The Linear Arrangement of Six Sex-Linking Factors in Drosophila, as Shown by their Mode of Association

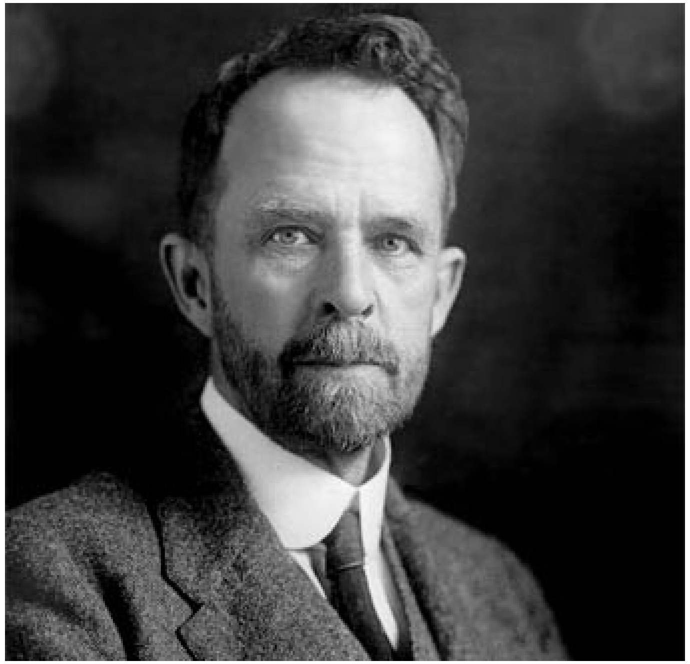
A. H. Sturtevant

Journal of Experimental Zoology; 1913

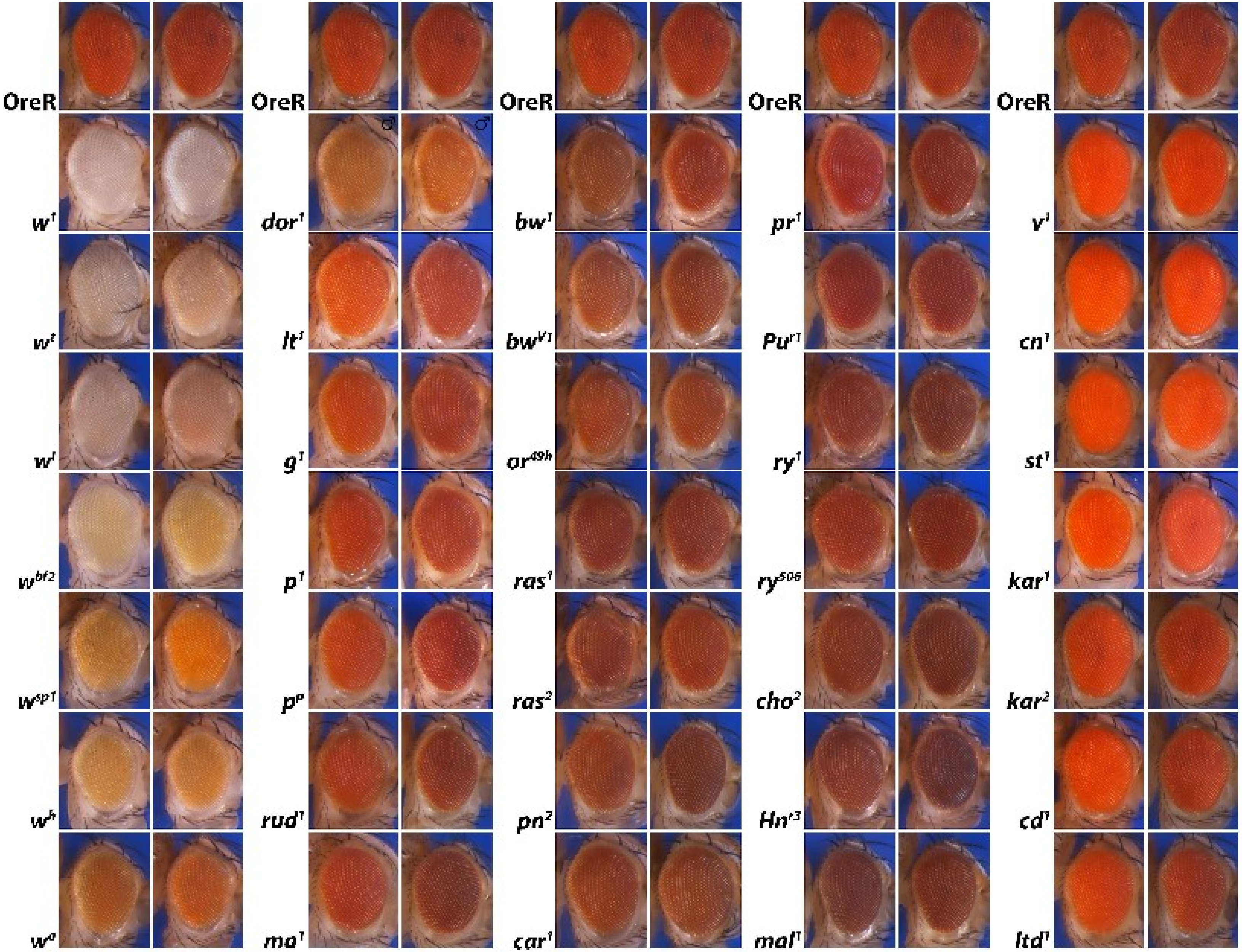
Methods & Logic

3.31.15

Thomas Hunt Morgan (1866-1945)



- Studied embryology and organism development
  - Associate Professor at Bryn Mawr
- After Mendel’s work was rediscovered, Morgan became interested in heredity and evolution
  - Professor at Columbia University
  - Initially found Darwin’s and Mendel’s work lacking
- Began working with *Drosophila melanogaster*
  - Mutated flies, then cross-bred to try and follow hereditable mutations
- Moved to Caltech in 1928


OreR
OreR
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♂
♂
w^{1}
dor^{1}
bw^{1}
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w^{t}
lt^{1}
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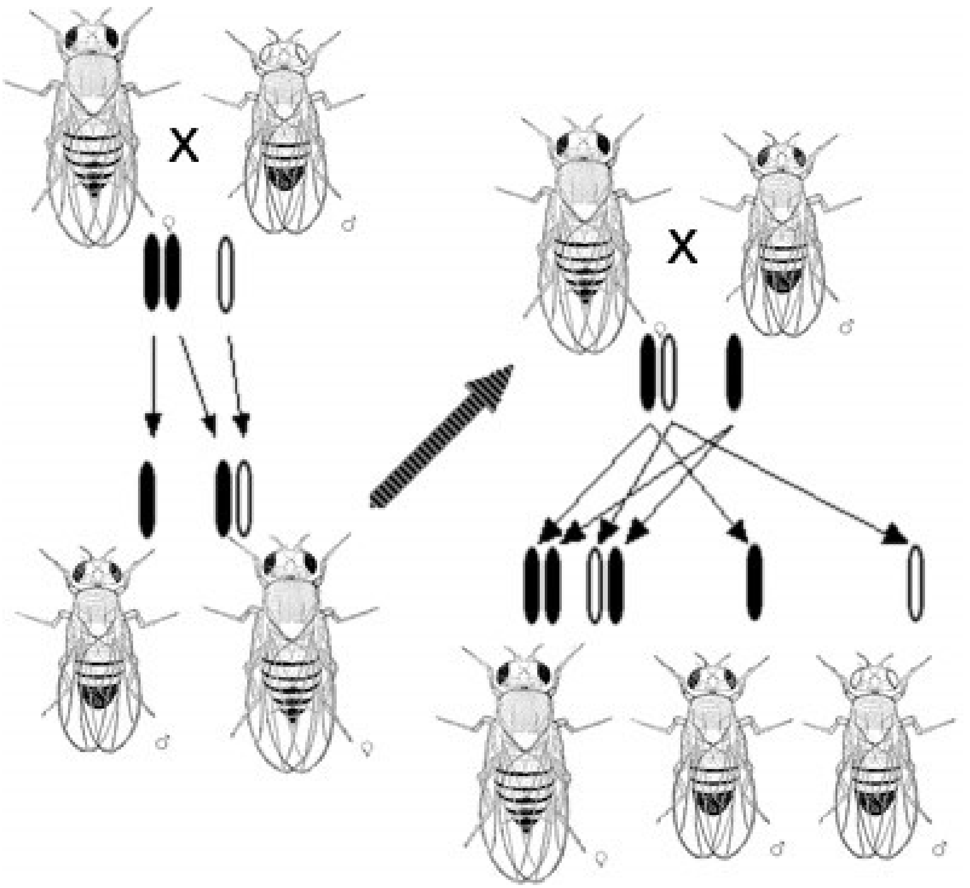
Hn^{r3}
cd^{1}
w^{a}
ma^{1}
car^{1}
mal^{1}
ltd^{1}

White eyed mutant

- 1910: Discovered a mutant white-eyed male
- *white* mutation was sex linked
- Discovered other sex-linked traits
- Introduced the idea that genes are arranged linearly on a chromosome
- Described the crossing-over phenomena
  - Based on observations when sex-linked traits sorted independently



Morgan’s Contributions

- 22 books:

  Evolution and Adaptation (1903); *A Critique of the Theory of Evolution* (1916); *Heredity and Sex* (1913); *The Mechanism of Mendelian Heredity* (1915); *The Theory of the Gene* (1926); *The Development of the Frog’s Egg: An Introduction to Experimental Embryology* (1897); *Experimental Embryology* (1927); *Embryology and Genetics* (1934)

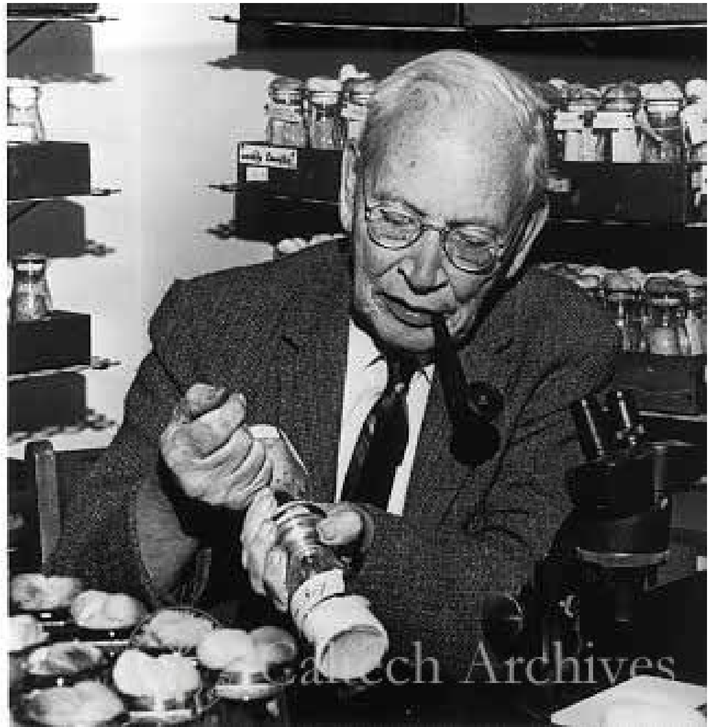
- 1933: Nobel Prize in Medicine or Physiology for his work on the role of chromosomes in heredity

  "It is conceivable that different batteries of genes come into action one after the other, as the embryo passes through its stages of development. This sequence might be assumed to be an automatic property of the chain of genes.”

  -Morgan, Nobel Prize address (1934)

Alfred H. Sturtevant (1891-1970)

- 1908-1911 Undergraduate at Columbia University
- 1911-1914 Ph.D. at Columbia University (Morgan)
- 1928 Professor at Caltech

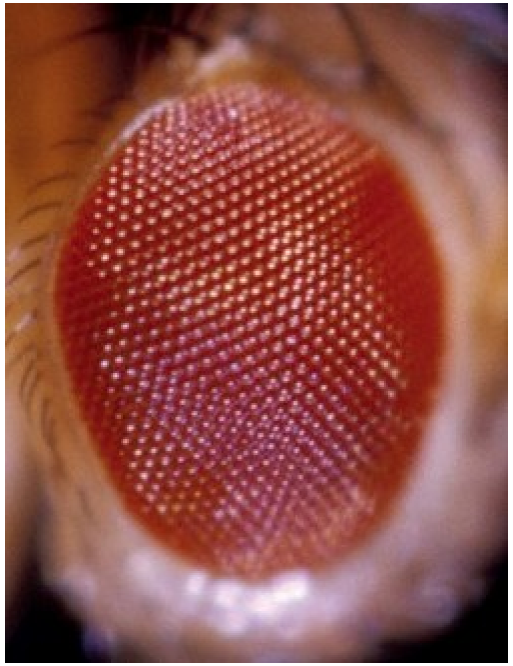


Six Traits

Trait (letter)	Dominant	Recessive
Body Color (B,b)	Gray	Yellow
Eye Color (C,c)**	Red	White
Eye Color (O,o)**	Red	Eosin
Eye Color (P,p)	Red	Vermilion
Wing Size (R,r)	Long	Miniature
Wing Shape (M,m)	Long	Rudimentary

** C & 0 are linked

Eye Color



Red (wild type)

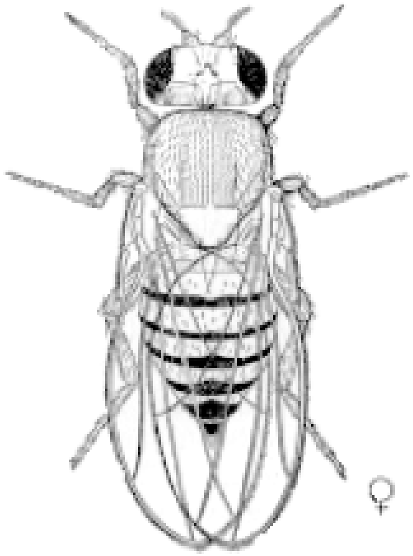
Vermillion

Eosin

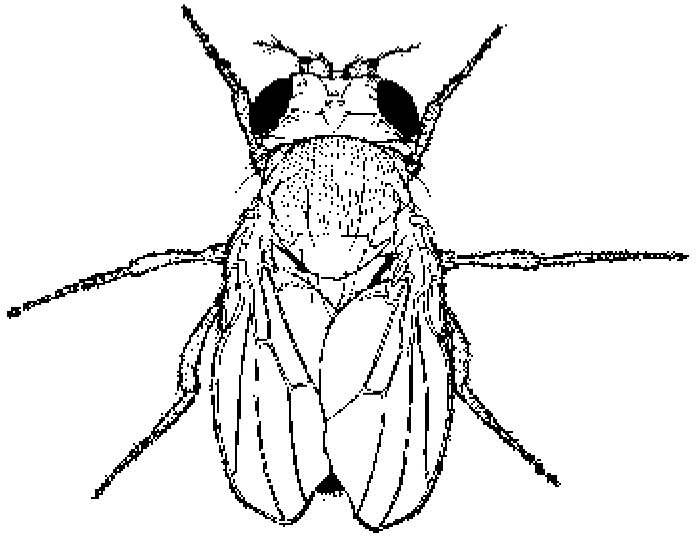
White

<u>Eosin:</u>
Males: white pinkish yellow
Females: dark yellowish pink

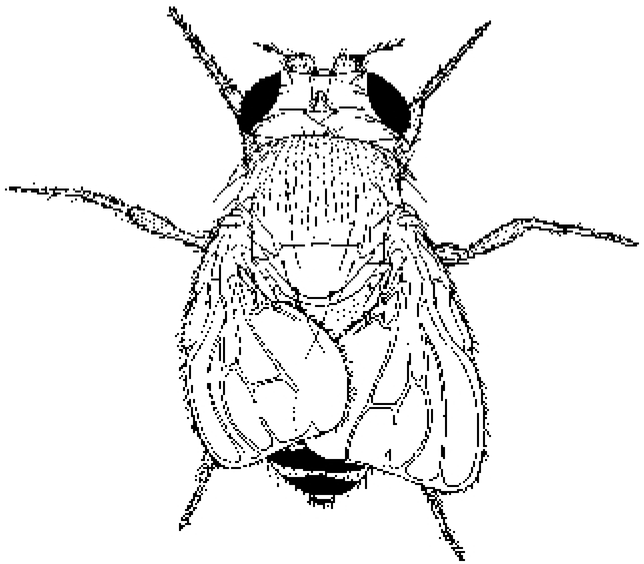
Wing Shape/Size



Wild type

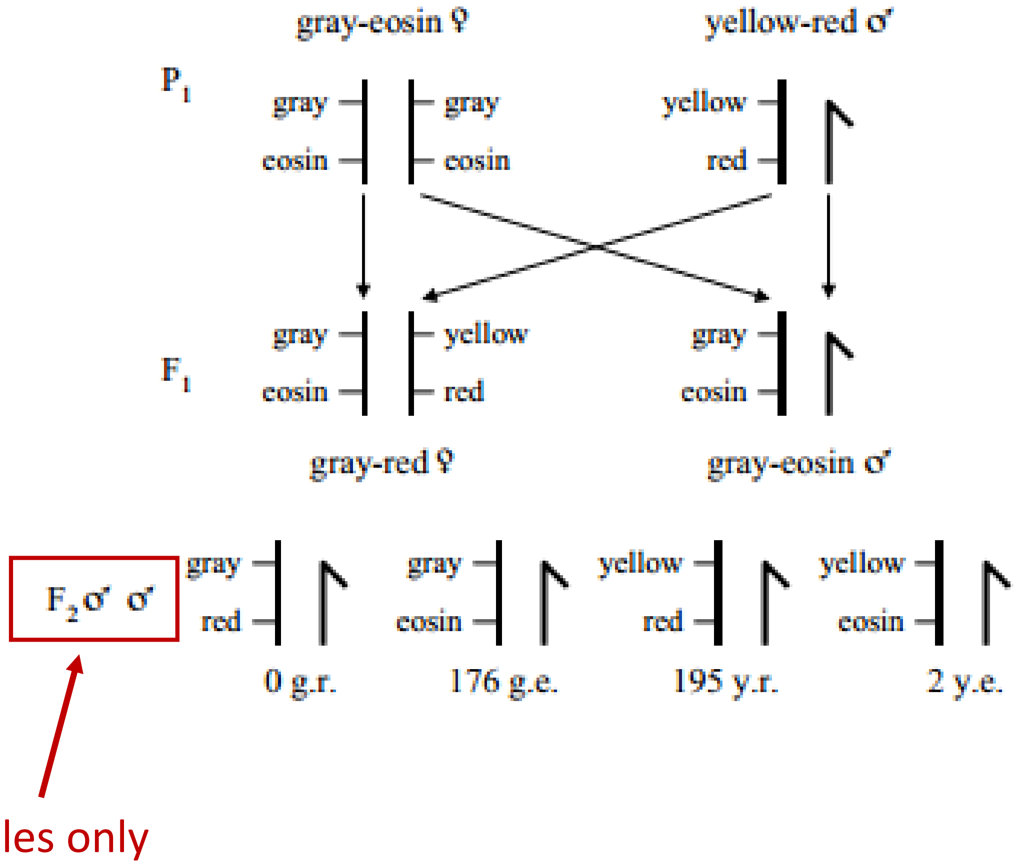


Miniature



Rudimentary

Cross-over calculation example



BO. P_1: gray-eosin ♀ × yellow-red ♂
F_1: gray-red ♀ × gray-eosin ♂
F_2: ♀ ♀, g.r. 241, g.e. 196
♂ ♂, g.r. 0, g.e. 176, y.r. 195, y.e. 2

Proportion of crossovers, $\frac{2}{373}$

$$\frac{2}{373} \times 100 = 0.5 \text{ map unit or ‘centimorgan’}$$

Cross-over calculations

Table 8

(The meaning of the phrase 'proportion of crossovers' is given on pp. 5-6)

BO.	P_1:		gray-eosin ♀ × yellow-red ♂			
	F_1:		gray-red ♀ × gray-eosin ♂			
	F_2:	♀ ♀,	g.r. 241,	g.e. 196		
		♂ ♂,	g.r. 0,	g.e. 176,	y.r. 195,	y.e. 2

Proportion of crossovers, $\frac{2}{373}$

BP.	P_1:		gray-red ♀ × yellow-vermilion ♂			
	F_1:		gray-red ♀ × gray-red ♂			
	F_2:	♀ ♀,	g.r. 98;			
		♂ ♂,	g.r. 59,	g.v. 16,	y.r. 24,	y.v. 33
			Back cross, F_1 gray-red ♀ ♀ from above × yellow-vermilion ♂ ♂			
	F_2:	♀ ♀	g.r. 31,	g.v. 11,	y.r. 12,	y.v. 41
		♂ ♂	g.r. 23,	g.v. 13,	y.r. 8,	y.v. 21
	P_1:		gray-vermilion ♀ × yellow-red ♂			
	F_1:		gray-red ♀ × gray-vermilion ♂			
	F_2:	♀ ♀,	g.r. 199,	g.v. 182		
		♂ ♂	g.r. 54,	g.v. 149,	y.r. 119,	y.v. 41
	P_1:		yellow-vermilion ♀ × gray-red ♂			
	F_1:		gray-red ♀ × yellow-vermilion ♂			
	F_2:	♀ ♀,	g.r. 472,	g.v. 240,	y.r. 213,	y.v. 414
		♂ ♂	g.r. 385,	g.v. 186,	y.r. 189,	y.v. 324
	P_1:		gray-vermilion × yellow-red (sexes not recorded)			
	F_1:		gray-red ♀ ♀. These were mated to yellow-vermilion ♂ ♂ of other stock			
	F_2:	♀ ♀	g.r. 50,	g.v. 96,	y.r. 68,	y.v. 41
		♂ ♂	g.r. 44,	g.v. 105,	y.r. 86,	y.v. 47

Proportion of crossovers, adding from BOPR (below), $\frac{1464}{4551}$

BR.	P_1:		miniature-yellow ♀ × long-gray ♂			
	F_1:		long-gray ♀ × miniature-yellow ♂			
	F_2:	♀ ♀	l.g. 14,	l.y. 2,	m.g. 7,	m.y. 6
		♂ ♂	l.g. 10,	l.y. 1,	m.g. 6,	m.y. 8
	P_1:		long-yellow ♀ × miniature-gray ♂			
	F_1:		long-gray ♀ × long-yellow ♂			
	F_2:	♀ ♀,	l.g. 148,	l.y. 130		
		♂ ♂	l.g. 51,	l.y. 82,	m.g. 89,	m.y. 48

Proportion of crossovers, $\frac{115}{324}$

BM.	P_1:		long-yellow ♀ × rudimentary-gray ♂			
	F_1:		long-gray ♀ × long-yellow ♂			
	F_2:	♀ ♀,	l.g. 591,	l.y. 549		
		♂ ♂,	l.g. 228,	l.y. 371,	r.g. 20,	r.y. 3
	P_1:		long-gray ♀ × rudimentary-yellow ♂			
	F_1:		long-gray ♀ × long-gray ♂			
	F_2:	♀ ♀,	l.g. 152			
		♂ ♂,	l.g. 42,	l.y. 29,	r.g. 0,	r.y. 0

Proportion of crossovers, $\frac{260}{693}$

COP.	P_1:		vermilion ♀ × white ♂		
	F_1:		red ♀ × vermilion ♂		
	F_2:	♀ ♀,	r. 320,	v. 294	
		♂ ♂,	r. 86,	v. 206,	w. 211

(7 of the vermilion ♀ ♀ known from tests to be CC, 2 known to be Cc. 7 white ♂ ♂, Pp, 2 pp.)

Back cross. F_1 red ♀ ♀ from above × white ♂ ♂ gave

F_2:	♀ ♀,	r. 195,	w. 227,	
	♂ ♂,	r. 66,	v. 164,	w. 184

Out cross, F_1 ♀ ♀ as above × white ♂ ♂ recessive in P, gave

F_2:	♀ ♀,	r. 35,	v. 65,	w. 98
	♂ ♂,	r. 33,	v. 75,	w. 95

Proportion of crossovers, $\frac{224}{748}$

COR.	P_1:		miniature-white ♀ × long-red ♂			
	F_1:		long-red ♀ × miniature-white ♂			
	F_2:	♀ ♀,	l.r. 193,	l.w. 109,	m.r. 124,	m.w. 208
		♂ ♂,	l.r. 202,	l.w. 114,	m.r. 123,	m.w. 174
	P_1:		long-white ♀ × miniature-red ♂			
	F_1:		long-red ♀ × long-white ♂			
	F_2:	♀ ♀,	l.r. 194,	l.w. 160		
		♂ ♂,	l.r. 52,	l.w. 124,	m.r. 97,	m.w. 41

Proportion of crossovers, $\frac{563}{1561}$

or, adding such available figures from Morgan (1911d) and Morgan and Cattell (1912) as are not complicated by the presence of yellow or brown flies,

$\frac{1643}{4749}$

Cross-over calculation continued

COM. P₁: long-white ♀ × rudimentary-red ♂

F₁: long-red ♀ × long-white ♂

F₂: ♀ ♀, l.r. 157, l.w. 127

♂ ♂, l.r. 74, l.w. 8 2, ru.r. 3, ru.w. 2

Proportion of crossovers, $\frac{76}{161}$

OP. P₁: black-red ♀ × black eosin-vermilion ♂

F₁: black-red ♀ × black-red ♂

F₂: (all black) ♀ ♀, r. 885

♂ ♂, r. 321, v. 125, e. 122, e.-v. 268

Proportion of crossovers, $\frac{247}{836}$

OR. P₁: long-red ♀ × miniature-eosin ♂

F₁: long-red ♀ × long-red ♂

F₂: ♀ ♀, l.r. 408

♂ ♂, l.r. 145, l.e. 67, m.r. 70, m.e. 100

P₁: long-eosin ♀ × miniature-red ♂

F₁: long-red ♀ × long-eosin ♂

F₂: ♀ ♀, l.r. 100, l.e. 95

♂ ♂, l.r. 27, l.e. 54, m.r. 56, m.e. 19

Proportion of crossovers, $\frac{183}{538}$

OM. P₁: long-eosin ♀ × rudimentary-red ♂

F₁: long-red ♀ × long-eosin ♂

F₂: ♀ ♀, l.r. 368, l.e. 266

♂ ♂, l.r. 194, l.e. 146, ru.r. 40, ru.e. 24

Proportion of crossovers, $\frac{218}{404}$

CR. P₁: long-white ♀ × miniature-eosin ♂

F₁: long-eosin ♀ × long-white ♂

F₂: ♀ ♀, l.e. 185, l.w. 205

♂ ♂, l.e. 54, l.w. 147, m.e. 149, m.w. 42

P₁: long-eosin ♀ × miniature-white ♂

F₁: long-eosin ♀ × long-eosin ♂

F₂: ♀ ♀, l.e. 527

♂ ♂, l.e. 169, l.w. 85, m.e. 55, m.w. 128

Proportion of crossovers, $\frac{236}{829}$

CM. P₁: long-white ♀ × rudimentary-eosin ♂

F₁: long-eosin ♀ × long-white ♂

F₂: ♀ ♀, l.e. 328, l.w. 371

♂ ♂, l.e. 112, l.w. 217, ru.e. 4, ru.w. 0

Proportion of crossovers, $\frac{112}{333}$

PR. P₁: long-vermilion (yellow) ♀ × miniature-red (yellow) ♂

F₁: long-red-yellow ♀ × long-vermilion-yellow ♂

F₂: (all y.) ♀ ♀, l.r. 138, l.v. 110

♂ ♂, l.r. 8, l.v. 117, m.r. 97, m.v. 1

P₁: long-vermilion (gray) ♀ × miniature-red ♂

F₁: long-red ♀ × long-vermilion ♂

F₂: ♀ ♀, l.r. 116, l.v. 110

♂ ♂, l.r. 2, l.v. 81, m.r. 96, m.v. 1

P₁: miniature-red ♀ × long-vermilion ♂

F₁: long-red ♀ × miniature-red ♂

F₂: ♀ ♀, l.r. 45, m.r. 49

♂ ♂, l.r. 1, l.v. 27, m.r. 26, m.v. 0

F₁: long-red ♀ ♀, from above × miniature-red ♂ ♂ of other stock, gave

F₂: ♀ ♀, l.r. 74, m.r. 52

♂ ♂, l.r. 3, l.v. 66, m.r. 46, m.v. 1

Proportion of crossovers, $\frac{17}{573}$

PM. P₁: long-vermilion ♀ × rudimentary-red ♂

F₁: long-red ♀ × long-vermilion ♂

F₂: ♀ ♀, l.r. 451, l.v. 417

♂ ♂, l.r. 105, l.v. 316, ru.r. 33, ru.v. 4

Proportion of crossovers, $\frac{109}{405}$

OPR. P₁: long-vermilion ♀ × miniature eosin ♂

F₁: long-red ♀ × long-vermilion ♂

F₂: ♀ ♀, l.r. 205, l.v. 182

♂ ♂, l.r. 1, l.v. 109, l.e. 8, l.e.-v. 53, m.r. 49, m.v. 3, m.e. 85, m.e.-v. 0

BOM. P₁: long-red-yellow ♀ × rudimentary-eosin-gray ♂

F₁: long-red-gray ♀ × long-red-yellow ♂

F₂: ♀ ♀, l.r.g. 530, l.r.y. 453

♂ ♂, l.r.g. 1, l.r.y. 274, l.e.g. 156, l.e.y. 0, ru.r.g. 0, ru.r.y. 4, ru.e.g. 4, ru.e.y. 0

BOPR. P₁: long-vermilion-brown ♀ × miniature-eosin-black ♂

F₁: long-red-black ♀ × long-vermilion-brown ♂

F₂: ♀ ♀, l.r.bl. 305, l.r.br. 113, l.v.bl. 162, l.v.br. 256

♂ ♂, l.r.bl. 0, l.r.br. 2, l.v.bl. 3, l.v.br. 185, l.e.bl. 9, l.e.br. 0, l.e.-v.bl. 127, l.e.-v.br. 0, m.r.bl. 1, m.r.br. 76, m.v.bl. 1, m.v.br. 10, m.e.bl. 208, m.e.br. 3, m.e.-v.bl. 0, m.e.-v.br. 0

Summary

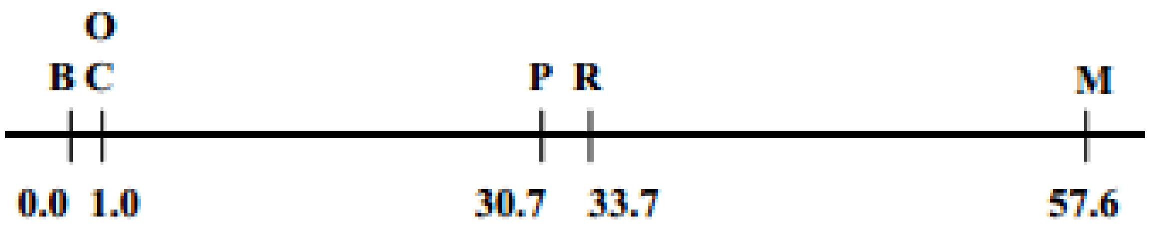


Diagram 1

Table 3

Factors	Calculated distance	Observed per cent of crossovers
BP	30.7	32.2
BR	33.7	35.5
BM	57.6	37.6
(C, O) R	32.7	33.7
(C, O) M	56.6	45.2

Table 2

Factors concerned	Proportion of crossovers	Percent of crossovers
BCO	$\frac{193}{16287}$	1.2
BO	$\frac{2}{373}$	0.5
BP	$\frac{1464}{4551}$	32.2
BR	$\frac{115}{324}$	35.5
BM	$\frac{260}{693}$	37.6
COP	$\frac{224}{748}$	30.0
COR	$\frac{1643}{4749}$	34.6
COM	$\frac{76}{161}$	47.2
OP	$\frac{247}{836}$	29.4
OR	$\frac{183}{538}$	34.0
OM	$\frac{218}{404}$	54.0
CR	$\frac{236}{829}$	28.5
CM	$\frac{112}{333}$	33.6
B(C, O)	$\frac{214}{21736}$	1.0
(C, O) P	$\frac{471}{1584}$	29.7
(C, O) R	$\frac{2062}{6116}$	33.7
(C, O) M	$\frac{406}{898}$	45.2
PR	$\frac{17}{573}$	3.0
PM	$\frac{109}{405}$	26.9

Double & Triple Cross Over Events

Table 4

No crossing over	Single crossing over		Double crossing over
B	B	B	B
CO	CO	CO	CO
R	R	R	R
6972	3454	60	9

Table 5

No crossing over	Single crossing over		Double crossing over
O	O	O	O
P	P	P	P
R	R	R	R
194	102	11	1

Table 6

No crossing over	Single crossing over		Double crossing over
B	B	B	B
O	O	O	O
M	M	M	M
278	160	1	0

Table 7

B	B	B	B	B	B	B	B
O	O	O	O	O	O	O	O
P	P	P	P	P	P	P	P
R	R	R	R	R	R	R	R
393	203	19	6	2	1	1	0

Things to note:

- Distance does not represent ‘physical’ distance
- Rudimentary winged flies are less viable than long winged flies

- Sturtevant developed the cross-over calculation when he was an undergraduate

Summary

- Mapping the fly X chromosome
- Double Cross-overs
- Interference

The Mechanism of Mendelian Heredity (1915)

- Written by Morgan, Sturtevant, Muller & Bridges

Group I	Group II	Group III	Group IV
Abnormal	Antlered	Band	Bent
Bar	Apterous	Beaded	Eyeless
Bifid	Arc	Cream III	
Bow	Balloon	Deformed	
Cherry	Black	Dwarf	
Chrome	Blistered	Ebony	
Cleft	Comma	Giant	
Club	Confluent	Kidney	
Depressed	Cream II	Low crossover	
Dotted	Curved	Maroon	
Eosin	Dachs	Peach	
Facet	Extra vein	Pink	
Forked	Fringed	Rough	
Furrowed	Jaunty	Safranin	
Fused	Limited	Sepia	
Green	Little crossover	Sooty	
Jaunty I	Morula	Spineless	
Lemon	Olive	Spread	
Lethal 1	Plexus	Truncate intens.	
Lethal 1a	Purple	Trident	
Lethal 2	Speck	White head	
Lethal 3	Strap	White ocelli	
Lethal 3a	Streak		
Lethal 4	Tip		
Lethal 5	Trefoil		
Lethal 6	Truncate		
Lethal 7	Vestigial		
Lethal B			
Lethal Sa			
Lethal Sb			
Lethal Sc			
Miniature			
Notch			
Reduplicated			
Ruby			
Rudimentary			
Sable			
Shifted			
Short			
Skee			
Spoon			
Spot			
Tan			
Truncate intens.			
Vermilion			
White			
Yellow