are carriers. When these daughters are married to a colour blind man, colour blind grandsons and grand daughters are produced in equal numbers. So it follows ***criss-cross inheritance.***

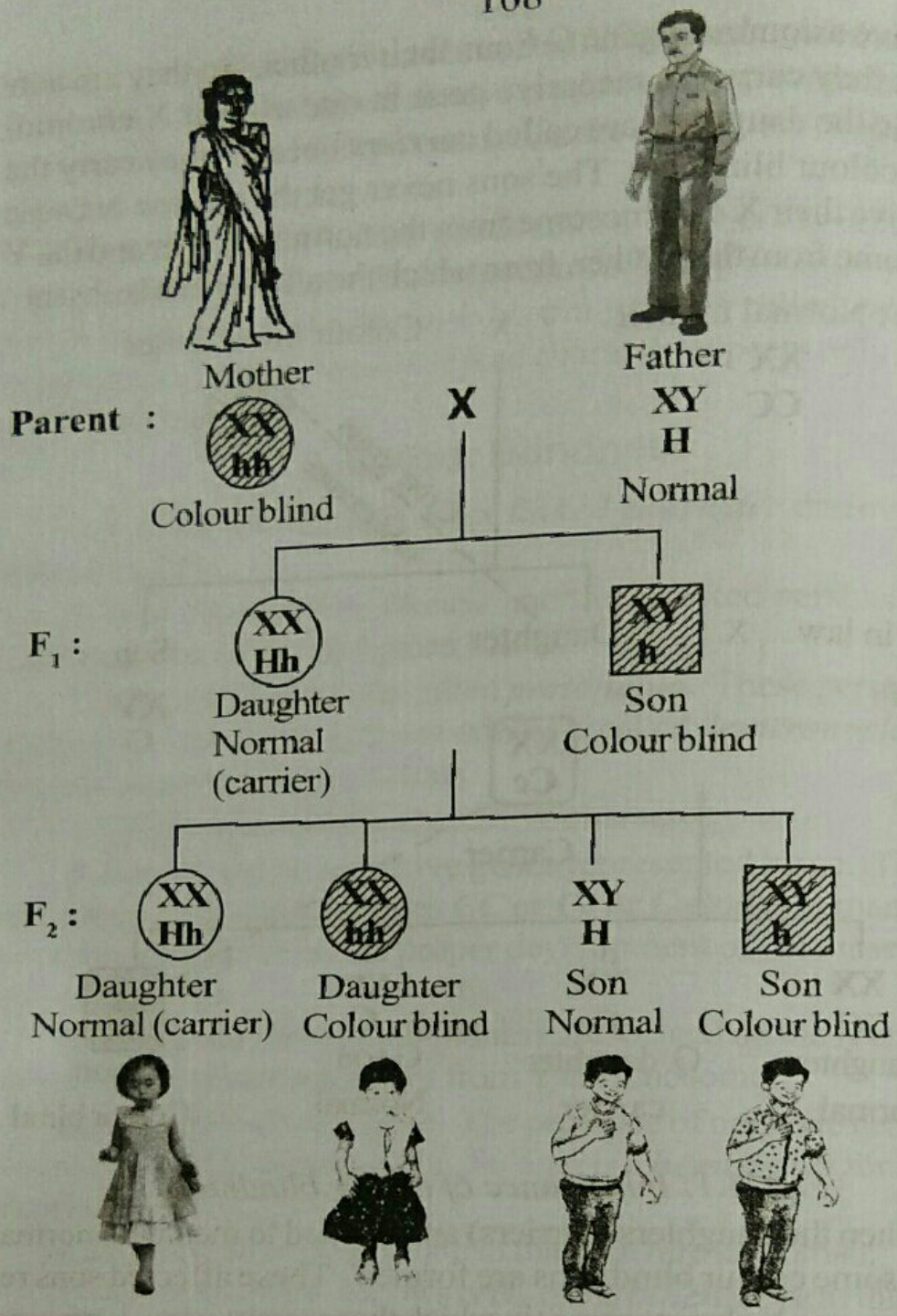


Fig.11.2: Inheritance of colour blindness.

2. Haemophilia (Bleeder's disease)

1. It is a ***hereditary blood disease*** discovered by ***John Cotto*** in 1803.

2. This disease is characterized by ***delayed blood clotting.*** This is because of the absence of a factor in the blood called ***antihaemophilic globulin*** which plays an important role in blood

clotting. In normal persons, the blood clots in 2 to 8 minutes. But in haemophilic patients, clotting is delayed for 20 minutes to 24 hours. Hence they bleed continuously from the wound. So haemophilia is also called ***bleeders disease.***

3. This disease appeared as a mutant in ***Queen Victoria*** and from her it was transmitted to her descendants. Hence this disease is common among the ***Royal family of Queen Victoria.*** So this disease is also called ***Royal disease.***

4. Haemophilia is a ***sex linked recessive character.***

5. It is caused by recessive genes represented by ***hh*** and the normal condition is due to dominant gene ***H.***

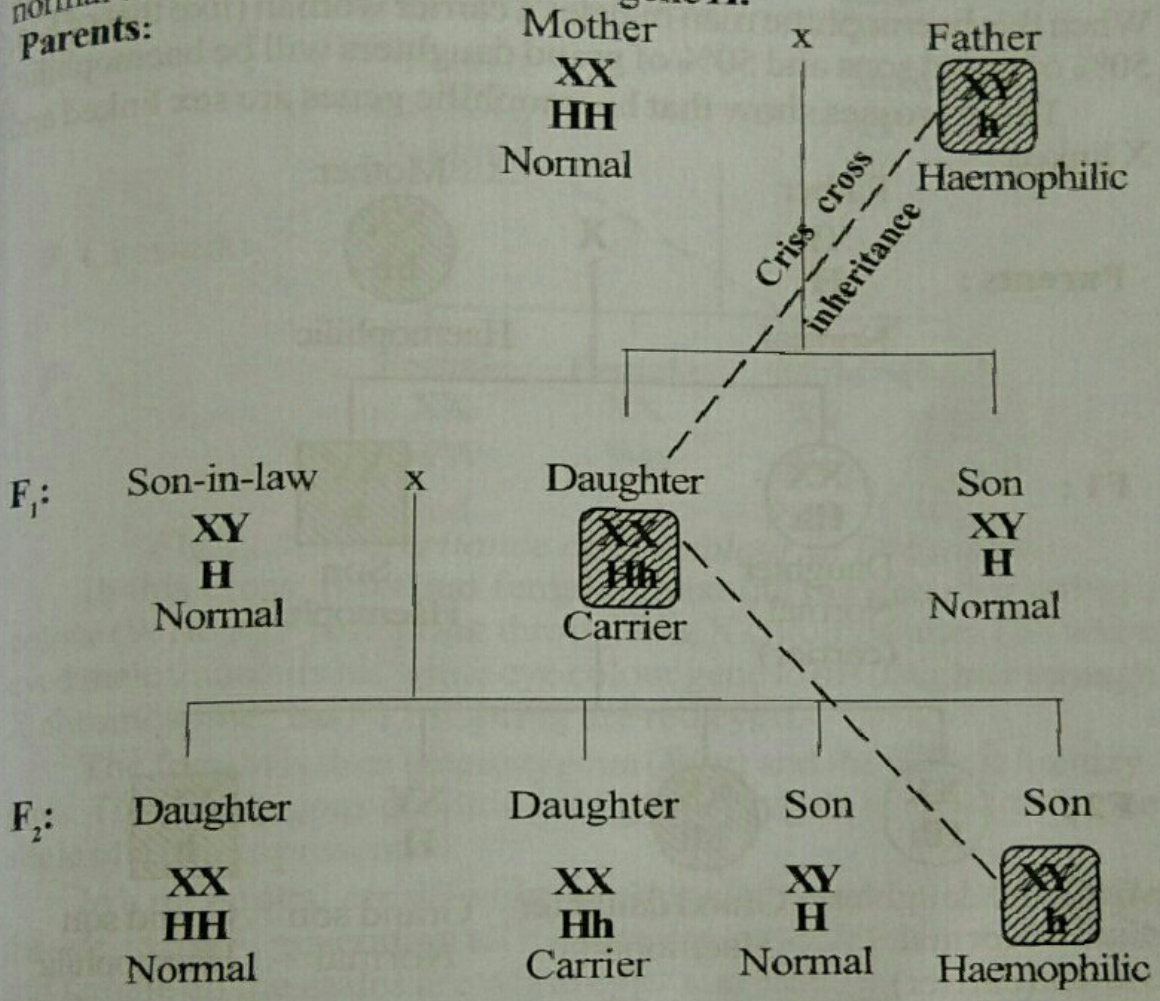


Fig.11.3: Inheritance of haemophilia.

6. The genes are located on the X chromosome. The Y chromosome has no gene. So the male has only one gene for this character. So the male is called ***hemizygous.***

7. As other sex linked characters, it is common in men but rare in women.

8. Haemophilia follows ***criss-cross inheritance.*** It is transmitted from the father to his grandson through his daughter.

9. Generally haemophilic patients will die before reaching reproductive stage, if they are exposed to severe bleeding.

When a normal woman marries a haemophilic man, their sons and daughters will be normal, but the daughters are carriers containing a recessive gene for haemophilia. When this carrier daughter marries a normal man, in the F_2 all grand daughters are normal, but 50% of their sons are haemophilic.

When a normal man marries a haemophilic woman, their sons will be ***haemophilic*** and the daughters will be normal but carriers. When this haemophilic man marries a carrier woman (like that of F1), 50% of grand sons and 50% of grand daughters will be haemophilic.

These crosses show that haemophilic genes are sex linked and X linked.

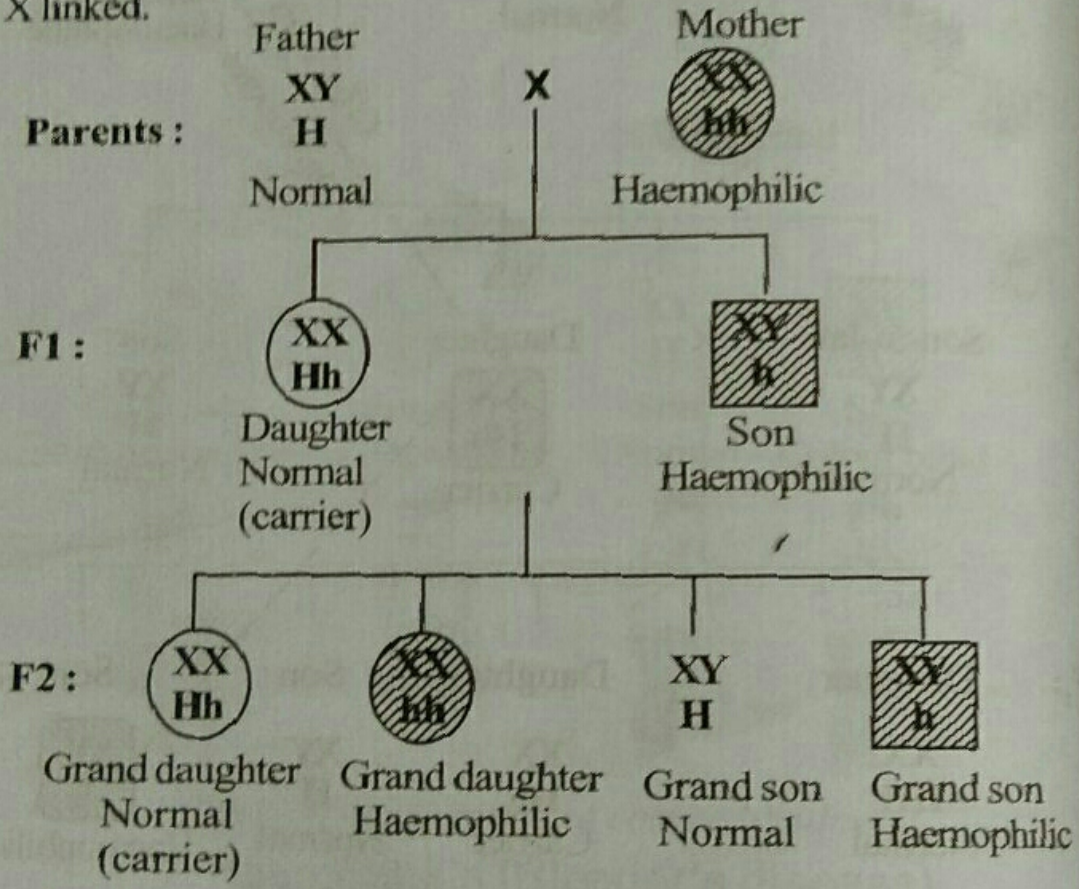


Fig.11.4: Inheritance of Haemophilia.

3. Eye Colour in Drosophila

In *Drosophila,* ***red eye*** colour (W) is dominant over ***white eye*** (w). The genes for eye colour are located in the X chromosomes. The Y chromosome does not carry any allele for eye colour.

T.H. Morgan in 1910 crossed a ***red eyed*** pure breeding female fly with a ***white eyed*** male. In the F_1 generation, all the offspring are red eyed.

When the F_1 is inbred, white eye appears in ¼ th of the F_2 generation as in Mendel's monohybrid experiment. Of the F_2 offspring, all the females are red. But among the males, half are white eyed.

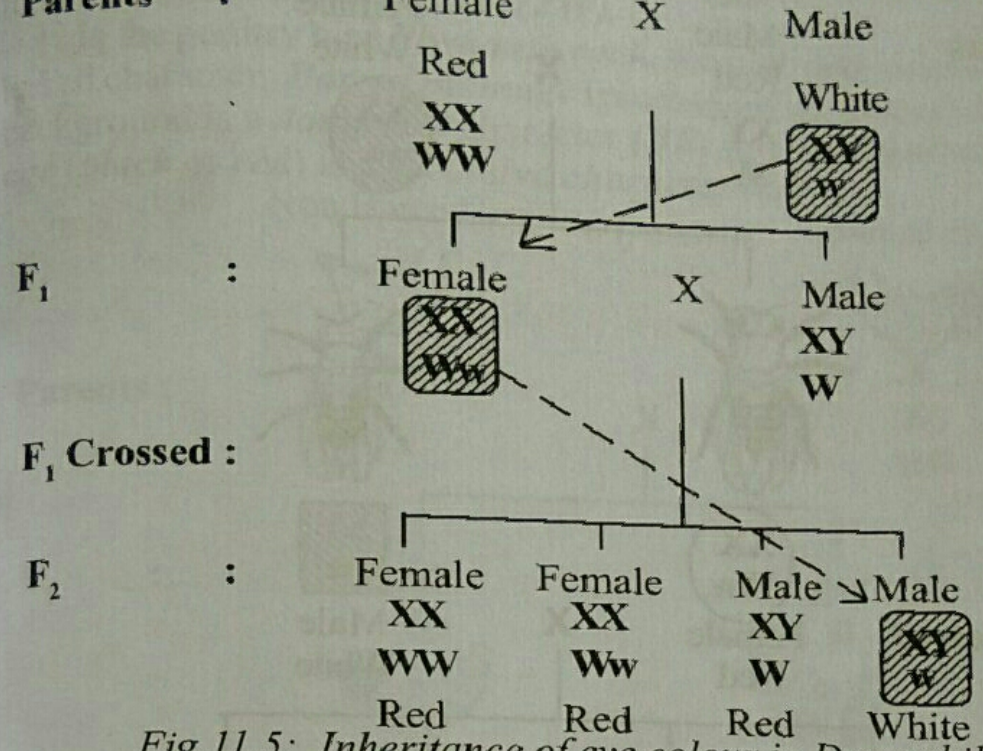


Fig.11.5: Inheritance of eye colour in Drosophila.

In this cross, red eyed female transmits the gene for red eye colour (W) to all F_1 offspring through her X chromosome. The white eyed male transmits his white eye colour gene to his daughter through X chromosome. So F1 offspring are red eyed.

The female is thus heterozygous (Ww) and the male is hemizygous. The ***hemizygous*** condition is a type of zygote in which only one allele of a pair is present.

In a reciprocal cross, when a ***red male*** is crossed with a ***white female,*** in the F_1 generation all the females are red eyed, and the male and female all the males are white eyed and the male and female are produced in equal numbers. When these F_1 offspring are interbred, F_2 offspring consist of red and white eyed individuals in equal proportion in both the sexes.

In this cross, white eyed female transmits white eye colour gene (w) to all her sons and daughters through X chromosomes. The red eyed male transmits red eye colour gene W to his daughters through

X chromosome. So the F_1 females are red eyed and males are white eyed.

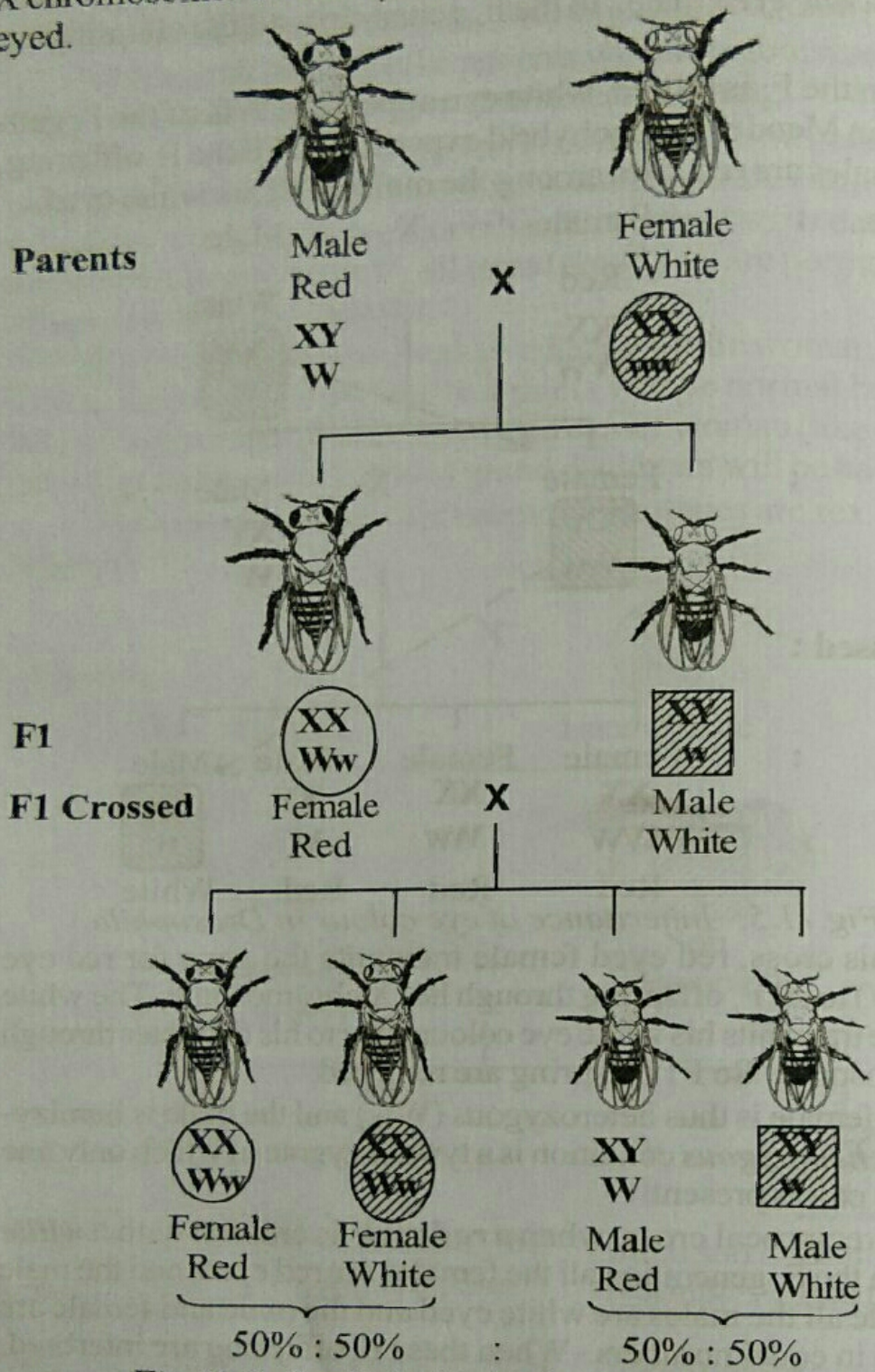


Fig.11.6: Sex linked inheritance in Drosophila.

Thus the transmission of white eye colour gene and the transmission of the X chromosome are similar. Hence ***T.H.Morgan*** concluded that the gene for eye colour in *Drosophila* is linked to X chromosome and Y chromosome carries no allele for eye colour.

ance is called ***XY linked inheritance.*** Eg. *Xeroderma pigmentosum, nephritis, retinitis pigmentosa,* etc.

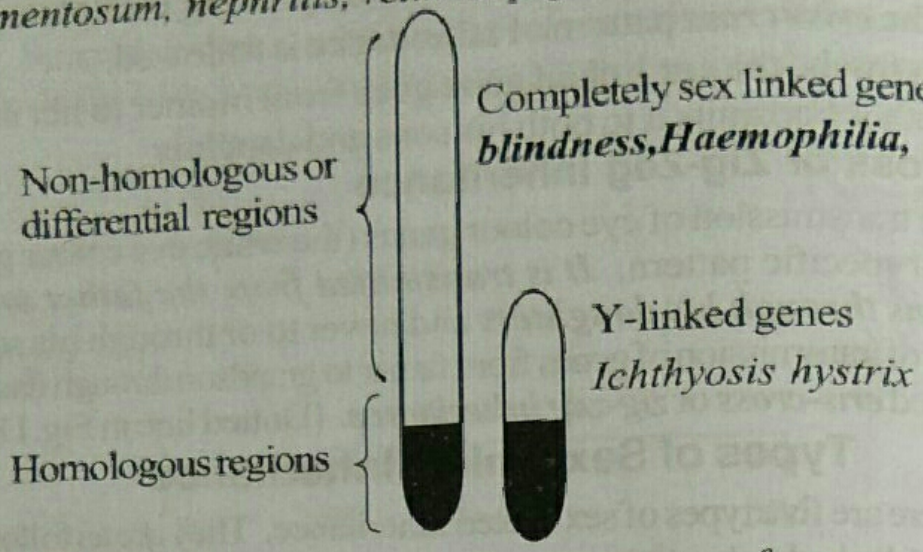


Fig.11.9: X and Y chromosomes of man.

4. Completely sex linked inheritance

The X and Y chromosomes are not similar. The X chromosome is larger and straight. But the Y chromosome is smaller and one end is curved. The lower part of X chromosome is similar to that of Y chromosome. These two parts are called ***homologous*** regions. They have the same type of genes. The remaining parts of the X and Y chromosomes are not similar. So they are called ***non-homologous regions*** or ***differential regions.*** They do not contain similar type of genes.

The genes located on non-homologous regions inherit together because crossing over does not occur in these regions. So the genes located on non-homologous regions are called ***completely sex linked genes*** and their inheritance is called ***completely sex linked inheritance.*** Eg. *Haemophilia, colour blindness*, etc.

5. Incompletely sex linked inheritance

The genes located on homologous regions of sex chromosomes do not inherit together because crossing over may occur in these regions. So these genes are called ***incompletely sex linked genes*** and their mode of inheritance is called ***incompletely sex linked inheritance.*** Eg. *Retinitis pigmentosa, nephritis,* etc.

Sex Limited Genes

Sex limited genes express characters in only one sex.

The sex limited genes may be located on any chromosome (sex linked genes are located only on the sex chromosome).

Their expression in the vertebrates is governed by the sex-hormones.

Sex limited genes are responsible for the secondary ***sexual characteristics*** as well as ***primary sexual characters.***

Examples

1. In man, the ***beard*** is produced by sex limited genes. A woman, normally, does not have a beard, yet she surely carries all the genes necessary to produce a beard. But the expression of that particular gene in ladies is prevented by the absence of a particular hormone. In rare cases, abnormalities in hormone secretion may occur in a woman which allow these genes to express themselves and the result is a bearded lady.

2. ***Breast development*** is normally limited to woman but hormone unbalance may cause breast development in a man.

3. The genes for the deep ***masculine voice*** and masculine musculature in man will express themselves only when the male hormone is present. Genes for the feminine musculature, express themselves in the absence of male hormone. They do not require the presence of the female hormone.

4. In cattles, the milk production is controlled by sex limited genes. The bulls also carry the gene for milk production. But it is not expressed in the male sex. In the cows, the genes for milk production makes its expression in the presence of female hormones. The brilliant plumage of peacock is also due to some sex limited genes.

5. An excellent illustration of sex limited inheritance is provided by the plumage pattern in birds. In domestic fowl of Leghorn, males have long curved, fringed feathers on tail and neck, but feathers of female are shorter, straighter and without fringe. Thus the males are ***cock feathered*** and females are ***hen feathered.***

Results of various crosses show that hen feather is due to a dominant gene ***H*** and cock feathering is due to it's recessive allele ***"h".***

It has been found that the expression of the genes ***H*** and ***h,*** depends upon the sex hormone. Any male that receives atleast one dominant gene will be hen feathered, but those males which are homozygous for the recessive gene ***(hh),*** will show the cock feathered condition.

Females are all hen feathered regardless of genotype. It shows that a particular type of feathering depends upon specific combination of genotype and sex hormones. The dominant gene ***H*** produces hen feathering in the presence of male or female sex hormone. The recessive gene, ***"h"*** produces cock feathering in the absence of female hormone and hen feathering in the presence of female hormone.

Table 11.1: Sex limited genes.

Genotype	Phenotypes	
	Male	Female
HH	Hen feathered	Hen feathered
Hh	Hen feathered	Hen feathered
hh	Cock feathered	Hen feathered

Sex Influenced Genes

The sex influenced genes are influenced by the sex of the bearer. They are located on the autosomes. The sex influenced genes express more frequently in one sex than in the other.

1. Baldness in Man

The ***baldness*** in man is a very good example for sex influenced character. This particular character is ***dominant*** in ***men*** and ***recessive*** in ***women.*** This is because the gene for baldness (B) in heterozygous condition (Bb) expresses itself in male but the heterozygous females are normal even though they carry the gene for baldness. It shows that only one gene is enough to produce a baldman, whereas a woman must require two such genes to be bald. In man, the single gene for baldness can operate only in the presence of male hormone.

Table 11.2: Influenced genes.

Genotype	Phenotypes	
	Male	Female
BB	Bald	Bald
Bb	Normal	Bald
bb	Normal	Normal

2. Index Finger

There is another interesting sex influenced gene in man which affects the ***length of the index finger***. The short index finger is due to a gene which is dominant in the male and recessive in the female.

3. Horns in Sheep

In sheep, the ***Dorset*** breed have horns while ***Suffolk*** breeds are hornless. The horned condition is dominant (HH) and the hornless condition is recessive (hh).

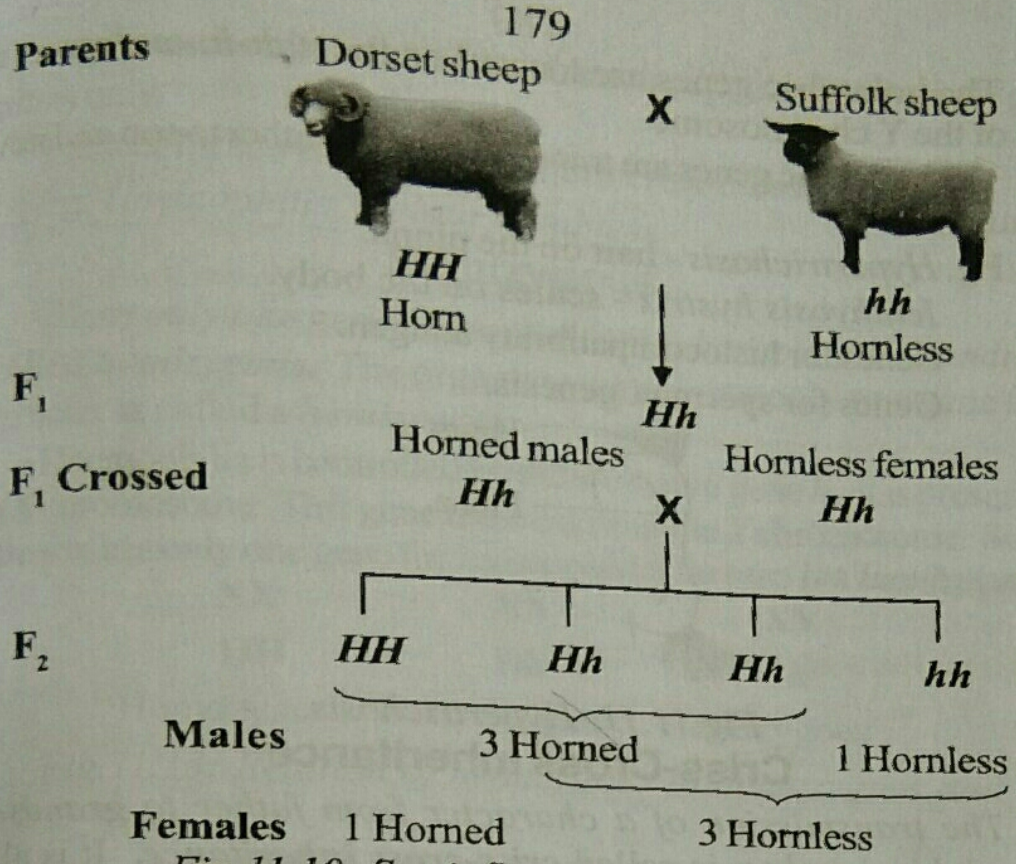


Fig.11.10: Sex influenced gene in sheep.

A pure horned Dorset breed is crossed with Suffolk hornless breed (hh). The F_1 offspring are heterozygous (Hh). The males are horned and females are hornless.

HH genotype produces horns in both sexes.

Hh genotype produces horns in male but not in female.

hh genotype produces hornless condition in both sexes.

In males, one dominant gene, in cooperation with male hormones, develops horns. But in females, one dominant gene cannot develop horns because of the absence of male hormones.

When the F_1 hybrids are crossed, In the F_2 the males having one or two dominant alleles, develop horns. The females having two dominant alleles alone develop horns. Thus horn in sheep is influenced by male sex.

Sex Linkage

The genes located on the sex chromosomes are inherited along with sex. This is called ***sex linkage.*** It is also called ***sex linked inheritance.***

Eg. *Haemophilia, colour blindness.*

Holandric Genes

The Y linked genes are called ***holandric genes*** *because they are present only in the male sex.* (***Holos*** = whole; ***Andros*** = male).