Linkage and crossing-over

Contents: Linkage- Background Information; Definition and characteristics of linkage; Types of linkage; Linkage groups; Theories of linkage; Significance of linkage; Crossing-over- Definition and characteristics of crossing-over; Types of crossing-over; When does crossing-over take place? Theories of crossing-over; Factors affecting crossing-over; Significance of crossing-over; Differences between linkage and crossing-over; Suggested reading.

Linkage

Background information

W. S. Sutton (1903): Proposed the chromosomal theory of heredity; all the units (factors/genes) on one chromosome must be linked, but he could not prove it. Bateson and Punnett (1905-06): Worked on the sweet pea *Lathyrus odoratus*; performed a dihybrid cross: Purple-Long × red-round and obtained 7: 1: 1: 7 ratios instead of classical 9: 3: 3: 1; they called parental types '**coupling**' and recombinant types '**repulsion**'. T. H. Morgan (1910): Worked on the fruit fly, *D. melanogaster* and proposed the terms '**linkage**' and '**crossing-over**' replacing 'coupling' and 'repulsion', respectively. J.B.S. Haldane (1942): Proposed the terms '*cis*-arrangement' for 3′- 5′ DNA molecule and '*trans*-arrangement' for 5′- 3′ DNA molecule.

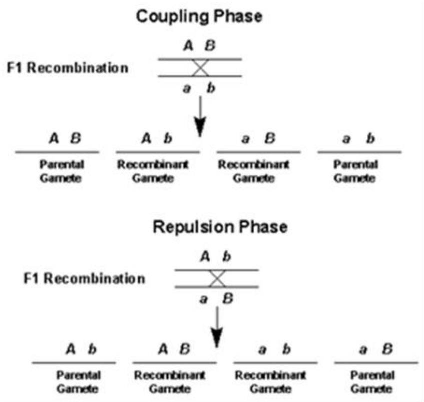

Fig. 5.1 Bateson and Punnett's (1905-06) 'coupling' and 'repulsion' hypothesis

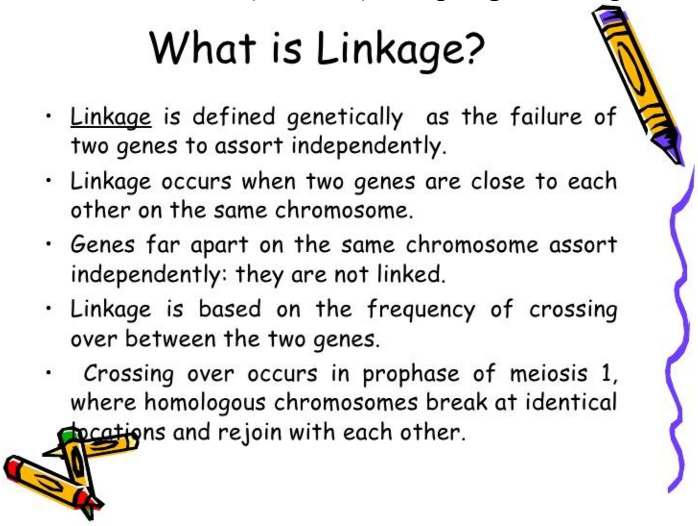

Fig. 5.2 Some relevant information on linkage

Definition of linkage

The tendency of genes located on the same chromosome to transmit together from parents to offspring is known as linkage.

Note: Mendel (1857-65) did not come across the phenomenon of linkage because the unit factors (genes) he considered were located on separate chromosomes in the garden peas.

Characteristics of linkage

1. Linkage is an exception to Mendel's law of independent assortment;
2. Linked genes are located on the same pair of homologous chromosomes;
3. Genes lying further apart show less linkage;
4. Linked genes tend to transmit together in groups from one generation to the next;
5. Separation of linked genes may take place by the phenomenon of crossing-over.

Types of linkage

Basically there are two types of linkage as follows:

(1) Complete linkage: Rare in nature, where only parental or non cross-over gametes are produced; *e.g*. male *D. melanogaster*, female *Bombyx mori* etc.

(2) Incomplete linkage: Frequently seen in nature, where both parental and recombinant (or cross-over) gametes are produced; *e.g*. female *D. melanogaster*, male *B. mori*, maize, pea, tomato etc.

An example of complete linkage: Morgan (1910) reported complete linkage in male *D. melanogaster*:

P: GGLL × ggll

(Gray body, Long wing) (black body, vestigial wing)

F_1: GgLl (all Gray-Long)

Test cross: GgLl ♂♂ × ggll ♀♀

F_2: GgLl : ggll

(Gray-Long) (black-vestigial)

Phenotypic ratio: 1 : 1

Conclusion: Progenies are all parental types only, no cross-over types found, because no crossing-over took place in males between G (g) and L (l) genes due to complete linkage.

An example of incomplete linkage: Morgan (1910) reported incomplete linkage in female *D. melanogaster*:

P: GGLL × ggll

(Gray body, Long wing) (black body, vestigial wing)

F_1: GgLl (all Gray-Long)

Test cross: GgLl ♀♀ × ggll ♂♂

F_2: GgLl Ggll ggLl ggll

(Gray-Long) (Gray-vestigial (black-Long) (black-vestigial)

Ph. ratio: 6.56 (41%):1.44 (9%): 1.44 (9%): 6.56 (41%)

Conclusion: Progenies are 82% parental types and 18% cross-over or recombinant types, because crossing-over took place in females between G (g) and L (l) genes.

Linkage groups

Since all linked genes transmit in groups, the number of linkage groups for a species is equal to the haploid (n) number of chromosomes. A few examples of linkage groups in different organisms are presented below:

Organisms	Diploid (2n) No.	Linkage groups
Fruit fly	8	4
Maize	20	10
Lab mouse	40	20
Rabbit	44	22
Man	46	23

Ref: G.W. Burns (1980)

Theories of linkage

Two major theories of linkage are mentioned briefly here:

1. **Chromosomal theory** (Castle and Morgan, 1918)

Linkage occurs due to the location of linked genes on the homologous chromosome pairs.

2**. Differential multiplication theory** (Bateson, 1930)

Linkage occurs due to the increase in the number of coupled and linked genes during gamete formation.

Differences between linkage and independent assortment

Complete linkage	Independent assortment
P: AABB×aabb	P: AABB×aabb
Genes on same chromosome	Genes on separate chromosomes
F_1: AaBb	F1: AaBb
Test cross:	Test cross:
AaBb×aabb	AaBb×aabb
F_2: AaBb: aabb	F_2: AaBb, Aabb, aaBb, aabb
Phenotypic ratio: 1: 1	Phenotypic ratio: 1: 1: 1: 1

Significance of linkage

1. Linkage is very useful for economic and desirable traits during selection and hybridization in animals and plants.
2. Since parental characteristics are transmitted to offspring due to linkage, it is advantageous for the improvement of domesticated animals and plants.
3. Linkage is conservative in nature. So, it preserves characters but prevents variation in natural populations.

Definition of crossing-over

Crossing-over is a process by which exchange of genetic materials (DNA/RNA) takes place between the non-sister chromatids of homologous pair of chromosomes.

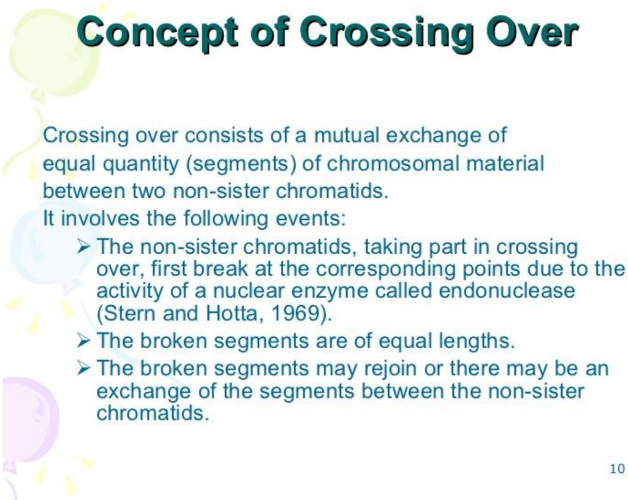

Fig. 5.3 The concept of crossing-over is clarified by mentioning some important events

Characteristics of crossing-over

1. Crossing-over takes place only in between the non-sister chromatids of a bivalent (synapsed homologous chromosomes);
2. The physical proof of the crossing-over is the presence of chiasma (pl. chiasmata);
3. In most organisms, it takes place by the end of pachytene stage of prophase-1 of meiosis;
4. The probability of crossing-over increases between the genes that lie far apart from each other;
5. The frequency of single crossing-over is greater than that of the double, triple or multiple crossing-overs.

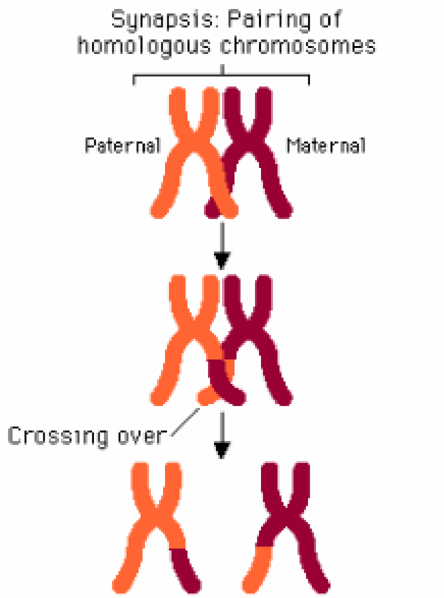

Fig. 5.4 The process of a single crossing-over between a pair of homologous chromosomes

Types of crossing-over
Crossing-over events could be single, double, triple or multiple as follows:

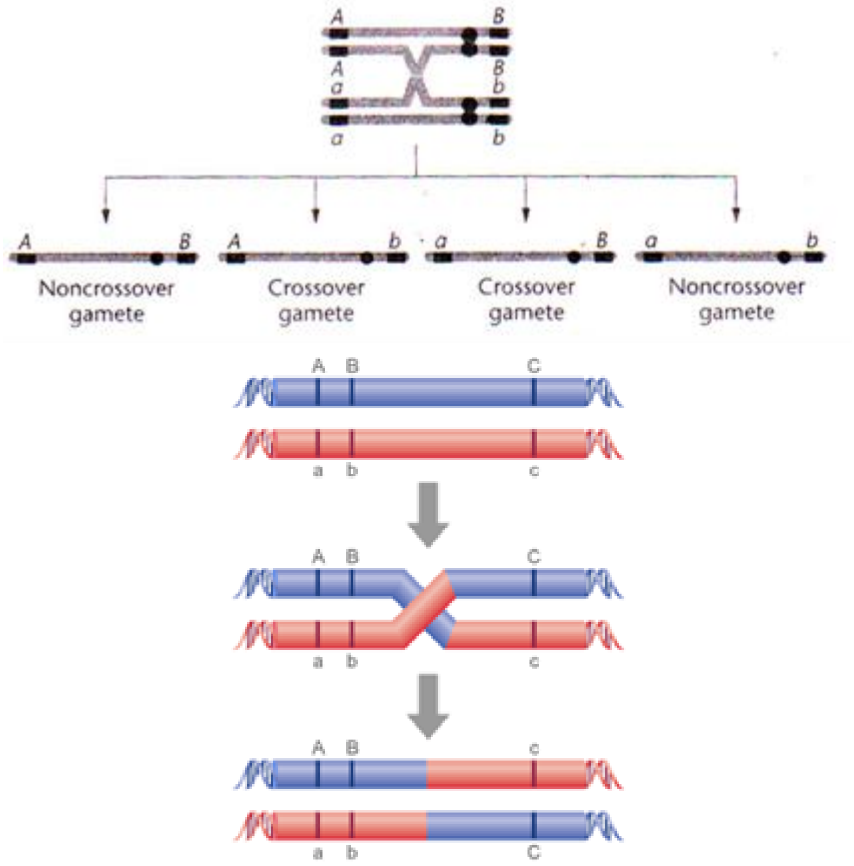

Fig. 5.5 Single crossing-over between B and C genes

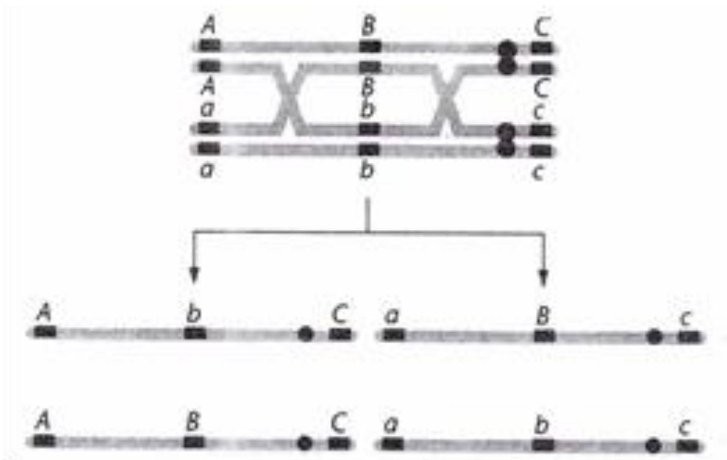

Fig. 5.6 Double crossing-over between A & B and B & C genes

Fig. 5.7 Photograph showing an event of multiple crossing-overs

Theories of crossing-over

A number of theories have been proposed to explain the mechanisms of crossing-over. Some of the main theories are as follows:

1. Janssen's classical theory (1909)
2. Belling's copy choice theory (1932)
3. Darlington's breakage and reunion theory (1937)
4. Serebrovsky's contact-first theory (?)
5. Muller's breakage-first theory (?)
6. Meselson and Weigle theory (1961)
7. Whitehouse (1963)
8. Uhl (1965)
9. Grell (1967) etc.

However, Belling's copy choice theory and Darlington's breakage and reunion theory are described below (Fig. 5.8).

Belling's copy choice theory (1932)

The theory assumes that the crossing-over is the direct result of the new chromatids copying partly from one strand (paternal) and partly from the other (maternal) homologous strand.

Darlington's breakage and reunion theory (1937)

It holds that the homologous chromosomes are intertwined during the four stranded stage of first meiosis; then break and reunion occurs between the non- sister chromatids (*i.e.*, paternal to maternal or *vice-versa*), as a consequence recombinants or cross-over types result.

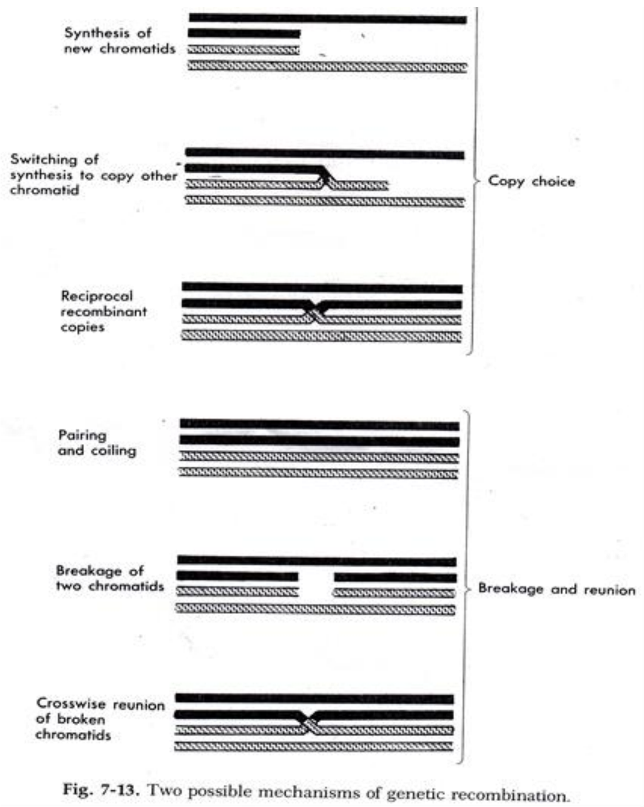

Fig. 5.8 The copy choice (top) and breakage and reunion (bottom) theories of crossing-over

When does crossing-over take place?

Experiments with *Neurospora*, *Drosophila*, *Zea mays* and others show the following inferences:

(a) Gonadal or germinal crossing-overs always take place in gonads at prophase of meiotic cell division;

(b) Synapsis or pairing of homologous chromosomes (= formation of bivalents) take place at **zygotene** stage;

(c) In **pachytene** stage, bivalents are split longitudinally into 4 chromatids (2 sister and 2 non-sister chromatids), known as tetrads;

(d) **By the end of pachytene**, 2 non-sister chromatids exchange their genetic materials, thus the phenomenon of crossing-over takes place here;

(e) The effects of crossing-over become visible as chiasmata (sing. chiasma) in **diplotene** stage.

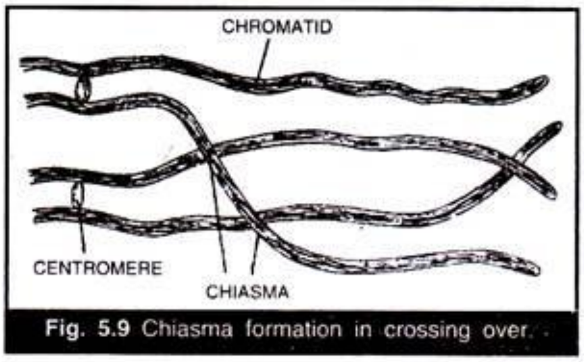

Fig. 5.9 Presence of chismata between non-sister chromatids

Factors affecting crossing-over

The rate of crossing-over is influenced by a number of extrinsic or intrinsic factors mentioned below:

1. **Age:** Older females show increased rate of crossing-over in *D. melanogaster*.
2. **Gender or sex:** Females of *Drosophila*, mice, guinea pigs > co than males.
3. **Inversion**: Inversions suppress the rate of crossing-over.
4. **Mutation:** It reduces crossing-over in all the chromosomes of *Drosophila*.
5. **Nutrition:** Higher nutritious diets decrease crossing-over in young *Drosophila*.
6. **Position of centromere:** Less crossing-overs near the centromere.
7. **Temperature:** Frequency of crossing-over increases below and above 17-29 °C.
8. **X-rays:** Increase the rate of crossing-overs.

Somatic crossing-overs

Somatic or mitotic crossing-over is an exceptional type of crossing-over that was first observed by Curt Stern (1936). An example of such an unusual event includes *Drosophila* heterozygous for yellow body and singed bristles (y^+/y and sn^+/sn).

Significance of crossing-over

1. Exchange of genetic materials takes place through crossing-over.
2. So, it is an important source of recombination and variation in natural populations.
3. Crossing-over has evolutionary significance for a species and it plays a significant role in the adaptation and evolution of organisms.

Differences between linkage and crossing-over

Differences between the phenomena of linkage and crossing-over are shown in the following table.

Linkage	Crossing-over
1. It keeps the genes together.	1. It leads to separation of linked genes.
2. It involves individual chromosomes.	2. It involves non-sister chromatids of homologous chromosomes.
3. Linkage groups can never be more than haploid (n) number of chromosomes.	3. Frequency of crossing-over can never be more than 50%.
4. It reduces variability by forming more parental types.	4. It increases variability by forming more recombinant types.
5. Linkage provides higher frequency of parental types than recombinant types in test cross progenies.	5. Crossing-over provides equal frequency of parental and recombinant types in test cross progenies.

Suggested reading:

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