Unit 9 · Linkage and Crossing Over

STUDY NOTES

WHAT NEB'S GRADE 12 EXAM ASKS

- **CDC's grid (2078):** Genetics (Units 7–10 together): 12 of 75 marks; 1 short question (4 marks: understanding 1, application 2, higher ability 1) and 1 long question (8 marks: understanding 2, application 3, higher ability 3)
- **The paper:** Botany 37 + Zoology 38; each part: MCQs × 1 (5 Botany, 6 Zoology) · 4 short × 4 · 2 long × 8; one OR in each short and long group; 3 hours; 1 mark per expected point
- **CDC's model paper:** long (OR): X-linked eye color in *Drosophila*: a white-eyed female crossed with a red-eyed male
- **MCQ (1 mark)**
  - 23 linkage groups in man; linked genes break independent assortment
  - *Drosophila*: 3 pairs of autosomes; eye-color gene on X
  - carrier mother × normal father: son 50% color-blind
  - fathers pass X-linked traits only to daughters
  - exchange in pachytene; chiasma; variation for survival; label a crossover
- **Short and long (in parts)**
  - linkage and its types; complete linkage; incomplete linkage in maize
  - why *Drosophila*; eye color in *Drosophila*; color blindness in man
  - crossing over: significance, role in variation
  - heterozygous red female × white male; color-blind man × normal woman
  - normal and vestigial wings: genotypes and a cross

Key terms

Linked genes: genes on the same chromosome.

Linkage: tendency of linked genes to be inherited together, in the parent's combination.

Linkage group: all genes of one chromosome; number = **haploid number** (n).

Parental gametes: the parent's combinations; **recombinant**: new combinations from crossing over.

Complete linkage: never separated: parental gametes only.

Incomplete linkage: some crossing over: parental (more) and recombinant (fewer).

Test cross: a cross with the homozygous recessive.

Map unit (centimorgan): distance giving 1% recombinant gametes.

Autosomes: non-sex chromosomes; **sex chromosomes**: X, Y.

Sex-linked inheritance: characters passed by genes on a sex chromosome, differently to sons and daughters.

Hemizygous: one copy only (a male's X genes).

Carrier: heterozygous female, shows nothing.

Criss-cross inheritance: father → daughter (carrier) → grandson.

Crossing over: exchange of matching pieces between **non-sister chromatids** of homologs in prophase I.

Chiasma: X-shaped join where crossing over is seen.

$RF = \frac{\text{recombinants}}{\text{all offspring}} \times 100\%$	RF recombination frequency **Use:** test cross of a double heterozygote
1% recombinants = 1 map unit	centimorgan (cM) **Use:** distance between linked genes

Linkage

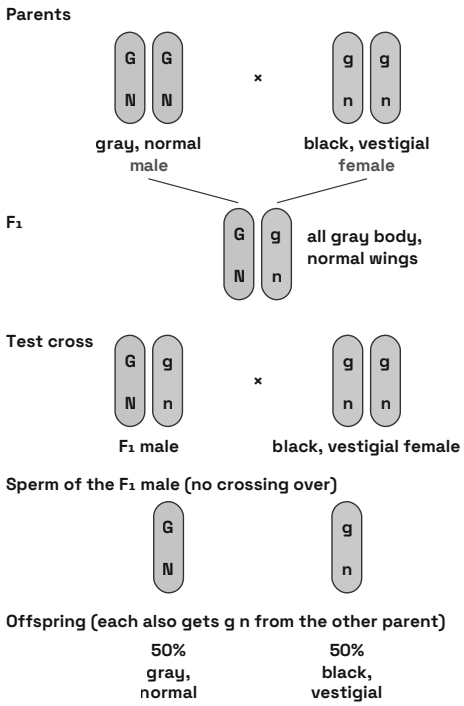
- ~20,000 genes, 23 kinds of chromosome → many genes per chromosome

- **linked genes don't follow independent assortment** (it holds for different chromosomes)

Organism	2n	Linkage groups
Drosophila	8	4
pea	14	7
maize	20	10
human	46	23 (male strictly 24)

Complete linkage: rare; genes very close, or no crossovers in one sex (male fruit fly, female silkworm)

- *Drosophila* chromosome 2: **G** gray > g black body; **N** normal > n vestigial wings
- GGNN ♂ × ggnn ♀ → F_1 GgNn (GN / gn), gray normal
- **F_1 male** × ggnn female → **2 kinds, 1 : 1**: gray normal (GgNn), black vestigial (ggnn); not 1 : 1 : 1 : 1
- F_1 **female** tested instead: ~41.5% + 41.5% parental, ~8.5% + 8.5% recombinant (~17%)



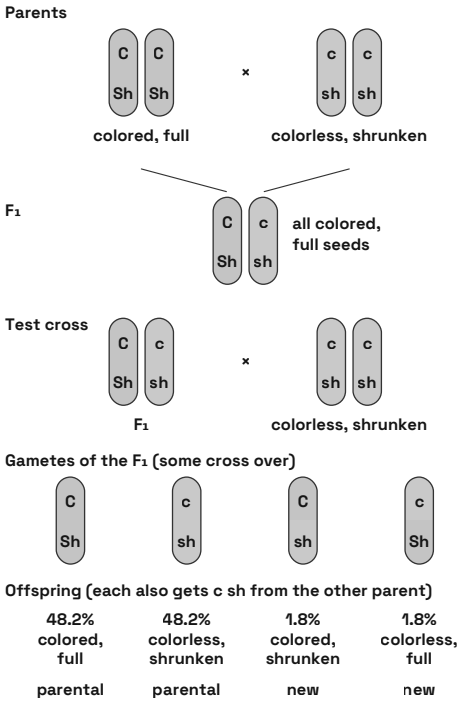
Complete linkage in a male fruit fly.

Incomplete linkage: common; genes some distance apart

- maize chromosome 9 (**Hutchinson**, 1922): **C** colored > c colorless; **Sh** full > sh shrunken
- CC ShSh × cc shsh → F_1 Cc Shsh (C Sh / c sh) → test cross with cc shsh

Seeds	Kind	Number	Share
colored full	parental	4,032	48.2%
colorless shrunken	parental	4,035	48.2%
colored shrunken	recombinant	149	1.8%
colorless full	recombinant	152	1.8%

- 96.4% parental, **3.6%** recombinant → ~3.6 map units
- closer genes → fewer recombinants → **gene maps**; double crossovers hide; never above 50%
- 420 AaBb, 410 aabb, 88 Aabb, 82 aaBb → recombinants 170/1000 = **17%** → 17 map units



Incomplete linkage in maize.

	Complete	Incomplete
crossing over between genes	none	in some cells
gametes	parental only	parental (more) + recombinant
test cross	2 kinds, 1 : 1	4 kinds, parental more
new combinations	none	some
how common	rare	common
example	body, wings in F_1 male *Drosophila*	seed color, shape in maize

Sex-linked inheritance

- human: **22 pairs autosomes + XX or XY** (44 + XX, 44 + XY); *Drosophila*: **3 pairs + XX/XY**
- X large, ~800 protein genes; Y small, a few dozen
- examples: hemophilia, red–green color blindness, *Drosophila* eye color

Features (X-linked)

1. genes on sex chromosomes, nearly all on **X**
2. most disorders **recessive**
3. **more common in males** (hemizygous); females need two copies
4. **father can't pass to son** (gives Y)
5. mother passes to sons and daughters
6. **criss-cross**: grandfather → carrier daughter → grandson

Color blindness

- red, green cone pigments: genes side by side on **X**; normal dominant, color blindness **recessive**
- ~1 man in 12 (N. European), 1 woman in 200

	Normal	Carrier	Color-blind
woman	X^CX^C	X^CX^c	X^cX^c
man	X^CY	none	X^cY

Marriage	Daughters	Sons
a. $X^cY \times X^CX^C$	all carriers	all normal
b. $X^CY \times X^CX^c$	½ normal, ½ carrier	½ normal, ½ color-blind
c. $X^CY \times X^cX^c$	all carriers	all color-blind
d. $X^cY \times X^CX^c$	½ carrier, ½ color-blind	½ normal, ½ color-blind

- b: son color-blind **50%**; next child a color-blind son **25%**
- color-blind man × normal woman → all children normal (a)
- only women are carriers; color-blind woman: father color-blind, **all sons** color-blind
- color-blind daughter only if the father is color-blind (d)

Eye color in Drosophila

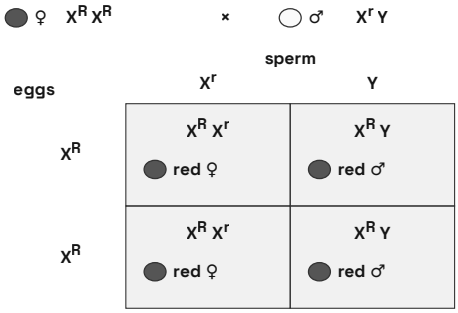
- **T. H. Morgan**, Columbia, Fly Room; Nobel 1933 (chromosomes in heredity)

Why *Drosophila*

- kept in bottles on cheap food
- breeds fast, hundreds of offspring
- life cycle ~10–15 days
- breeds all year
- **4 pairs** of chromosomes
- sexes easy: male smaller, dark rounded abdomen tip, **sex comb**; female larger, pointed striped abdomen
- 1910: one **white-eyed male**; X^R red, X^r white

Cross I: red ♀ X^RX^R × white ♂ X^rY

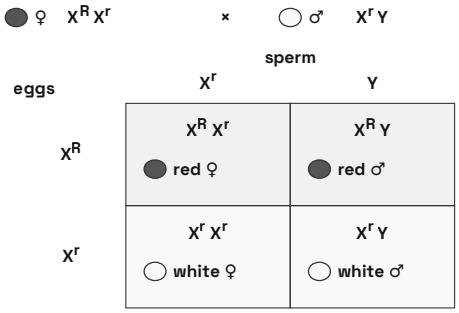
- F_1 all **red** (X^RX^r, X^RY): red dominant
- F_2: all females red; males ½ red, ½ white; **3 : 1**, every white fly male (2,459 : 1,011 : 782)



Cross I.

Cross II: F_1 red ♀ X^RX^r × white ♂ X^rY

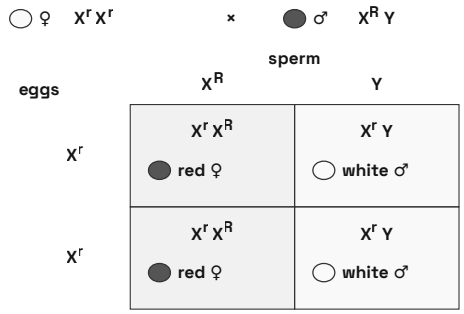
- red ♀, white ♀, red ♂, white ♂: **1 : 1 : 1 : 1**; white not limited to males



Cross II.

Cross III (reciprocal): white ♀ X^rX^r × red ♂ X^RY

- gametes: X^r; X^R, Y
- **all females red** (X^RX^r), **all males white** (X^rY)
- differs from Cross I → gene on X (autosomal genes give the same either way)



Cross III, the reciprocal cross.

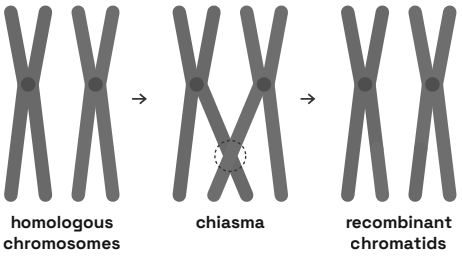
Conclusions

- white eye **sex-linked**, more in males
- red **dominant**
- gene on **X**, white recessive; Y has none
- white-eyed male → F_1 daughters → ½ grandsons (criss-cross)
- male passes it only to **daughters**

X-linked trait	Dominant/recessive	More often
hemophilia A	recessive	males
red–green color blindness	recessive	males
Duchenne muscular dystrophy	recessive	males
G6PD deficiency	recessive	males
hypophosphatemic rickets	dominant	females

Crossing over

- term by Morgan (with Cattell, 1912); in **prophase I**; makes **recombinant chromatids**
- **zygotene**: synapsis (synaptonemal complex)
- **pachytene**: **actual exchange**
- **diplotene**: homologs part, joined at **chiasmata**
- **diakinesis**: terminalization; separate at anaphase I
- only **2 of 4** chromatids per crossover → recombinants ≤ 50%



Crossing over.

- **single** (1 chiasma), **double** (2), **multiple** (> 2); ~26 per cell in men, > 40 in women
- crossovers make recombinants only **between** the genes (paper strips)

Significance

1. **genetic variation**: new combinations
2. offspring differ from parents and each other
3. variety for **natural selection**, evolution
4. helps populations **adapt**
5. population variety against disease ("immunity" only in this sense)
6. breeders combine **useful characters**
7. **gene maps**: P–Q 8%, Q–R 12%, P–R 20% → P — Q — R

COMMON MISTAKES

✗ Linked genes assort independently
✓ they break **independent assortment**.

✗ Linkage groups = diploid number
✓ **haploid** (23 in man).

✗ Complete linkage in any F_1 fly
✓ only the **F_1 male** (no crossovers in male flies).

✗ Recombinants are the large classes
✓ the **small** classes are recombinant.

✗ A father passes color blindness to his son
✓ only to **daughters** (carriers).

✗ Men can be carriers
✓ only **women**; a man shows it or lacks it.

✗ Crossing over between sister chromatids
✓ **non-sister** chromatids.

✗ Exchange happens in diplotene
✓ in **pachytene**; chiasmata seen in diplotene.