Linkage

Problem with chromosome theory:

There are more genes than chromosomes

Sex linkage

Fly room at Columbia ~1920

white eyed fly (*w*) wild type (R)

The white-eyed male, bred to his red-eyed sisters, produced 1,237 red-eyed offspring, (F_1), and 3 white-eyed males. The occurrence of these three white-eyed males (F_1) (due evidently to further sporting) will, in the present communication, be ignored.

The F_1 hybrids, inbred, produced:

2,459 red-eyed females,
1,011 red-eyed males,
782 white-eyed males.

No white-eyed females appeared. The new character showed itself therefore to be sex limited in the sense that it was transmitted only to the grandsons. But that the character is not incompatible with femaleness is shown by the following experiment.

The white-eyed male (mutant) was later crossed with some of his daughters (F_1), and produced:

129 red-eyed females,
132 red-eyed males,
88 white-eyed females,
86 white-eyed males.

Morgan, 1910

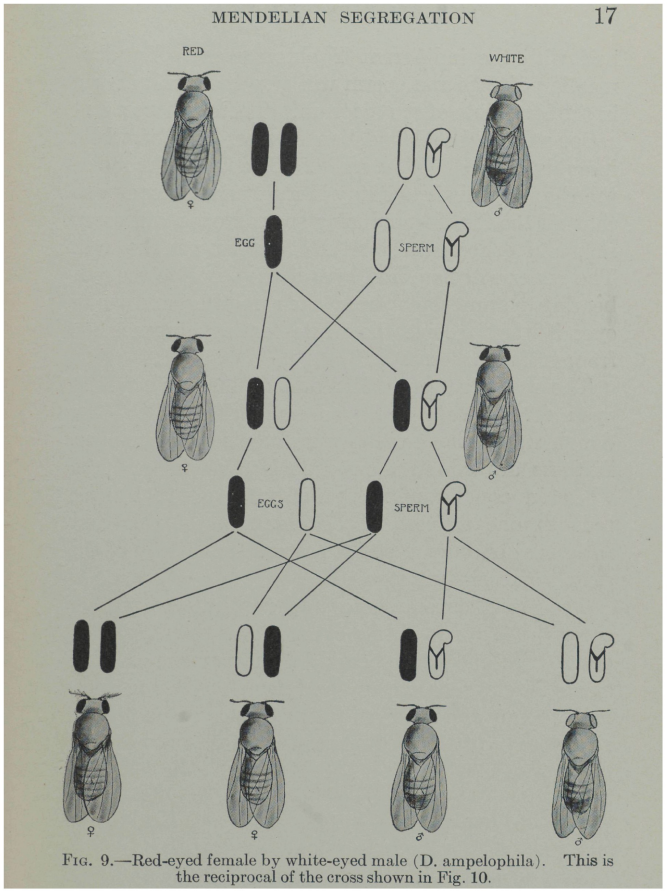
Sex linkage

P ♀ × ♂

♀ \ ♂	WX	Y
RX	RX/WX ♀	RX/Y ♂

F1 ♀ × ♂

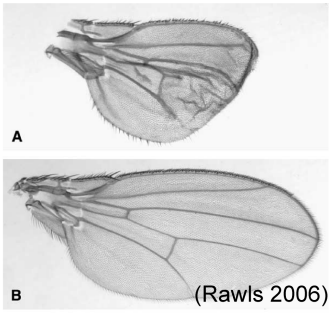
♀ \ ♂	RX	Y
RX	RX/RX ♀	RX/Y ♂
WX	RX/WX ♀	WX/Y ♂



Morgan, Sturtevant, Muller, Bridges, 1915

Crossing over

rudimentary

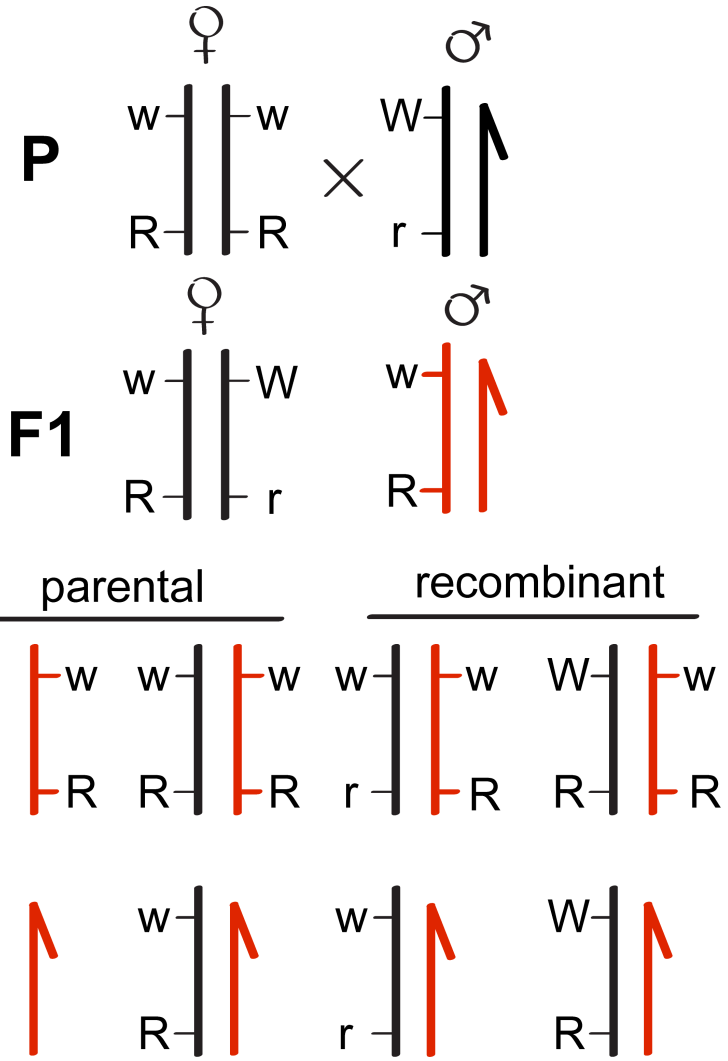


Normal Wing

P ♀ white Normal Wing ×
♂ Red rudimentary

F1 ♀ Red Normal Wing ×
♂ white Normal Wing

F2	♀ white Normal Wing	520
	♀ Red Normal Wing	480
	♂ Red Normal Wing	160
	♂ Red rudimentary	368
	♂ white Normal Wing	402
	♂ white rudimentary	170



Three-factor cross/ crossover interference

P ♀ $\frac{y\ w\ r}{y\ w\ r}$ × ♂ $\frac{+\ +\ +}{}$

F1 ♀ $\frac{YWR}{y\ w\ r}$ × ♂ $\frac{y\ w\ r}{}$

F2 ♂

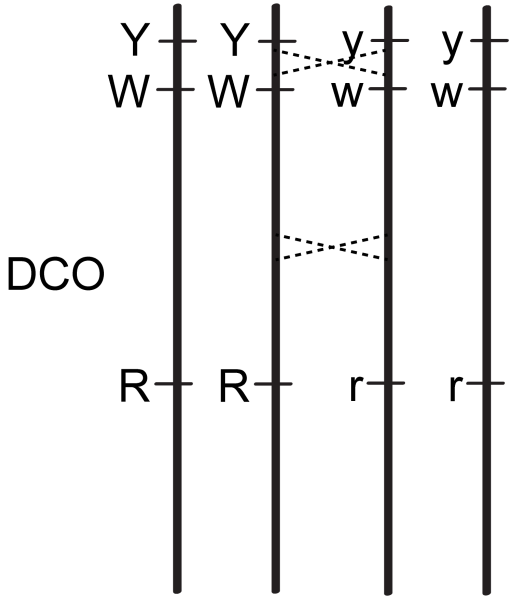
y w r / YWR	6972	NCO
yWR / Ywr	60	SCO
YWr / ywR	3454	SCO
yWr / YwR	9	DCO

TABLE 4

NO CROSSING OVER	SINGLE CROSSING OVER		DOUBLE CROSSING OVER
B CO R	B CO R	B CO R	B CO R
6972	3454	60	9

Sturtevant, 1913

Female meiosis:



DCO expected: 0.188%

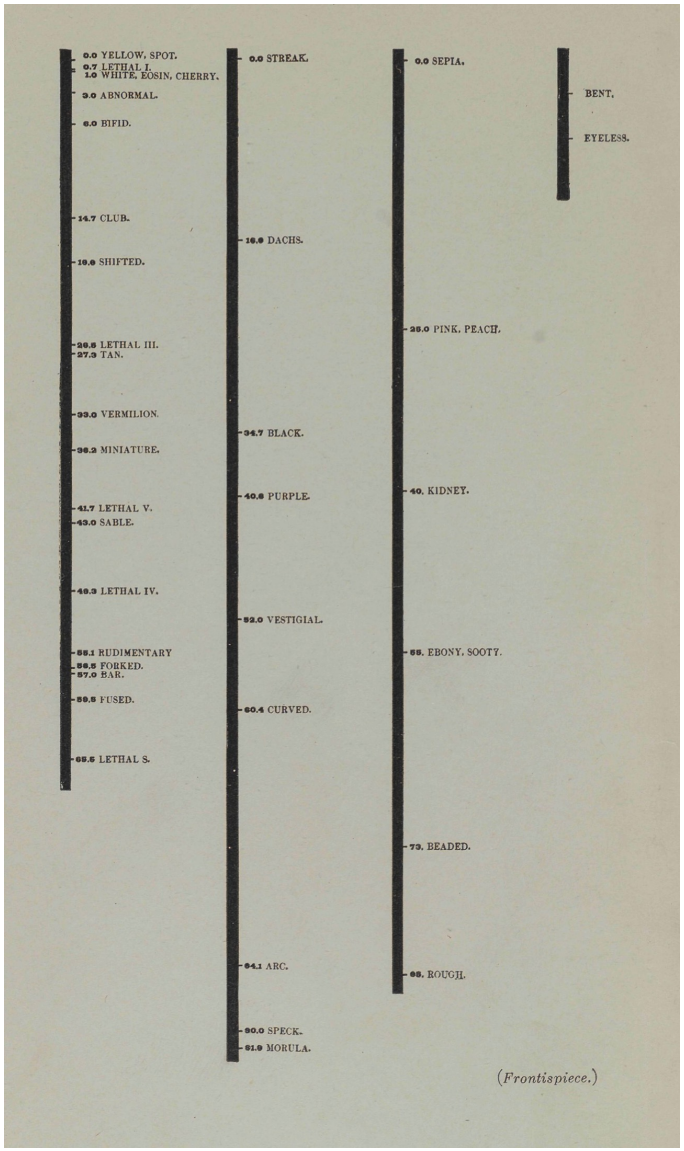
DCO observed: 0.086%

COI = .046

Genetic Mapping

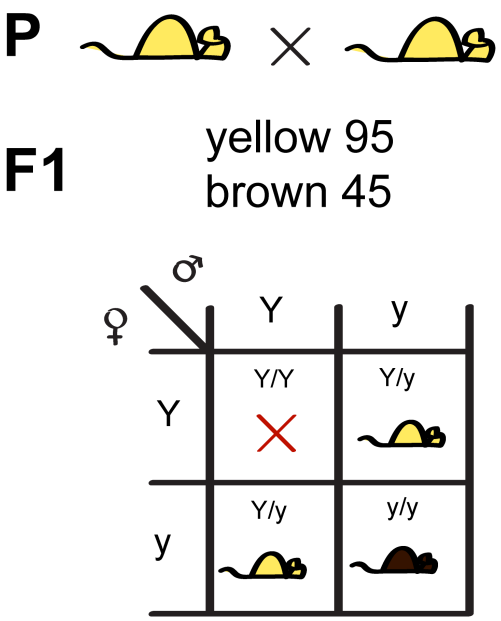
Fig. 1.

Sturtevant, 1913

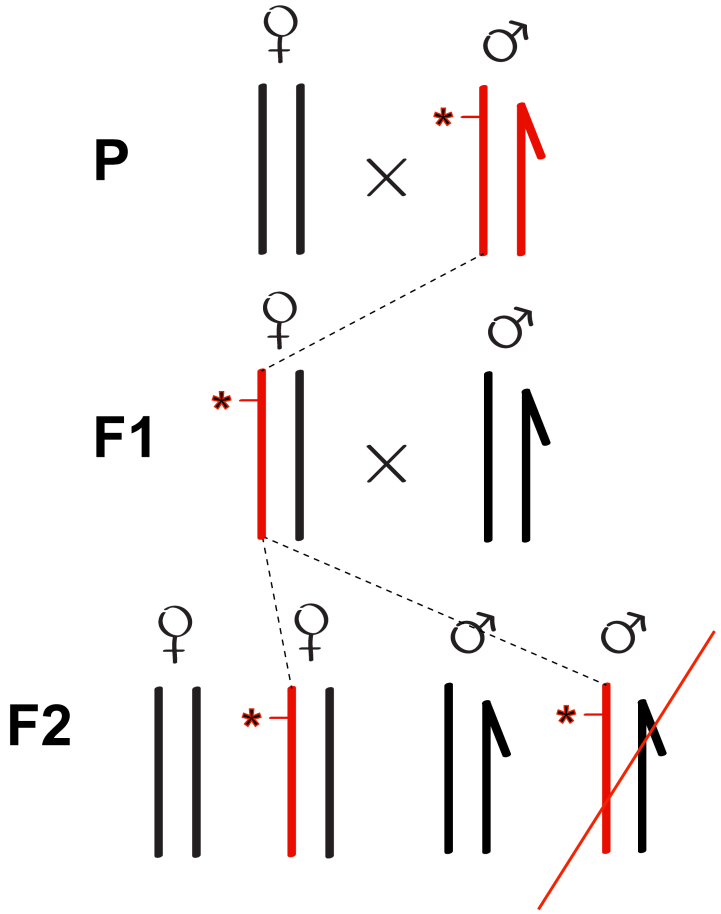


Morgan, Sturtevant, Bridges, Muller ~1931

Sex-linked lethal mutations

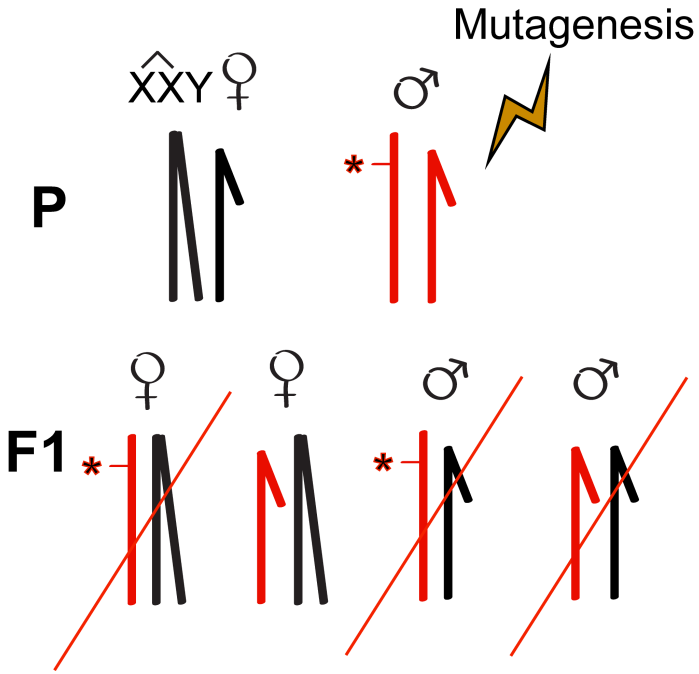


Correns 1905



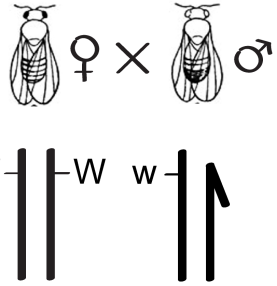
2 : 1 female : male ratio
reveals sex-linked lethal

Attached X



No males
reveals sex-linked lethal

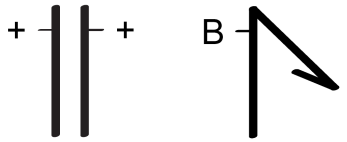
Non disjunction

P 

The white-eyed male, bred to his red-eyed sisters, produced 1,237 red-eyed offspring, (F_1), and 3 white-eyed males. The occurrence of these three white-eyed males (F_1) (due evidently to further sporting) will, in the present communication, be ignored.

Morgan, 1910

P X X ♀ × B $\hat{X}$Y ♂



F1

♀ \ ♂	wX (regular sperm)	Y (regular sperm)	wX/Y (non-disjunction sperm)	O (non-disjunction sperm)
WX (regular ova)	WX/wX ♀	WX/Y ♂	WX/wX/Y ♀	WX/O ♂
WX/WX (non-disjunction ova)	✕	WX/WX/Y ♀		
O (non-disjunction ova)	wX/O ♂	✕		

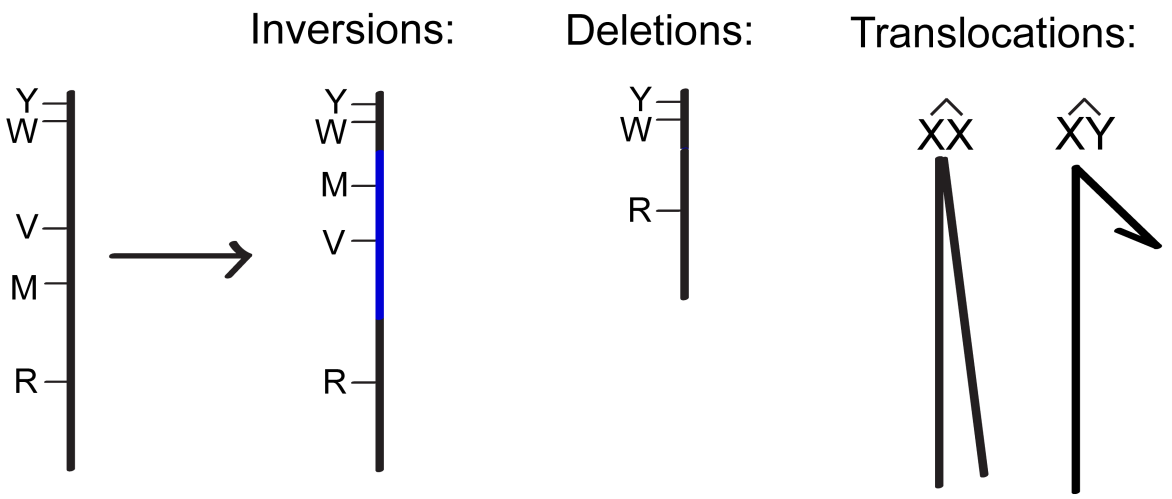
F1

♀ \ ♂	O	$\hat{X}$Y
X (regular ova)	XO + ♂	WX/Y B ♀
XX (non-disjunction ova)	+ ♀	✕
O (non-disjunction ova)	✕	B ♂

Mutagenesis

1927 Hermann Muller demonstrates that X-rays are mutagenic
- Irradiated flies and measured mutations in the offspring
- Focused on lethal mutations
  - 88/758 lethal mutations in treated cultures
  - 1/947 lethal mutations arose in control cultures
  - These data were later used to estimate the size of a gene

Chromosomal abberations were now easier to isolate:



Somatic crossing over: mosaic generation

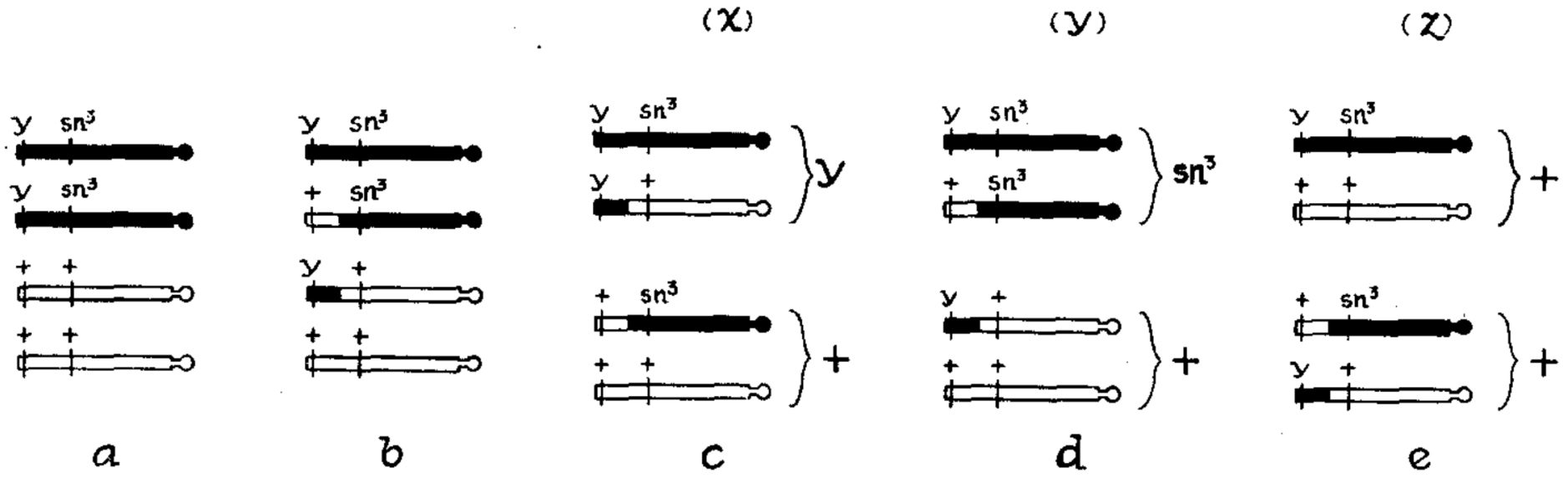


FIGURE 2. *y sn³/+*. Crossing over between *y* and *sn³* at a four strand stage. a. Non-crossover chromatids. b. Two crossover and two non-crossover chromatids. c-e. Three different types of chromatid segregation.

Stern 1936

Polytene chromosomes

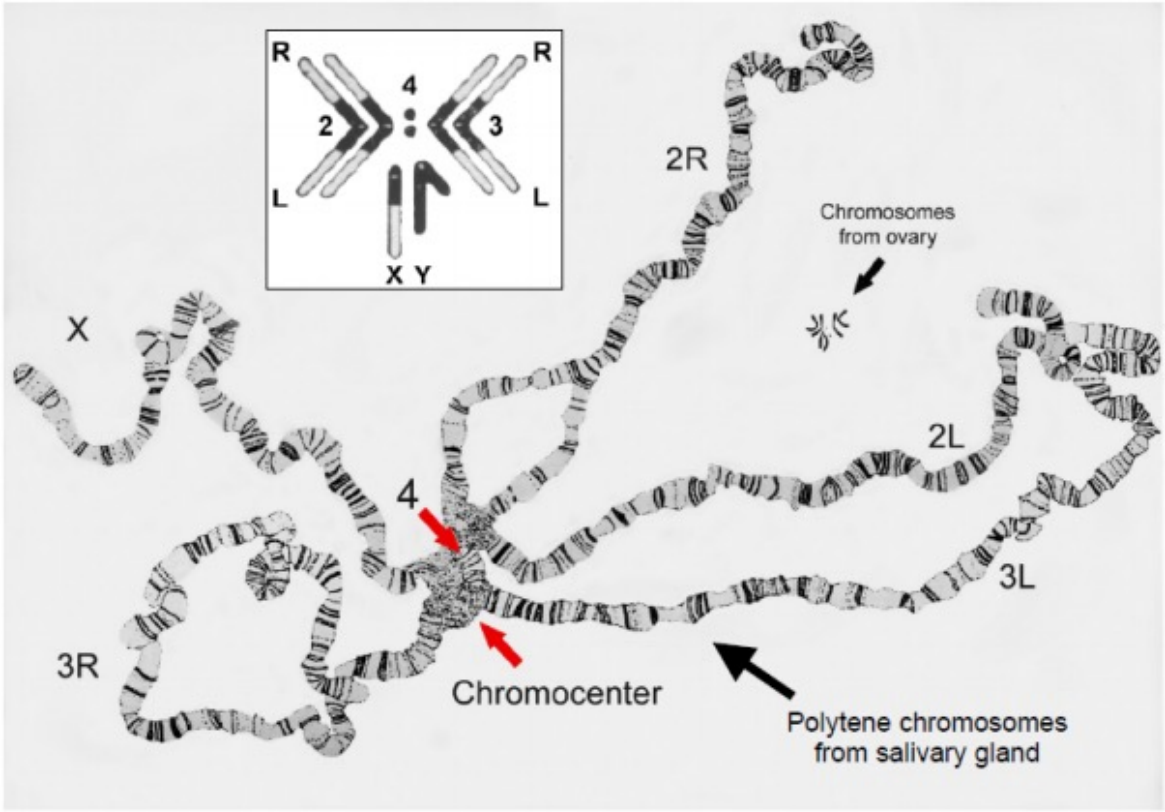


Figure 1. *Drosophila melanogaster* chromosomes (from Painter, 1934; used with permission from Oxford University Press)

- Banding patterns used to verify translocations, inversions, deletions, etc.
- What are chromosomes made of and how do they carry heredity information?

Painter, 1934