

Hypothesis: *pr* and *vg* are independently assorted

		Observed
Parental	$pr^+ \cdot vg^+$	86
	$pr \cdot vg$	93
Recombinant	$pr^+ \cdot vg$	34
	$pr \cdot vg^+$	55
Total: 268		

Phenotype	Expected
$pr^+ vg^+$	67
$pr vg$	67
$pr^+ vg$	67
$pr vg^+$	67

$$\chi^2 = \sum (O - E)^2 / E$$

Phenotype	Observed	Expected	(O-E) ²	(O-E) ² /E
$pr^+ vg^+$	86	67	361	5.3880597
$pr vg$	93	67	676	10.0895522
$pr^+ vg$	34	67	1089	16.2537313
$pr vg^+$	55	67	144	2.14925373
			SUM	33.880597

Critical value



Critical value is then used to determine the confidence level

TABLE 3-1 Critical Values of the χ^2

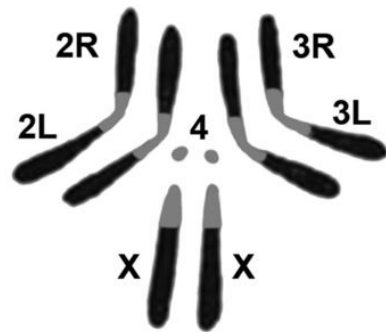
df	p									df
	0.995	0.975	0.9	0.5	0.1	0.05	0.025	0.01	0.005	
1	.000	.000	0.016	0.455	2.706	3.841	5.024	6.635	7.879	1
2	0.010	0.051	0.211	1.386	4.605	5.991	7.378	9.210	10.597	2
3	0.072	0.216	0.584	2.366	6.251	7.815	9.348	11.345	12.838	3
4	0.207	0.484	1.064	3.357	7.779	9.488	11.143	13.277	14.860	4
5	0.412	0.831	1.610	4.351	9.236	11.070	12.832	15.086	16.750	5
6	0.676	1.237	2.204	5.348	10.645	12.592	14.449	16.812	18.548	6
7	0.989	1.690	2.833	6.346	12.017	14.067	16.013	18.475	20.278	7
8	1.344	2.180	3.490	7.344	13.362	15.507	17.535	20.090	21.955	8
9	1.735	2.700	4.168	8.343	14.684	16.919	19.023	21.666	23.589	9
10	2.156	3.247	4.865	9.342	15.987	18.307	20.483	23.209	25.188	10
11	2.603	3.816	5.578	10.341	17.275	19.675	21.920	24.725	26.757	11
12	3.074	4.404	6.304	11.340	18.549	21.026	23.337	26.217	28.300	12
13	3.565	5.009	7.042	12.340	19.812	22.362	24.736	27.688	29.819	13
14	4.075	5.629	7.790	13.339	21.064	23.685	26.119	29.141	31.319	14
15	4.601	6.262	8.547	14.339	22.307	24.996	27.488	30.578	32.801	15

df: **degree of freedom** (number of independent value -1)

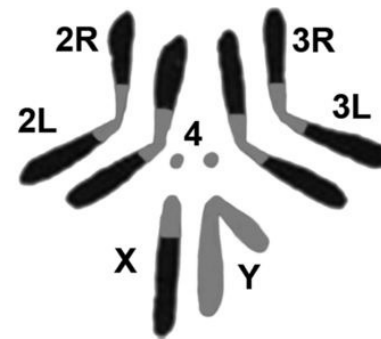
$p=0.05$ means that there is 5% chance of getting observed number even if independent assortment is true. If $p < 0.05$, you can reject the hypothesis with the confidence level of 95% or greater

Linkage & Mapping

Ch4.1- Ch4.2



Female



Males

Morgan's finding

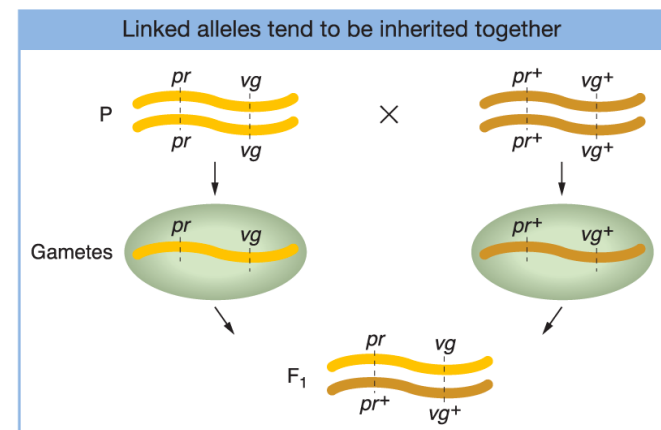
two recessive mutations
pr: purple eyes instead of red
vg: small wings

$$\begin{array}{lcl}
 \text{P} & & pr/pr \cdot vg/vg \times pr^+/pr^+ \cdot vg^+/vg^+ \\
 & \downarrow & \\
 \text{Gametes} & & pr \cdot vg \quad pr^+ \cdot vg^+ \\
 & \downarrow & \\
 \text{F}_1 \text{ dihybrid} & & pr^+/pr \cdot vg^+/vg
 \end{array}$$

Testcross

$$\begin{array}{lcl}
 pr^+/pr \cdot vg^+/vg \text{ ♀} & \times & pr/pr \cdot vg/vg \text{ ♂} \\
 \text{F}_1 \text{ dihybrid female} & & \text{Tester male}
 \end{array}$$

Parental	$pr^+ \cdot vg^+$	1339
	$pr \cdot vg$	1195
Recombinant	$pr^+ \cdot vg$	151
	$pr \cdot vg^+$	154
		<hr/> 2839



Griffiths et al., *Introduction to Genetic Analysis*, 12e, © 2020
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Fig 4-2

Thomas Hunt Morgan: “Chromosome theory of inheritance”



The Nobel Prize in Physiology or Medicine 1933

“His work confirmed that genes are stored in chromosomes inside cell nuclei. He came to understand that genes are organized in a long row inside chromosomes and how traits related to each other correspond to genes that lie close to one another on the chromosomes. He also discovered the crossover phenomenon, in which parts of different chromosomes can trade places with one another.”

<https://www.nobelprize.org/prizes/medicine/1933/morgan/facts/>

Recombinants are produced during meiosis

$pr^+ \cdot vg^+$	1339
$pr \cdot vg$	1195
$pr^+ \cdot vg$	151
$pr \cdot vg^+$	154
	<hr/> 2839

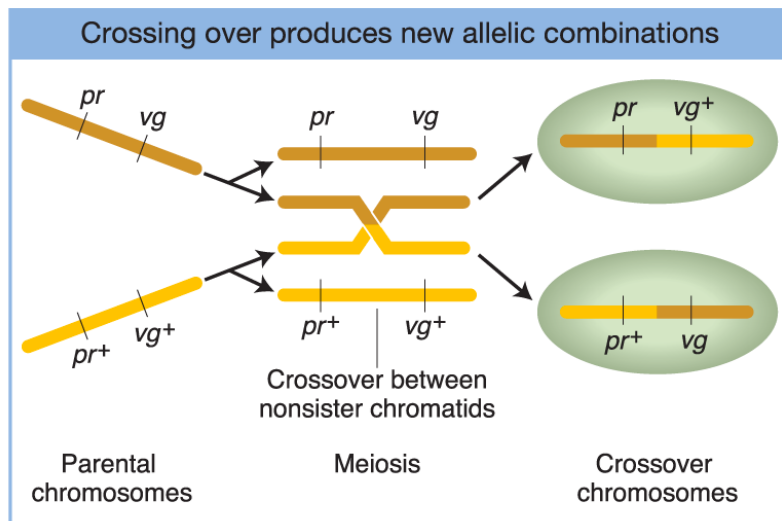


Fig 4-3

Crossover

Chiasmata are the sites of crossing over

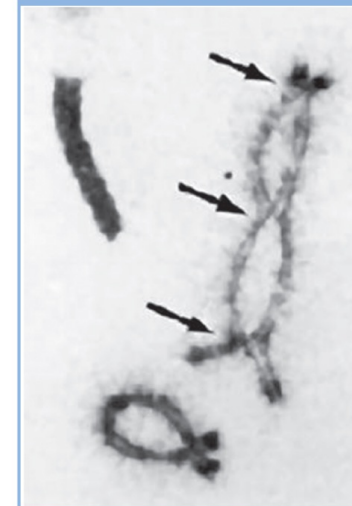


Fig 4-4

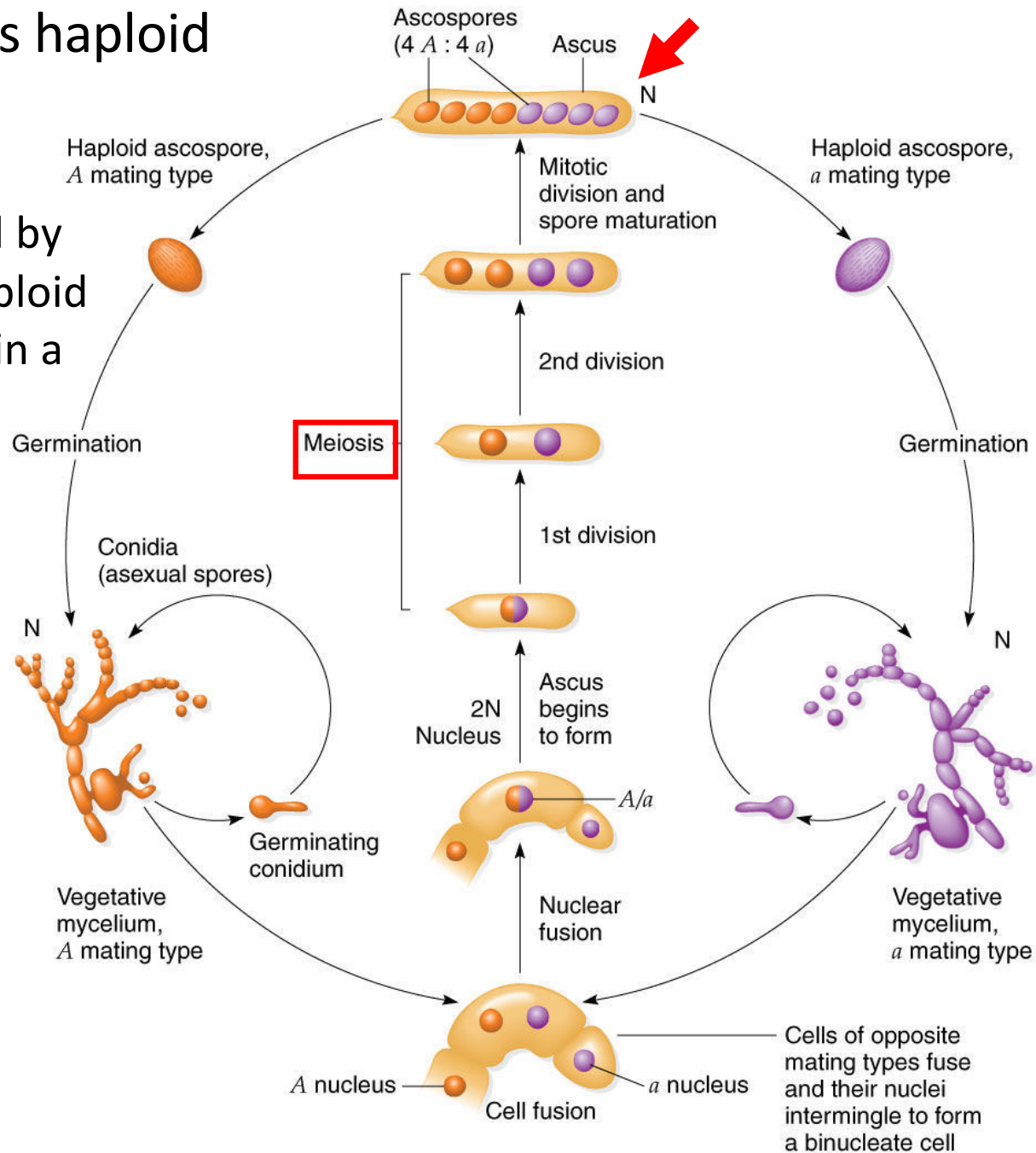
When does crossover take place during meiosis, before or after DNA replication?

Could there be multiple crossovers in a single meiosis event?

Neurospora Life cycle

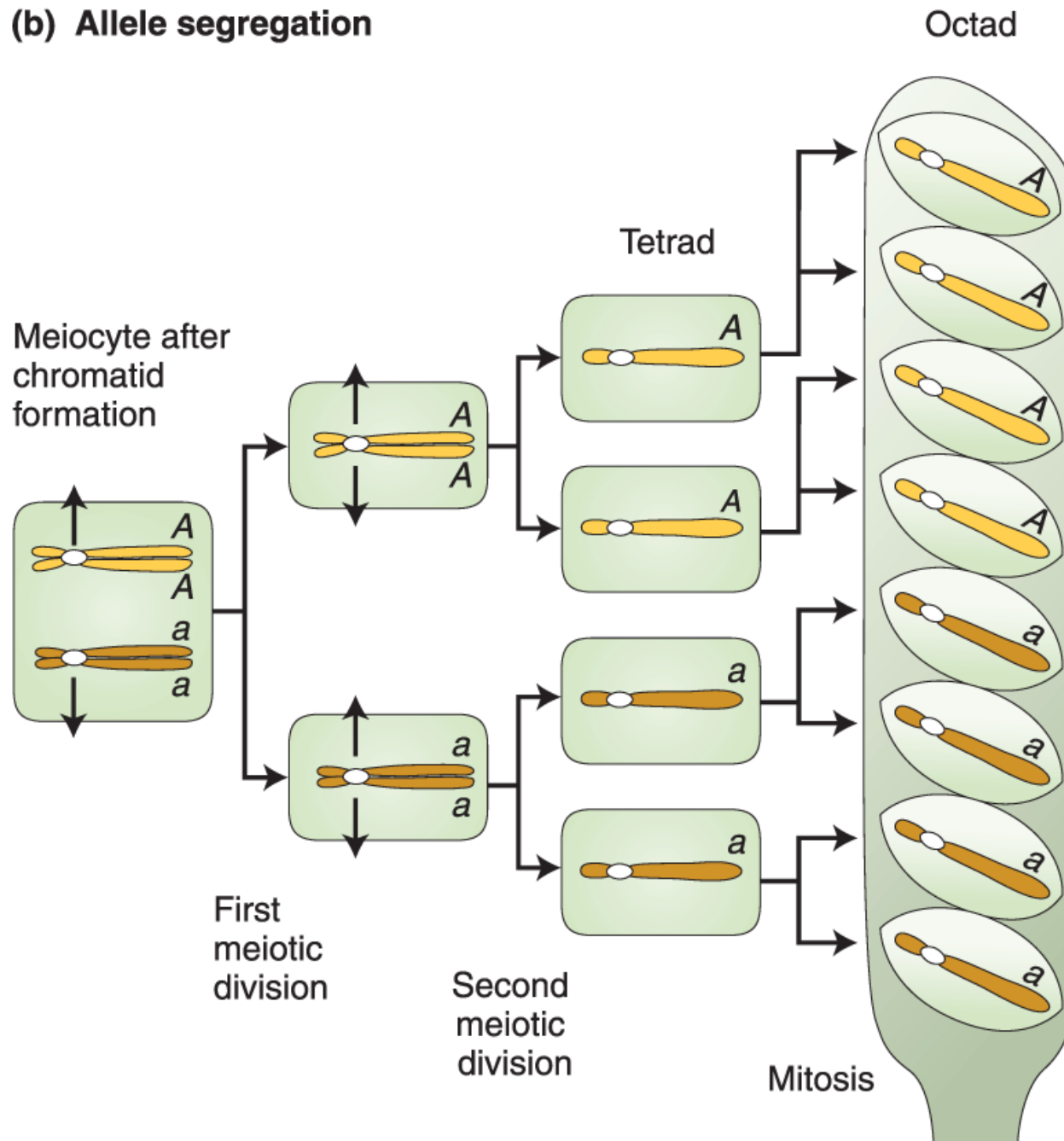
Mold, grows as haploid

Ascospores produced by meiosis of a single diploid cell remain together in a sac called **ascus**.

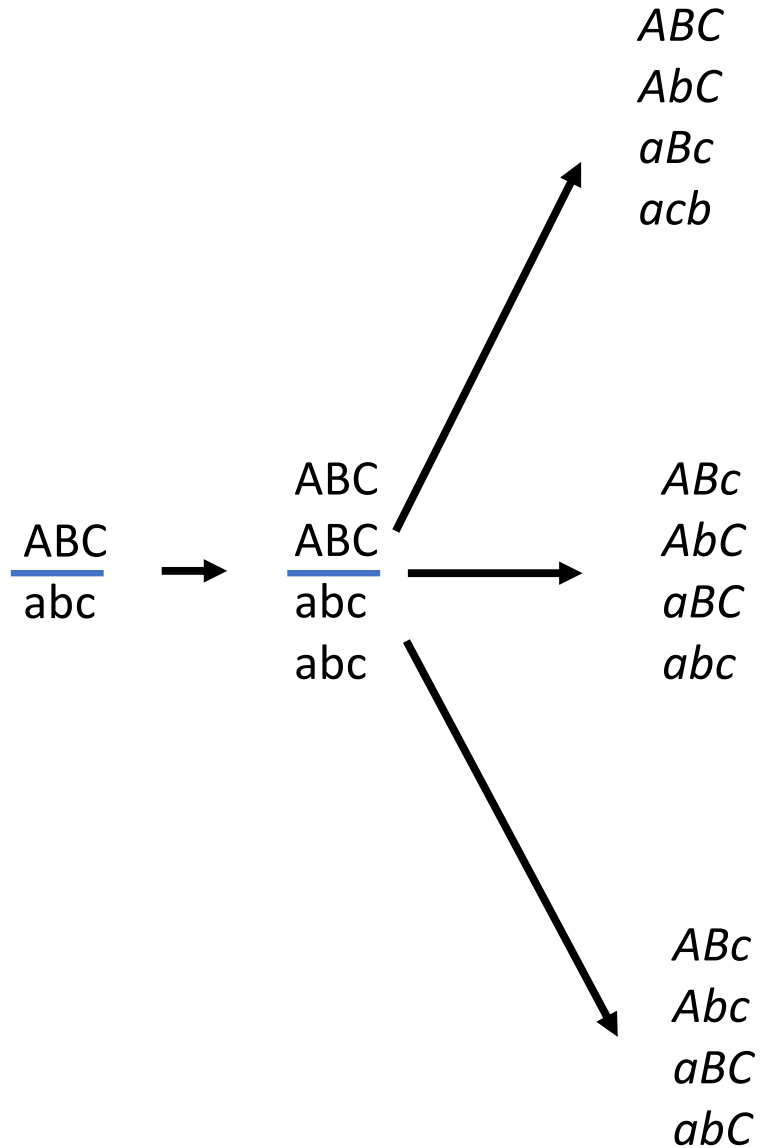


Ascus contain products of a single meiotic event

(b) Allele segregation



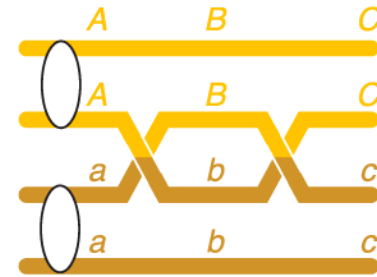
Multiple crossovers between two haploids: $ABC \times abc$



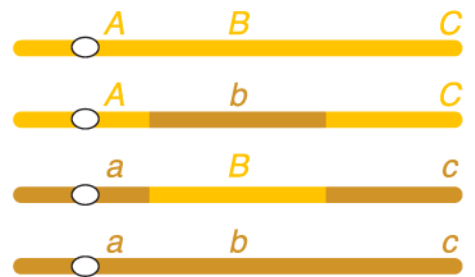
Multiple crossovers can include two or more chromatids

(a) Two chromatids

Position of crossovers

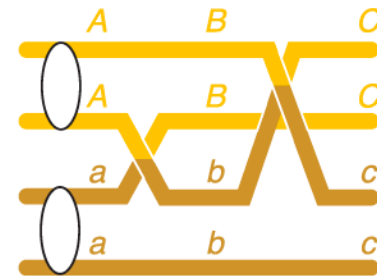


Tetrad genotypes

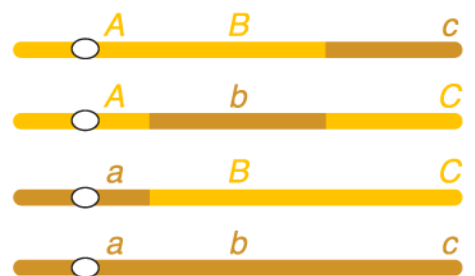


(b) Three chromatids

Position of crossovers

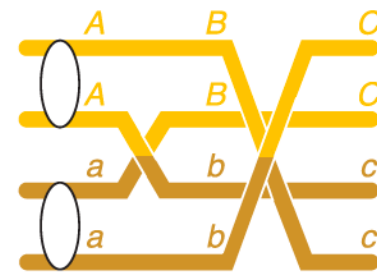


Tetrad genotypes

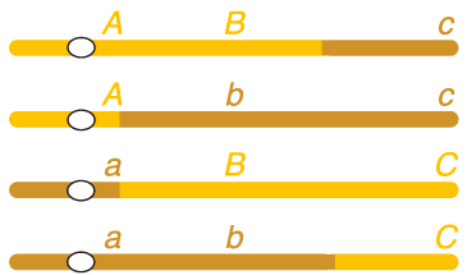


(c) Four chromatids

Position of crossovers



Tetrad genotypes



Crossover and the physical distance of the genes

Farther apart the genes are, they are more likely to crossover, higher chance of producing recombinant.

Chiasmata are the sites of crossing over

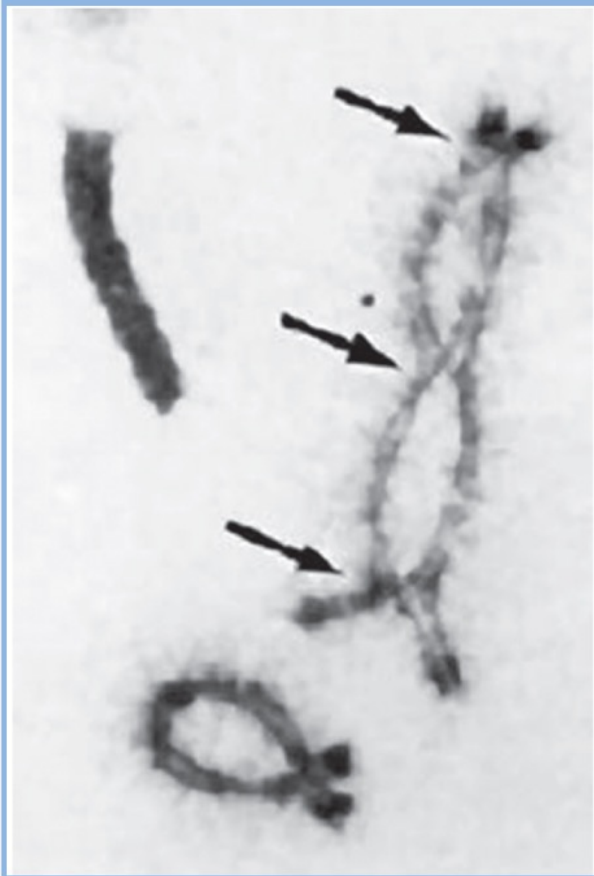
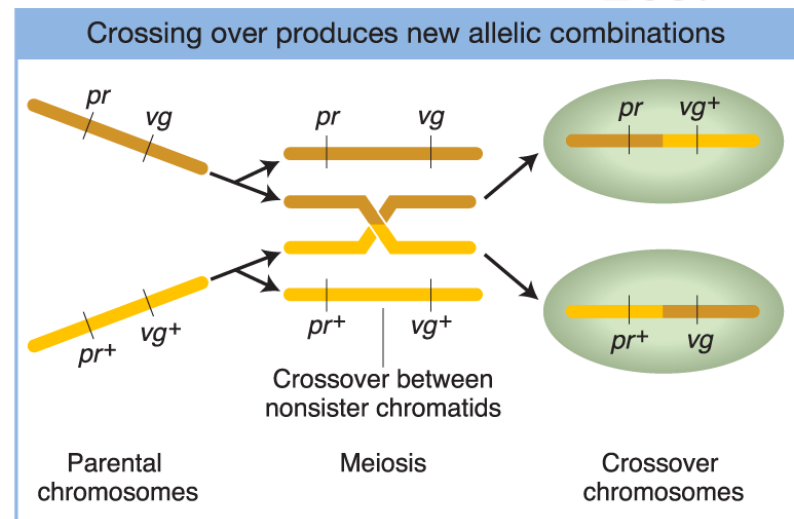


Fig 4-4

Parental	$pr^{+} \cdot vg^{+}$	1339
	$pr \cdot vg$	1195
Recombinant	$pr^{+} \cdot vg$	151
	$pr \cdot vg^{+}$	154
		<hr/> 2839



Frequency of recombinant production is determined by their physical distance!!!

Genetic map unit (centimorgan)

1 genetic map unit (m.u.) = the frequency at which one out of 100 meiosis products is recombinant.



Alfred Henry Sturtevant
Photo courtesy of Cold Spring Harbor
Laboratory Archives.

$pr^{+} \cdot vg^{+}$	1339
$pr \cdot vg$	1195
$pr^{+} \cdot vg$	151
$pr \cdot vg^{+}$	154
	<hr/>
	2839

$$(151+154)/2839 \times 100 = 10.7\%$$

Alfred Sturtevant
A student of Thomas Morgan

FRs between linked genes can generate a map of a genome.

Therefor the distance between pr and vg is 10.7 m.u. (centimorgan (cM) in honor of Thomas Hunt Morgan).

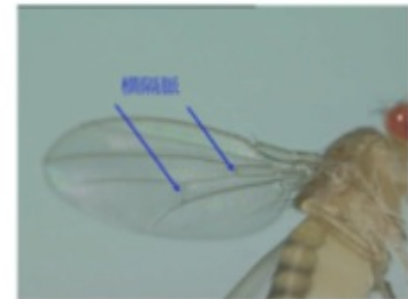
In theory, RF of two genes cannot exceed 50%, independent assortment.

Three point testcross

v vermillion eyes
("vermillion")



cv wings lacking cross veins
("cross-veinless")



ct cut or snapped wing edges
("cut")



Three point testcross

P $v^+/v^+ \cdot cv/cv \cdot ct/ct \times v/v \cdot cv^+/cv^+ \cdot ct^+/ct^+$



Gametes $v^+ \cdot cv \cdot ct$ $v \cdot cv^+ \cdot ct^+$

F₁ trihybrid $v/v^+ \cdot cv/cv^+ \cdot ct/ct^+$

$v/v^+ \cdot cv/cv^+ \cdot ct/ct^+ \text{♀} \times v/v \cdot cv/cv \cdot ct/ct \text{♂}$

F₁ trihybrid female

Tester male

parental types: $v \cdot cv^+ \cdot ct^+$ & $v^+ \cdot cv \cdot ct$

Gametes of F1

$v \cdot cv^+ \cdot ct^+$	580
$v^+ \cdot cv \cdot ct$	592
$v \cdot cv \cdot ct^+$	45
$v^+ \cdot cv^+ \cdot ct$	40
$v \cdot cv \cdot ct$	89
$v^+ \cdot cv^+ \cdot ct^+$	94
$v \cdot cv^+ \cdot ct$	3
$v^+ \cdot cv \cdot ct^+$	5
	1448

RF

parental types: $v \cdot cv^+ \cdot ct^+$ & $v^+ \cdot cv \cdot ct$

Gametes of F1	<i>Recombinant for loci</i>	
	v and cv	
$v \cdot cv^+ \cdot ct^+$	580	
$v^+ \cdot cv \cdot ct$	592	
$v \cdot cv \cdot ct^+$	45	R
$v^+ \cdot cv^+ \cdot ct$	40	R
$v \cdot cv \cdot ct$	89	R
$v^+ \cdot cv^+ \cdot ct^+$	94	R
$v \cdot cv^+ \cdot ct$	3	
$v^+ \cdot cv \cdot ct^+$	5	
	1448	268
	RF	18.5%

parental types: $v \cdot cv^+ \cdot ct^+$ & $v^+ \cdot cv \cdot ct$

Gametes of F1		<i>Recombinant for loci</i>	
		<i>v and ct</i>	
$v \cdot cv^+ \cdot ct^+$	580		
$v^+ \cdot cv \cdot ct$	592		
$v \cdot cv \cdot ct^+$	45		
$v^+ \cdot cv^+ \cdot ct$	40		
$v \cdot cv \cdot ct$	89		R
$v^+ \cdot cv^+ \cdot ct^+$	94		R
$v \cdot cv^+ \cdot ct$	3		R
$v^+ \cdot cv \cdot ct^+$	5		R
	1448		191
	RF		13.2%

parental types: $v \cdot cv^+ \cdot ct^+$ & $v^+ \cdot cv \cdot ct$

Gametes of F1		<i>Recombinant for loci</i>	
		<i>cv and ct</i>	
$v \cdot cv^+ \cdot ct^+$	580		
$v^+ \cdot cv \cdot ct$	592		
$v \cdot cv \cdot ct^+$	45		R
$v^+ \cdot cv^+ \cdot ct$	40		R
$v \cdot cv \cdot ct$	89		
$v^+ \cdot cv^+ \cdot ct^+$	94		
$v \cdot cv^+ \cdot ct$	3		R
$v^+ \cdot cv \cdot ct^+$	5		R
	1448		93
	RF		6.4%

parental types: $v \cdot cv^+ \cdot ct^+$ & $v^+ \cdot cv \cdot ct$

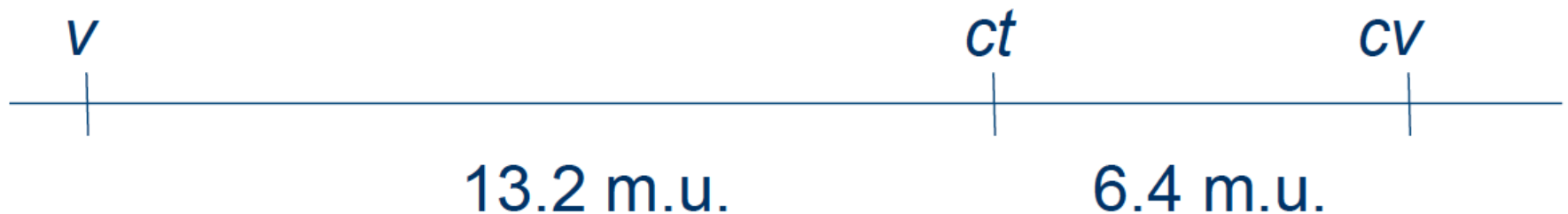
Gametes of F1		<i>Recombinant for loci</i>		
		v and cv	v and ct	cv and ct
$v \cdot cv^+ \cdot ct^+$	580			
$v^+ \cdot cv \cdot ct$	592			
$v \cdot cv \cdot ct^+$	45	R		R
$v^+ \cdot cv^+ \cdot ct$	40	R		R
$v \cdot cv \cdot ct$	89	R	R	
$v^+ \cdot cv^+ \cdot ct^+$	94	R	R	
$v \cdot cv^+ \cdot ct$	3		R	R
$v^+ \cdot cv \cdot ct^+$	5		R	R
	1448	268	191	93
	RF	18.5%	13.2%	6.4%

v & cv = 18.5%

v & ct = 13.2%

cv & ct = 6.4%

Therefore the map looks like:

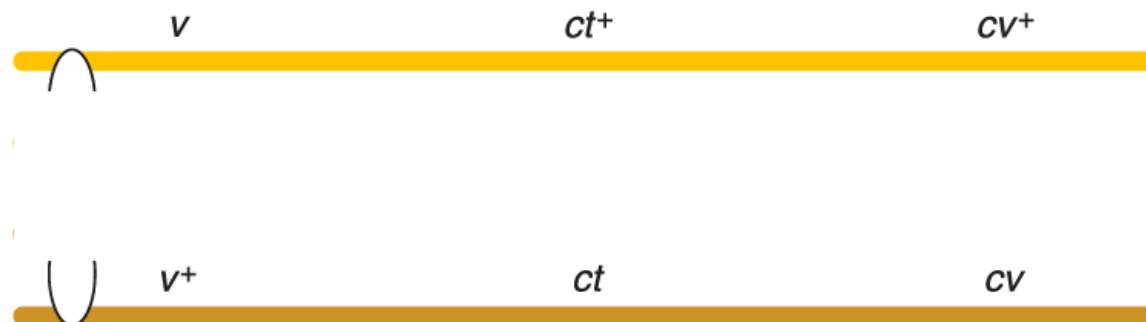


But $13.2 + 6.4 = 19.6$ not 18.5..... Why?

parental types: $v \cdot cv^+ \cdot ct^+$ & $v^+ \cdot cv \cdot ct$

		<i>Recombinant for loci</i>		
Gametes		v and cv	v and ct	cv and ct
$v \cdot cv^+ \cdot ct^+$	580			
$v^+ \cdot cv \cdot ct$	592			
$v \cdot cv \cdot ct^+$	45	R		R
$v^+ \cdot cv^+ \cdot ct$	40	R		R
$v \cdot cv \cdot ct$	89	R	R	
$v^+ \cdot cv^+ \cdot ct^+$	94	R	R	
→ $v \cdot cv^+ \cdot ct$	3		R	R
→ $v^+ \cdot cv \cdot ct^+$	5		R	R
1448		268	191	93

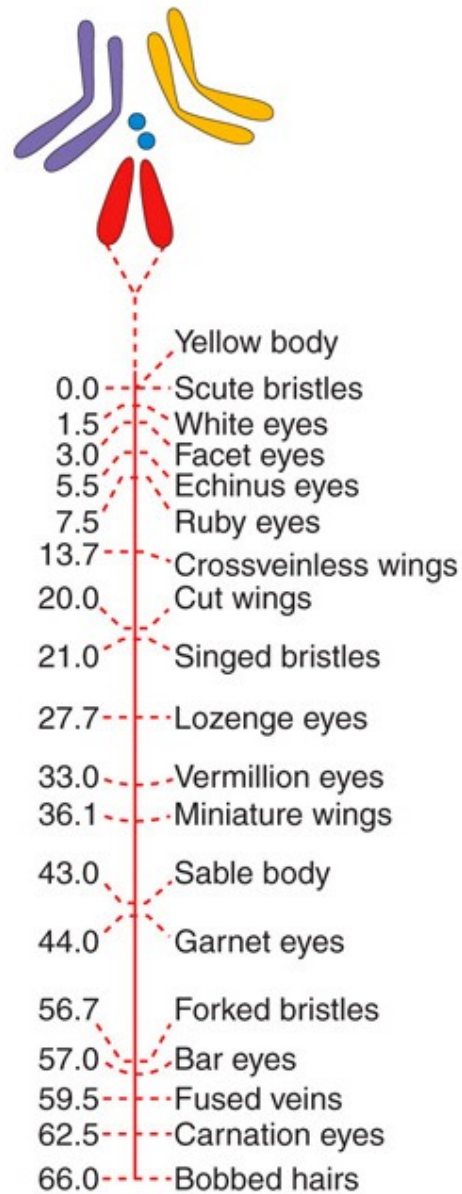
Double recombinants arising from two crossovers



Griffiths et al., *Introduction to Genetic Analysis*, 12e, © 2020
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Two recombination events between v and cv : $2(3+5) + 268 = 284$ recombination events
 $284/1448 \times 100 = 19.6$

Map of Drosophila genes



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