4

Mapping Eukaryotic Chromosomes by Recombination

WORKING WITH THE FIGURES

(The first 11 problems require inspection of text figures.)

1. In Figure 4-3, would there be any noncrossover meiotic products in the meiosis illustrated? If so, what colors would they be in the color convention used?

   Answer: Figure 4-3 is drawn to show how crossing over can produce new combinations of alleles, so only the crossover meiotic products are shown for simplicity. In addition to those, there would be two noncrossover products: \( pr \) \( vg \) designated with brown, and \( pr^+ \) \( vg^+ \) designated yellow.

2. In Figure 4-6, why does the diagram not show meioses in which two crossovers occur between the same two chromatids (such as the two inner ones)?

   Answer: Figure 4-6 is drawn to show the result of double crossovers involving more than two chromatids (three or four). A double crossover between the inner two chromatids only would not meet this condition.

3. In Figure 4-8, some meiotic products are labeled parental. Which parent is being referred to in this terminology?

   Answer: The parental meiotic products are chromosomes that have descended intact from one of the two original parents (\( P_1 \)) in the cross. In this case, the parent for the \( AB/ab \) genotype would be the \( AB/AB \) parent (homozygous brown) and the parent for the \( ab/ab \) genotype would be the \( ab/ab \) (homozygous yellow).

4. In Figure 4-9, why is only locus A shown in a constant position?
5. In Figure 4-10, what is the mean frequency of crossovers per meiosis in the region A–B? The region B–C?

Answer: Figure 4-10 shows the four products of one meiosis, depicting crossovers at various locations along the chromosome. There are five total crossovers in the A-C region of this chromosome. One crossover occurs in the A-B region, for a frequency of 0.20. Four crossovers (two singles and a three-stranded double) occur in the B-C region for a frequency of 0.80. Because A and C are near the ends of the chromosome, but not at the ends, crossovers could occur outside the A-C interval. To calculate the overall frequency of crossovers that occurred in the two designated regions, the number of meiocytes for which crossovers occurred outside the A-C region would have to be known.

6. In Figure 4-11, is it true to say that from such a cross the product $v\, cv^+$ can have two different origins?

Answer: Yes. Ignoring the middle gene $ct$, the product $v\, cv^+$ can arise from either a nonrecombinant parental chromosome or a double crossover. If only the two outside genes, $v$ and $cv$ were involved in the cross, the nonparental double crossover product would not be detectable phenotypically and would appear as a parental chromosome.

7. In Figure 4-14, in the bottom row four colors are labeled SCO. Why are they not all the same size (frequency)?

Answer: Figure 4-14 represents a trihybrid testcross with linked genes, so there are two genetic intervals to consider. In a typical three-point testcross, those intervals will be different sizes with correspondingly different frequencies of SCOs. The colored boxes depicting SCOs are different sizes to reflect a difference in the number of single crossovers. Note that the two adjacent colors in each pair (green/brown, purple/gray) are about the same size, reflecting the roughly equal number of reciprocal products in each crossover.

8. Using the conventions of Figure 4-15, draw parents and progeny classes from a cross

$$PM''/p\, M' \times p\, M'/p\, M'''$$
Answer: In this cross, the dominant disease gene $P$ is linked to the microsatellite allele $M''$. The progeny classes of the cross shown would be $\frac{1}{4} P M''/p M'$ (affected by the disease), $\frac{1}{4} P M''/p M'''$ (affected), $\frac{1}{4} p M'/p M'$, (unaffected) and $\frac{1}{4} p M'/p M'''$ (unaffected).

9. In Figure 4-17, draw the arrangements of alleles in an octad from a similar meiosis in which the upper product of the first division segregated in an upside-down manner at the second division.

Answer: A reversal in the orientation of the upper product would produce a second division pattern of $aAAAa$, and an octad of $aaAAAAaa$.

10. In Figure 4-19, what would be the RF between $A/a$ and $B/b$ in a cross in which purely by chance all meioses had four-strand double crossovers in that region?
Answer: Figure 4-19 shows that a single four-stranded double crossover produces 100% RF for that meiosis. If by chance all meioses had four-stranded double crossovers, the overall RF would be 100%.

11. a. In Figure 4-21, let GC = A and AT = a, then draw the fungal octad that would result from the final structure (5).

b. (Challenging) Insert some closely linked flanking markers into the diagram, say P/p to the left and Q/q to the right (assume either cis or trans arrangements). Assume neither of these loci show non-Mendelian segregation. Then draw the final octad based on the structure in part 5.

Answer:

a. The heteroduplex DNA in the upper chromatid would produce a non-identical spore pair with GC (= A) on top and AT (= a) on bottom. The bottom chromatid would replicate to produce a normal identical spore pair. Thus, the final octad would be A-A a-a a-a a-a.

b. That the two loci show no non-Mendelian segregation means that both lie outside the heteroduplex region. If P and Q were in cis and positioned to
the left and right, respectively, of the gene $A$ crossover region, they would recombine due to the crossover. The final octad would be $PQ PQ Pq Pq pQ pQ pQ pq pq$.

**BASIC PROBLEMS**

12. A plant of genotype

\[
\begin{array}{c|c}
A & B \\
\hline
a & b \\
\end{array}
\]

is testcrossed with

\[
\begin{array}{c|c}
a & b \\
\hline
a & b \\
\end{array}
\]

If the two loci are 10 m.u. apart, what proportion of progeny will be $AB/ab$?

Answer: You perform the following cross and are told that the two genes are 10 m.u. apart.

\[ A B/a b \times a b/a b \]

Among their progeny, 10 percent should be recombinant ($A b/a b$ and $a B/a b$) and 90 percent should be parental ($A B/a b$ and $a b/a b$). Therefore, $A B/a b$ should represent $1/2$ of the parentals or 45 percent.

13. The $A$ locus and the $D$ locus are so tightly linked that no recombination is ever observed between them. If $Ad/Ad$ is crossed with $aD/aD$ and the $F_1$ is intercrossed, what phenotypes will be seen in the $F_2$ and in what proportions?
Answer:

\[
P: \quad A^d/A^d \quad \text{and} \quad a^D/a^D \\
F_1: \quad A^d/a^D \\
F_2: \quad 1 \quad A^d/A^d \quad \text{phenotype: } A^d \\
\quad 2 \quad A^d/a^D \quad \text{phenotype: } A^D \\
\quad 1 \quad a^D/a^D \quad \text{phenotype: } a^D
\]

14. The \( R \) and \( S \) loci are 35 m.u. apart. If a plant of genotype

\[
\begin{array}{c|c|c}
R & S \\
\hline
r & s
\end{array}
\]

is selfed, what progeny phenotypes will be seen and in what proportions?

Answer:

\[
P: \quad R/S \times r/s
\]

Gametes:
\[
\frac{1}{2} (1-0.35) \quad R\ S \\
\frac{1}{2} (1-0.35) \quad r\ s \\
\frac{1}{2} \ (0.35) \quad R\ s \\
\frac{1}{2} \ (0.35) \quad r\ S
\]

\[
F_1 \text{ genotypes: } 0.1056 \quad R\ S/R\ S \quad 0.1138\ r\ s/r\ s \\
\quad 0.1056 \quad r\ s/r\ s \quad 0.1138 \quad r\ s/R\ s \\
\quad 0.2113 \quad R\ S/r\ s \quad 0.0306 \quad R\ s/R\ s \\
\quad 0.1138 \quad R\ S/r\ s \quad 0.0306 \quad r\ S/r\ S \\
\quad 0.1138 \quad R\ S/r\ s \quad 0.0613 \quad R\ s/r\ S
\]

\[
F_1 \text{ phenotypes: } 0.6058 \quad R\ S \\
\quad 0.1056 \quad r\ s \\
\quad 0.1444 \quad R\ s \\
\quad 0.1444 \quad r\ S
\]

15. The cross \( E/E \cdot F/F \times e/e \cdot f/f \) is made, and the \( F_1 \) is then backcrossed with the recessive parent. The progeny genotypes are inferred from the phenotypes. The progeny genotypes, written as the gametic contributions of the heterozygous parent, are in the following proportions:

\[
\begin{align*}
E \cdot F & : 2/6 \\
E \cdot f & : 1/6 \\
e \cdot F & : 1/6 \\
e \cdot f & : 2/6
\end{align*}
\]

Explain these results.
Answer: The cross is $E/e \times F/f$. If independent assortment exists, the progeny should be in a 1:1:1:1 ratio, which is not observed. Therefore, there is linkage. $E/f$ and $e/F$ are recombinants equaling one-third of the progeny. The two genes are 33.3 map units (m.u.) apart.

$$RF = 100\% \times \frac{1}{3} = 33.3\%$$

16. A strain of *Neurospora* with the genotype $H \cdot I$ is crossed with a strain with the genotype $h \cdot i$. Half the progeny are $H \cdot I$, and the other half are $h \cdot i$. Explain how this outcome is possible.

Answer: Because only parental types are recovered, the two genes must be tightly linked and recombination must be very rare. Knowing how many progeny were looked at would give an indication of how close the genes are.

17. A female animal with genotype $A/a \cdot B/b$ is crossed with a double-recessive male ($a/a \cdot b/b$). Their progeny include 442 $A/a \cdot B/b$, 458 $a/a \cdot b/b$, 46 $A/a \cdot b/b$, and 54 $a/a \cdot B/b$. Explain these results.

Answer: The problem states that a female that is $A/a \cdot B/b$ is testcrossed. If the genes are unlinked, they should assort independently, and the four progeny classes should be present in roughly equal proportions. This is clearly not the case. The $A/a \cdot B/b$ and $a/a \cdot b/b$ classes (the parentals) are much more common than the $A/a \cdot b/b$ and $a/a \cdot B/b$ classes (the recombinants). The two genes are on the same chromosome and are 10 map units apart.

$$RF = 100\% \times \frac{46 + 54}{1000} = 10\%$$

18. If $A/A \cdot B/B$ is crossed with $a/a \cdot b/b$ and the $F_1$ is testcrossed, what percentage of the testcross progeny will be $a/a \cdot B/b$ if the two genes are (a) unlinked; (b) completely linked (no crossing over at all); (c) 10 m.u. apart; (d) 24 m.u. apart?

Answer: The cross is $A/A \cdot B/B \times a/a \cdot a/a$. The $F_1$ would be $A/a \cdot B/b$.

a. If the genes are unlinked, all four progeny classes from the testcross (including $a/a \cdot b/b$) would equal 25 percent.

b. With completely linked genes, the $F_1$ would produce only $A B$ and $a b$ gametes. Thus, there would be a 50 percent chance of having $a b/a b$ progeny from a testcross of this $F_1$. 
c. If the two genes are linked and 10 map units apart, 10 percent of the test-cross progeny should be recombinants. Since the F₁ is \(A\ B/a\ b\), \(a\ b\) is one of the parental classes (\(A\ B\) being the other) and it should equal 1/2 of the total parents or 45 percent.

d. 38 percent (see part c).

19. In a haploid organism, the \(C\) and \(D\) loci are 8 m.u. apart. From a cross \(C\ d\times c\ D\), give the proportion of each of the following progeny classes: (a) \(C\ D\); (b) \(c\ d\); (c) \(C\ d\); (d) all recombinants.

Answer: Meiosis is occurring in an organism that is \(C\ d/c\ D\), ultimately producing haploid spores. The parental genotypes are \(C\ d\) and \(c\ D\), in equal frequency. The recombinant types are \(C\ D\) and \(c\ d\), in equal frequency. Eight map units means 8 percent recombinants. Thus, \(C\ D\) and \(c\ d\) will each be present at a frequency of 4 percent, and \(C\ d\) and \(c\ D\) will each be present at a frequency of \((100\% - 8\%)/2 = 46\%\).

a. 4 percent  
b. 4 percent  
c. 46 percent  
d. 8 percent

20. A fruit fly of genotype \(B\ R/b\ r\) is testcrossed with \(b\ r/b\ r\). In 84 percent of the meioses, there are no chiasmata between the linked genes; in 16 percent of the meioses, there is one chiasma between the genes. What proportion of the progeny will be \(B\ r/b\ r\)?

Answer: To answer this question, you must realize that

(1) One chiasma involves two of the four chromatids of the homologous pair so if 16 percent of the meioses have one chiasma, it will lead to 8 percent recombinants observed in the progeny (one half of the chromosomes of such a meiosis are still parental), and

(2) Half of the recombinants will be \(B\ r\), so the correct answer is 4 percent.

21. A three-point testcross was made in corn. The results and a recombination analysis are shown in the display below, which is typical of three-point testcrosses (\(p\) = purple leaves, + = green; \(v\) = virus-resistant seedlings, + = sensitive; \(b\) = brown midriff to seed, + = plain). Study the display and answer parts \(a\) through \(e\).

\[
P \quad +/+ \cdot +/+ \cdot +/+ \times p/p \cdot v/v \cdot B/b
\]
Gametes $+ \cdot + \cdot + \quad p \cdot v \cdot b$

a. Determine which genes are linked.

b. Draw a map that shows distances in map units.

c. Calculate interference, if appropriate.

<table>
<thead>
<tr>
<th>Class</th>
<th>Progeny phenotypes</th>
<th>F$_1$ gametes</th>
<th>Numbers</th>
<th>$p–b$</th>
<th>$p–v$</th>
<th>$v–b$</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>gre sen pla</td>
<td>$+ \cdot + \cdot +$</td>
<td>3,210</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>pur res bro</td>
<td>$p \cdot v \cdot b$</td>
<td>3,222</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>gre res pla</td>
<td>$+ \cdot v \cdot +$</td>
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<td>R</td>
<td>R</td>
<td></td>
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<td>pur sen bro</td>
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<td>R</td>
<td>R</td>
<td></td>
</tr>
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<tr>
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<td>gre sen bro</td>
<td>$+ \cdot + \cdot b$</td>
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<td>R</td>
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<td>R</td>
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<td>R</td>
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<td></td>
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<td>Total</td>
<td></td>
<td>10,000</td>
<td>1,500</td>
<td>2,200</td>
<td>3,436</td>
</tr>
</tbody>
</table>

**Unpacking Problem 21**

1. Sketch cartoon drawings of the P, F$_1$, and tester corn plants, and use arrows to show exactly how you would perform this experiment. Show where seeds are obtained.

Answer: There is no correct drawing; any will do. Pollen from the tassels is placed on the silks of the females. The seeds are the F$_1$ corn kernels.

2. Why do all the +’s look the same, even for different genes? Why does this not cause confusion?

Answer: The +’s all look the same because they signify wild type for each gene. The information is given in a specific order, which prevents confusion, at least initially. However, as you work the problem, which may require you to reorder the genes, errors can creep into your work if you do not make sure that you reorder the genes for each genotype in exactly the same way. You may find it easier to write the complete genotype, $p^+$ instead of +, to avoid confusion.

3. How can a phenotype be purple and brown, for example, at the same time?

Answer: The phenotype is purple leaves and brown midriff to seeds. In other words, the two colors refer to different parts of the organism.
4. Is it significant that the genes are written in the order $p$-$v$-$b$ in the problem?

Answer: There is no significance in the original sequence of the data.

5. What is a tester and why is it used in this analysis?

Answer: A tester is a homozygous recessive for all genes being studied. It is used so that the meiotic products in the organism being tested can be seen directly in the phenotype of the progeny.

6. What does the column marked “Progeny phenotypes” represent? In class 1, for example, state exactly what “gre sen pla” means.

Answer: The progeny phenotypes allow you to infer the genotypes of the plants. For example, gre stands for “green,” the phenotype of $p^+/-$; sen stands for “virus-sensitive,” the phenotype of $v^+/-$; and pla stands for “plain seed,” the phenotype of $b^+/-$. In this testcross, all progeny have at least one recessive allele so the “gre sen pla” progeny are actually $p^+/p \cdot v^+/v \cdot b^+/b$.

7. What does the line marked “Gametes” represent, and how is it different from the column marked “F1 gametes”?

In what way is comparison of these two types of gametes relevant to recombination?

Answer: Gametes refers to the gametes of the two pure-breeding parents. $F_1$ gametes refers to the gametes produced by the completely heterozygous $F_1$ progeny. They indicate whether crossing-over or independent assortment have occurred. In this case, because there is either independent assortment or crossing-over, or both, the data indicate that the three genes are not so tightly linked that zero recombination occurred.

8. Which meiosis is the main focus of study? Label it on your drawing.

Answer: The main focus is meiosis occurring in the $F_1$ parent.

9. Why are the gametes from the tester not shown?

Answer: The gametes from the tester are not shown because they contribute nothing to the phenotypic differences seen in the progeny.

10. Why are there only eight phenotypic classes? Are there any classes missing?
Answer: Eight phenotypic classes are expected for three autosomal genes, whether or not they are linked, when all three genes have simple dominant-recessive relationships among their alleles. The general formula for the number of expected phenotypes is $2^n$, where $n$ is the number of genes being studied.

11. What classes (and in what proportions) would be expected if all the genes are on separate chromosomes?

Answer: If the three genes were on separate chromosomes, the expectation is a 1:1:1:1:1:1:1:1 ratio.

12. To what do the four pairs of class sizes (very big, two intermediates, very small) correspond?

Answer: The four classes of data correspond to the parentals (largest), two groups of single crossovers (intermediate), and double crossovers (smallest).

13. What can you tell about gene order simply by inspecting the phenotypic classes and their frequencies?

Answer: By comparing the parentals with the double crossovers, gene order can be determined. The gene in the middle flips with respect to the two flanking genes in the double-crossover progeny. In this case, one parental is +++ and one double crossover is p++. This indicates that the gene for leaf color ($p$) is in the middle.

14. What will be the expected phenotypic class distribution if only two genes are linked?

Answer: If only two of the three genes are linked, the data can still be grouped, but the grouping will differ from that mentioned in (12) above. In this situation, the unlinked gene will show independent assortment with the two linked genes. There will be one class composed of four phenotypes in approximately equal frequency, which combined will total more than half the progeny. A second class will be composed of four phenotypes in approximately equal frequency, and the combined total will be less than half the progeny. For example, if the cross were $a b/+ +; c/+ \times a b/a b; c/c$, then the parental class (more frequent class) would have four components: $a b c$, $a b +$, $+ + c$, and $+ + +$. The recombinant class would be $a + c$, $a + +$, $+ b c$, and $+ b +$. 
15. What does the word “point” refer to in a three-point testcross? Does this word usage imply linkage? What would a four-point testcross be like?

Answer: *Point* refers to locus. The usage does not imply linkage but rather a testing for possible linkage. A four-point testcross would look like the following: \(a/+ \cdot b/+ \cdot c/+ \cdot d/+ \times a/a \cdot b/b \cdot c/c \cdot d/d\).

16. What is the definition of *recombinant*, and how is it applied here?

Answer: A *recombinant* refers to an individual who has alleles inherited from two different grandparents, both of whom were the parents of the individual’s heterozygous parent. Another way to think about this term is that in the recombinant individual’s heterozygous parent, recombination took place among the genes that were inherited from his or her parents. In this case, the recombination took place in the F1, and the recombinants are among the F2 progeny.

17. What do the “Recombinant for” columns mean?

Answer: The “recombinant for” columns refer to specific gene pairs and progeny that exhibit recombination between those gene pairs.

18. Why are there only three “Recombinant for” columns?

Answer: There are three “recombinant for” columns because three genes can be grouped in three different gene pairs.

19. What do the *R*’s mean, and how are they determined?

Answer: *R* refers to recombinant progeny, and they contain different configurations of alleles than were present in their heterozygous parent.

20. What do the column totals signify? How are they used?

Answer: Column totals indicate the number of progeny that experience crossing-over between the specific gene pairs. They are used to calculate map units between the two genes.

21. What is the diagnostic test for linkage?
Answer: The diagnostic test for linkage is a recombination frequency of significantly less than 50 percent.

22. What is a map unit? Is it the same as a centimorgan?

Answer: A map unit represents 1 percent crossing over and is the same as a centimorgan.

23. In a three-point testcross such as this one, why aren’t the F₁ and the tester considered to be parental in calculating recombination? (They are parents in one sense.)

Answer: In the tester, recombination cannot be detected in the gamete contribution to the progeny because the tester is homozygous. The F₁ individuals have genotypes fixed by their parents’ homozygous state and, again, recombination cannot be detected in their phenotypes. Recombination between the P configurations occurs when the F₁ forms gametes and is detected in the phenotypes of the F₂ progeny.

24. What is the formula for interference? How are the “expected” frequencies calculated in the coefficient-of-coincidence formula?

Answer: Interference $I = 1 – \text{coefficient of coincidence} = 1 – (\text{observed double crossovers/expected double crossovers})$. The expected double crossovers are equal to the (frequency of crossing over in the first region, in this case between $v$ and $p$) $\times$ (frequency of crossing over in the second region, between $p$ and $b$) $\times$ number of progeny.

25. Why does part c of the problem say “if appropriate”?

Answer: If the three genes are not all linked, then interference cannot be calculated.

26. How much work is it to obtain such a large progeny size in corn? Which of the three genes would take the most work to score? Approximately how many progeny are represented by one corncob?

Answer: A great deal of work is required to obtain 10,000 progeny in corn because each seed on a cob represents one progeny. Each cob may contain as many as 200 seeds. While seed characteristics can be assessed at the cob stage, for other characteristics such as leaf color, viral sensitivity, and midriff color,
each seed must be planted separately and assessed after germination and growth. The bookkeeping task is also enormous.

**Solution to the Problem**

a. The three genes are linked.

b. Comparing the parentals (most frequent) with the double crossovers (least frequent), the gene order is \( v p b \). There were 2200 recombinants between \( v \) and \( p \), and 1500 between \( p \) and \( b \). The general formula for map units is:

\[
m.u. = \frac{100\% \text{ (number of recombinants)}}{\text{total number of progeny}}
\]

Therefore, the map units between \( v \) and \( p \) = \( \frac{100\% (2200)}{10,000} = 22 \) m.u., and the map units between \( p \) and \( b \) = \( \frac{100\% (1500)}{10,000} = 15 \) m.u.

The map is

\[
\begin{array}{ccc}
\text{\( v \)} & \text{\( p \)} & \text{\( b \)} \\
\hline
22 \text{ m.u.} & 15 \text{ m.u.}
\end{array}
\]

c. \( I = 1 - \frac{\text{observed double crossovers}}{\text{expected double crossovers}} \)

\[
= 1 - \frac{132}{(0.22)(0.15)(10,000)} \\
= 1 - 0.4 = 0.6
\]

22. You have a *Drosophila* line that is homozygous for autosomal recessive alleles \( a, b, \) and \( c \), linked in that order. You cross females of this line with males homozygous for the corresponding wild-type alleles. You then cross the F

\( 1 \) heterozygous males with their heterozygous sisters. You obtain the following F

\( 2 \) phenotypes (where letters de note recessive phenotypes and pluses denote wild-type phenotypes): 1364 + + +, 365 \( a b c \), 87 \( a b + \), 84 + + c, 47 \( a + + \), 44 + + c, 5 \( a + c \), and 4 + + b.

a. What is the recombinant frequency between \( a \) and \( b \)? Between \( b \) and \( c \)? 
(Remember, there is no crossing over in *Drosophila* males.)

b. What is the coefficient of coincidence?

Answer:

\[
P(a \ b \ c/a \ b \ c \times a^+ b^+ c^+/a^+ b^+ c^+)
\]

\[
F_1 a^+ b^+ c^+/a \ b \ c \times a^+ b^+ c^+/a \ b \ c
\]

\[
F_2 1364 a^+ b^+ c^+ \\
365 a b c \\
87 a b c^+ \\
84 a^+ b^+ c \\
47 a b^+ c^+ \\
44 a^+ b c
\]
This problem is somewhat simplified by the fact that recombination does not occur in male *Drosophila*. Also, only progeny that received the *a b c* chromosome from the male will be distinguishable among the F2 progeny.

**a.** Because you cannot distinguish between $a^+ b^+ c^+/a^+ b^+ c^+$ and $a^+ b^+ c^+/a b c$, use the frequency of $a b c/a b c$ to estimate the frequency of $a^+ b^+ c^+$ (parental) gametes from the female.

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Parents</strong></td>
<td>730</td>
<td>$2 \times 365$</td>
</tr>
<tr>
<td><strong>CO a–b:</strong></td>
<td>91</td>
<td>$(a b^+ c^+, a^+ b c = 47 + 44)$</td>
</tr>
<tr>
<td><strong>CO b–c:</strong></td>
<td>171</td>
<td>$(a b c^+, a^+ b^+ c = 87 + 84)$</td>
</tr>
<tr>
<td><strong>DCO:</strong></td>
<td>9</td>
<td>$(a^+ b c^+, a b c = 4 + 5)$</td>
</tr>
</tbody>
</table>

$a–b$: $100\%(91 + 9)/1001 = 10$ m.u.  
$b–c$: $100\%(171 + 9)/1001 = 18$ m.u.

**b.** Coefficient of coincidence = (observed DCO)/(expected DCO)  
$= 9/[(0.1)(0.18)(1001)] = 0.5$

23. R. A. Emerson crossed two different pure-breeding lines of corn and obtained a phenotypically wild-type F1 that was heterozygous for three alleles that determine recessive phenotypes: *an* determines anther; *br*, brachytic; and *f*, fine. He testcrossed the F1 with a tester that was homozygous recessive for the three genes and obtained these progeny phenotypes: 355 anther; 339 brachytic, fine; 88 completely wild type; 55 anther, brachytic, fine; 21 fine; 17 anther, brachytic; 2 brachytic; 2 anther, fine.

**a.** What were the genotypes of the parental lines?  
**b.** Draw a linkage map for the three genes (include map distances).  
**c.** Calculate the interference value.

**Answer:**  
**a.** By comparing the two most frequent classes (parentals: *an* *br* $^+ f^+$, *an* $^+$ *br* *f*)  
to the least frequent classes (DCO: *an* $^+$ *br* $^+ f^+$, *an* *br* $^+ f$), the gene order can  
be determined. The gene in the middle switches with respect to the other  
two (the order is *an* $f$ *br*). Now the crosses can be written fully.

\[
\begin{align*}
\text{P} & \quad \text{an} \ f^+ \ br^+ / \text{an} \ f^+ \ br^+ \times \text{an}^+ \ f \ br / \text{an}^+ \ f \ br \\
\text{F}_1 & \quad \text{an}^+ \ f \ br / \text{an} \ f^+ \ br^+ \times \text{an} \ f \ br / \text{an} \ f \ br \\
\text{F}_2 & \quad 355 \quad \text{an} \ f^+ \ br^+ / \text{an} \ f \ br \quad \text{parental}
\end{align*}
\]
Chapter Four

<p>| | | | |</p>
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<tr>
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</thead>
<tbody>
<tr>
<td></td>
<td>339</td>
<td>$an^+ f\ br/an\ f\ br$</td>
<td>parental</td>
</tr>
<tr>
<td></td>
<td>88</td>
<td>$an^+ f^+\ br^+ /an\ f\ br$</td>
<td>CO $an–f$</td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>$an\ f\ br/an\ f\ br$</td>
<td>CO $an–f$</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>$an^+ f\ br^+ /an\ f\ br$</td>
<td>CO $f–br$</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>$an\ f^+\ br/an\ f\ br$</td>
<td>CO $f–br$</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>$an^+ f^+\ br/an\ f\ br$</td>
<td>DCO</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>$an\ f\ br^+ /an\ f\ br$</td>
<td>DCO</td>
</tr>
<tr>
<td></td>
<td>879</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

b. $an–f$: 100% $(88 + 55 + 2 + 2)/879 = 16.72$ m.u.
$f–br$: 100% $(21 + 17 + 2 + 2)/879 = 4.78$ m.u.

\[
\begin{array}{c|c|c}
\text{an} & \text{f} & \text{br} \\
\hline
16.72 \text{ m.u.} & & 4.78 \text{ m.u.}
\end{array}
\]

c. Interference = $1 – (\text{observed DCO/expected DCO})$
\[= 1 – 4/(0.1672)(0.0478)(879) = 0.431\]

24. Chromosome 3 of corn carries three loci ($b$ for plant-color booster, $v$ for virescent, and $lg$ for liguleless). A testcross of triple recessives with $F_1$ plants heterozygous for the three genes yields progeny having the following genotypes: $305 + v\ lg$, $275 b + +$, $128 b + lg$, $112 + v +$, $74 + + lg$, $66 b\ v +$, $22 + +$, and $18 b\ v\ lg$. Give the gene sequence on the chromosome, the map distances between genes, and the coefficient of coincidence.

Answer: By comparing the most frequent classes (parental: $+ v\ lg$, $b + +$) with the least frequent classes (DCO: $+ + +$, $b\ v\ lg$) the gene order can be determined. The gene in the middle switches with respect to the other two, yielding the following sequence: $v\ b\ lg$. Now the cross can be written:

\[
P \quad v\ b^+ lg/v\ b^+ lg \times v\ b\ lg/v\ b\ lg
\]

\[
\begin{array}{r|l}
\text{P} & \\
\hline
\text{F}_1 & 305 & v\ b^+ lg/v\ b^+ lg \text{ parental} \\
 & 275 & v^+ b\ lg/v\ b^+ lg \text{ parental} \\
 & 128 & v\ b\ lg/v\ b\ lg \text{ CO} b–lg \\
 & 112 & v\ b^+\ lg^+/v\ b\ lg \text{ CO} b–lg \\
 & 74 & v^+ b^+\ lg/v\ b\ lg \text{ CO} v–b \\
 & 66 & v\ b\ lg^+/v\ b\ lg \text{ CO} v–b \\
 & 22 & v^+ b^+\ lg^+/v\ b\ lg \text{ DCO} \\
 & 18 & v\ b\ lg/v\ b\ lg \text{ DCO}
\end{array}
\]

$v–b$: 100%(74 + 66 + 22 + 18)/1000 = 18.0 m.u.

$b–lg$: 100%(128 + 112 + 22 + 18)/1000 = 28.0 m.u.

\[
c.c. = \text{observed DCO/expected DCO} = (22 + 18)/(0.28)(0.18)(1000) = 0.79
\]
25. Groodies are useful (but fictional) haploid organisms that are pure genetic tools. A wild-type groody has a fat body, a long tail, and flagella. Mutant lines are known that have thin bodies, are tailless, or do not have flagella. Groodies can mate with one another (although they are so shy that we do not know how) and produce recombinants. A wild-type groody mates with a thin-bodied groody lacking both tail and flagella. The 1000 baby groodies produced are classified as shown in the illustration here. Assign genotypes, and map the three genes. (Problem 25 is from Burton S. Guttman.)

Answer: Let $F =$ fat, $L =$ long tail, and $Fl =$ flagella. The gene sequence is $FLFl$ (compare most frequent with least frequent). The cross is:

$$P \quad FLFl/flfl \times flfl/flfl$$

<table>
<thead>
<tr>
<th>F1</th>
<th>398</th>
<th>FLFl/flfl</th>
<th>parental</th>
</tr>
</thead>
<tbody>
<tr>
<td>370</td>
<td>flfl/flfl</td>
<td>parental</td>
<td></td>
</tr>
<tr>
<td>72</td>
<td>FLfl/flfl</td>
<td>CO $L$–$Fl$</td>
<td></td>
</tr>
<tr>
<td>67</td>
<td>flFL/flfl</td>
<td>CO $L$–$Fl$</td>
<td></td>
</tr>
<tr>
<td>44</td>
<td>FL FL/flfl</td>
<td>CO $F$–$L$</td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>F l fl/f l fl</td>
<td>CO $F$–$L$</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>fl FL/flfl</td>
<td>DCO</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>FL fl/f l fl</td>
<td>DCO</td>
<td></td>
</tr>
</tbody>
</table>

$L$–$Fl$: $100\%(72 + 67 + 9 + 5)/1000 = 15.3$ m.u.

$F$–$L$: $100\%(44 + 35 + 9 + 5)/1000 = 9.3$ m.u.

$$\begin{array}{ccc}
F & L & Fl \\
9.3 \text{ m.u.} & 15.3 \text{ m.u.} & \\
\end{array}$$

26. In *Drosophila*, the allele $dp^+$ determines long wings and $dp$ determines short ("dumpy") wings. At a separate locus, $e^+$ determines gray body and $e$
determines ebony body. Both loci are autosomal. The following crosses were made, starting with pure-breeding parents:

\[
P \quad \text{long, ebony } \hat{\alpha} \times \text{short, gray } \delta
\]

\[
F_1 \quad \text{long, gray } \hat{\alpha} \times \text{short, ebony } \delta \text{ (pure)}
\]

\[
F_2 \quad \begin{array}{l}
\text{long, ebony} \quad 54 \\
\text{long, gray} \quad 47 \\
\text{short, gray} \quad 52 \\
\text{short, ebony} \quad 47 \\
\end{array}
\]

Use the \( \chi^2 \) test to determine if these loci are linked. In doing so, indicate (a) the hypothesis, (b) calculation of \( \chi^2 \), (c) \( p \) value, (d) what the \( p \) value means, (e) your conclusion, (f) the inferred chromosomal constitutions of parents, \( F_1 \), tester, and progeny.

Answer:

a. The hypothesis is that the genes are not linked. Therefore, a 1:1:1:1 ratio is expected.

\[
\chi^2 = \frac{(54-50)^2}{50} + \frac{(47-50)^2}{50} + \frac{(52-50)^2}{50} + \frac{(47-50)^2}{50} \\
= 0.32 + 0.18 + 0.08 + 0.18 = 0.76
\]

c. With three degrees of freedom, the \( p \) value is between 0.50 and 0.90.

d. Between 50 percent and 90 percent of the time values this extreme from the prediction would be obtained by chance alone.

e. Accept the initial hypothesis.

f. Because the \( \chi^2 \) value was insignificant, we conclude the two genes are assorting independently. The genotypes of all individuals are

\[
P \quad dp^+/dp^+ ; e/e \times dp/dp ; e^+/e^+
\]

\[
F_1 \quad dp^+/dp ; e^+/e
\]

tester \quad dp/dp ; e/e

progeny \quad \begin{array}{l}
\text{long, ebony} \quad dp^+/dp ; e/e \\
\text{long, gray} \quad dp^+/dp ; e^+/e \\
\text{short, gray} \quad dp/dp ; e^+/e \\
\text{short, ebony} \quad dp/dp ; e/e \\
\end{array}
27. The mother of a family with 10 children has blood type Rh⁺. She also has a very rare condition (elliptocytosis, phenotype E) that causes red blood cells to be oval rather than round in shape but that produces no adverse clinical effects. The father is Rh⁻ (lacks the Rh⁺ antigen) and has normal red blood cells (phenotype e). The children are 1 Rh⁺ e, 4 Rh⁺ E, and 5 Rh⁻ e. Information is available on the mother’s parents, who are Rh⁺ E and Rh⁻ e. One of the 10 children (who is Rh⁺ E) marries someone who is Rh⁺ e, and they have an Rh⁺ E child.

   a. Draw the pedigree of this whole family.
   b. Is the pedigree in agreement with the hypothesis that the Rh⁺ allele is dominant and Rh⁻ is recessive?
   c. What is the mechanism of transmission of elliptocytosis?
   d. Could the genes governing the E and Rh phenotypes be on the same chromosome? If so, estimate the map distance between them, and comment on your result.

   Answer:
   a. 
   
   b. Yes
   c. Dominant
   d. As drawn, the pedigree hints at linkage. If unlinked, expect that the phenotypes of the 10 children should be in a 1:1:1:1 ratio of Rh⁺ E, Rh⁻ e, Rh⁻ E, and Rh⁺ e. There are actually five Rh⁻ e, four Rh⁺ E, and one Rh⁺ e. If linked, this last phenotype would represent a recombinant, and the distance between the two genes would be 100% (1/10) = 10 m.u. However, there is just not enough data to strongly support that conclusion.

28. From several crosses of the general type A/A · B/B × a/a · B/b the F₁ individuals of type A/a · B/b were testcrossed with a/a · B/b. The results are as follows:


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Testcross progeny

<table>
<thead>
<tr>
<th>Testcross of F\textsubscript{1} from cross</th>
<th>A/a \cdot B/b</th>
<th>a/a \cdot B/b</th>
<th>A/a \cdot B/b</th>
<th>a/a \cdot B/b</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>310</td>
<td>315</td>
<td>287</td>
<td>288</td>
</tr>
<tr>
<td>2</td>
<td>36</td>
<td>38</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>3</td>
<td>360</td>
<td>380</td>
<td>230</td>
<td>230</td>
</tr>
<tr>
<td>4</td>
<td>74</td>
<td>72</td>
<td>50</td>
<td>44</td>
</tr>
</tbody>
</table>

For each set of progeny, use the $\chi^2$ test to decide if there is evidence of linkage.

**Answer:** Assume there is no linkage. (This is your hypothesis. If it can be rejected, the genes are linked.) The expected values would be that genotypes occur with equal frequency. There are four genotypes in each case ($n = 4$) so there are 3 degrees of freedom.

\[
\chi^2 = \sum \frac{(\text{observed} - \text{expected})^2}{\text{expected}}
\]

Cross 1: \[\chi^2 = \frac{[(310-300)^2 + (315-300)^2 + (287-300)^2 + (288-300)^2]}{300} = 2.1266; p > 0.50, nonsignificant; hypothesis cannot be rejected\]

Cross 2: \[\chi^2 = \frac{[(36-30)^2 + (38-30)^2 + (23-30)^2 + (23-30)^2]}{30} = 6.6; p > 0.10, nonsignificant; hypothesis cannot be rejected\]

Cross 3: \[\chi^2 = \frac{[(360-300)^2 + (380-300)^2 + (230-300)^2 + (230-300)^2]}{300} = 66.0; p < 0.005, significant; hypothesis must be rejected\]

Cross 4: \[\chi^2 = \frac{[(74-60)^2 + (72-60)^2 + (50-60)^2 + (44-60)^2]}{60} = 11.60; p < 0.01, significant; hypothesis must be rejected\]

29. In the two pedigrees diagrammed here, a vertical bar in a symbol stands for steroid sulfatase deficiency, and a horizontal bar stands for ornithine transcarbamylase deficiency.
a. Is there any evidence in these pedigrees that the genes determining the deficiencies are linked?
b. If the genes are linked, is there any evidence in the pedigree of crossing over between them?
c. Draw genotypes of these individuals as far as possible.

Answer:

d. Both disorders must be recessive to yield the patterns of inheritance that are observed. Notice that only males are affected, strongly suggesting X linkage for both disorders. In the first pedigree, there is a 100 percent correlation between the presence or absence of both disorders, indicating close linkage. In the second pedigree, the presence and absence of both disorders are inversely correlated, again indicating linkage. In the first pedigree, the two defective alleles must be cis within the heterozygous females to show 100 percent linkage in the affected males, while in the second pedigree the two defective alleles must be trans within the heterozygous females.

d. and c. Let a stand for the allele giving rise to steroid sulfatase deficiency (vertical bar) and b stand for the allele giving rise to ornithine transcarbamylase deficiency (horizontal bar). Crossing over cannot be detected without attaching genotypes to the pedigrees. When this is done, it can be seen that crossing over need not occur in either of the pedigrees to give rise to the observations.

First pedigree:

```
  a b/Y  A B/-
   |       |
  A B/a b  A B/Y

  A B/Y  A B/a b  a b/Y  A B/-  a b/Y  A B/Y

  A B/Y  a b/Y  A B/Y  A B/Y
```
30. In the accompanying pedigree, the vertical lines stand for protan color blindness, and the horizontal lines stand for deutan color blindness. These are separate conditions causing different misperceptions of colors; each is determined by a separate gene.

a. Does the pedigree show any evidence that the genes are linked?

b. If there is linkage, does the pedigree show any evidence of crossing over? Explain your answers to parts a and b with the aid of the diagram.

c. Can you calculate a value for the recombination between these genes? Is this recombination by independent assortment or by crossing over?

Answer:

a. Note that only males are affected by both disorders. This suggests that both are X-linked recessive disorders. Using $p$ for protan and $P$ for non-protan, and $d$ for deutan and $D$ for non-deutan, the inferred genotypes are listed on the pedigree below. The Y chromosome is shown, but the X is represented by the alleles carried.

b. Individual II-2 must have inherited both disorders in the trans configuration (on separate chromosomes). Therefore, individual III-2 inherited both traits...
as the result of recombination (crossing over) between his mother’s X chromosomes.

c. Because both genes are X-linked, this represents crossing over. The progeny size is too small to give a reliable estimate of recombination.

31. In corn, a triple heterozygote was obtained carrying the mutant alleles \( s \) (shrunken), \( w \) (white aleurone), and \( y \) (waxy endosperm), all paired with their normal wild-type alleles. This triple heterozygote was testcrossed, and the progeny contained 116 shrunken, white; 4 fully wild type; 2538 shrunken; 601 shrunken, waxy; 626 white; 2708 white, waxy; 2 shrunken, white, waxy; and 113 waxy.

a. Determine if any of these three loci are linked and, if so, show map distances.

b. Show the allele arrangement on the chromosomes of the triple heterozygote used in the testcross.

c. Calculate interference, if appropriate.

Answer:

a. and b. Again, the best way to determine whether there is linkage is through chi-square analysis, which indicates that it is highly unlikely that the three genes assort independently. To determine linkage by simple inspection, look at gene pairs. Because this is a testcross, independent assortment predicts a 1:1:1:1 ratio.

Comparing shrunken and white, the frequencies are:
\[
\begin{align*}
+ + & \quad (113 + 4)/\text{total} \\
\text{s wh} & \quad (116 + 2)/\text{total} \\
+ \text{wh} & \quad (2708 + 626)/\text{total} \\
\text{s +} & \quad (2538 + 601)/\text{total}
\end{align*}
\]

There is not independent assortment between shrunken and white, which means that there is linkage.

Comparing shrunken and waxy, the frequencies are:
There is not independent assortment between shrunken and waxy, which means that there is linkage.

Comparing white and waxy, the frequencies are:

\[
\begin{align*}
\text{++} & \quad (2538 + 4)/\text{total} \\
\text{s\ wa} & \quad (601 + 2)/\text{total} \\
\text{+ wa} & \quad (2708 + 113)/\text{total} \\
\text{s\ +} & \quad (2538 + 116)/\text{total}
\end{align*}
\]

There is not independent assortment between waxy and white, which means that there is linkage.

Because all three genes are linked, the strains must be \( + s+/wh + wa \) and \( wh\ s\ wa/wh\ s\ wa \) (compare most frequent, parentals, to least frequent, double crossovers, to obtain the gene order). The cross can be written as:

\[
P \quad + s+/wh + wa \times wh\ s\ wa/wh\ s\ wa
\]

\( F_1 \) as in problem

Crossovers between white and shrunken and shrunken and waxy are:

\[
\begin{array}{cc}
113 & 601 \\
116 & 626 \\
4 & 4 \\
\frac{2}{235} & \frac{2}{1233}
\end{array}
\]

Dividing by the total number of progeny and multiplying by 100 percent yields the following map:

\[
\begin{array}{c|c|c}
\text{white} & \text{shrunken} & \text{waxy} \\
\hline
3.5 \text{ m.u.} & & 18.4 \text{ m.u.}
\end{array}
\]

c. Interference = 1 – (observed double crossovers/expected double crossovers)

\[
= 1 - \frac{6}{(0.035)(0.184)(6,708)} = 0.86
\]

32. a. A mouse cross \( A/a \cdot B/b \times a/a \cdot b/b \) is made, and in the progeny there are
25% \( A/a \cdot B/b \), 25% \( a/a \cdot b/b \), 25\% \( A/a \cdot b/b \), 25\% \( a/a \cdot B/b \)

Explain these proportions with the aid of simplified meiosis diagrams.

b. A mouse cross \( C/c \cdot D/d \times c/c \cdot d/d \) is made, and in the progeny there are

45\% \( C/c \cdot d/d \), 45\% \( c/c \cdot D/d \),
5\% \( c/c \cdot d/d \), 5\% \( C/c \cdot D/d \)

Explain these proportions with the aid of simplified meiosis diagrams.

Answer:
a. The results of this cross indicate independent assortment of the two genes. This might be diagrammed as
b. The results of this cross indicate that the two genes are linked and 10 m.u. apart. Further, the recessive alleles are in repulsion in the dihybrid \((C\,d/c\,D\times c\,d/c\,d)\). This might be diagrammed as

![Diagram](image)

33. In the tiny model plant *Arabidopsis*, the recessive allele *hyg* confers seed resistance to the drug hygromycin, and *her*, a recessive allele of a different gene, confers seed resistance to herbicide. A plant that was homozygous *hyg/hyg \cdot her/her* was crossed with wild type, and the *F_1* was selfed. Seeds resulting from the *F_1* self were placed on petri dishes containing hygromycin and herbicide.

a. If the two genes are unlinked, what percentage of seeds are expected to grow?
b. In fact, 13 percent of the seeds grew. Does this percentage support the hypothesis of no linkage? Explain. If not, calculate the number of map units between the loci.

c. Under your hypothesis, if the F₁ is testcrossed, what proportion of seeds will grow on the medium containing hygromycin and herbicide?

Answer:

a. If the genes are unlinked, the cross becomes:

\[
\begin{align*}
P & \quad \text{hyg/\text{hyg} ; her/\text{her} \times \text{hyg}^+/\text{hyg}^+ ; her^+/\text{her}^+} \\
F_1 & \quad \text{hyg}^+/\text{hyg} ; \text{her}^+/\text{her} \times \text{hyg}^+/\text{hyg} ; \text{her}^+/\text{her} \\
F_2 & \quad 9/16 \quad \text{hyg}^+/- ; \text{her}^+/- \\
& \quad 3/16 \quad \text{hyg}^+/- ; \text{her/\text{her}} \\
& \quad 3/16 \quad \text{hyg/\text{hyg} ; her}^+/- \\
& \quad 1/16 \quad \text{hyg/\text{hyg} ; her/\text{her}}
\end{align*}
\]

So only 1/16 (or 6.25 percent) of the seeds would be expected to germinate.

b. and c. No. More than twice the expected seeds germinated so assume the genes are linked. The cross then becomes:

\[
\begin{align*}
P & \quad \text{hyg her/\text{hyg her} \times \text{hyg}^+/\text{hyg}^+ \text{ her}^+/\text{her}^+} \\
F_1 & \quad \text{hyg}^+/\text{hyg her} \times \text{hyg}^+/\text{hyg her} \text{ her}^+/- \\
F_2 & \quad 13\% \quad \text{hyg her/\text{hyg her}}
\end{align*}
\]

Because this class represents the combination of two parental chromosomes, it is equal to:

\[p(\text{hyg her}) \times p(\text{hyg her}) = (1/2 \text{ parentals})^2 = 0.13\]

and

parentals = 0.72 \quad \text{so recombinants} = 1 – 0.72 = 0.28

Therefore, a testcross of \text{hyg}^+ \text{ her}^+/\text{hyg her} should give:

\[
\begin{align*}
36\% & \quad \text{hyg}^+/\text{hyg her} \\
36\% & \quad \text{hyg her/\text{hyg her}} \\
14\% & \quad \text{hyg}^+ \text{ her/\text{hyg her}} \\
14\% & \quad \text{hyg her}^+/\text{hyg her}
\end{align*}
\]

and 36 percent of the progeny should grow (the \text{hyg her/\text{hyg her}} class).
34. In a diploid organism of genotype $A/a \; B/b \; D/d$, the allele pairs are all on different chromosome pairs. The two diagrams in the next column purport to show anaphases ("pulling apart" stages) in individual cells. State whether each drawing represents mitosis, meiosis I, or meiosis II or is impossible for this particular genotype.
Answer:
a. Meiosis I (crossing-over has occurred between all genes and their centromeres.)

b. Impossible

c. Meiosis I (crossing-over has occurred between gene B and its centromere.)

d. Meiosis I

e. Meiosis II

f. Meiosis II (crossing-over has occurred between genes A and B and their centromeres.)

g. Meiosis II

h. Impossible

i. Mitosis

j. Impossible

35. The *Neurospora* cross al-2+ × al-2 is made. A linear tetrad analysis reveals that the second-division segregation frequency is 8 percent.

a. Draw two examples of second-division segregation patterns in this cross.
b. What can be calculated by using the 8 percent value?

Answer:
a. al-2+ al-2

b. The 8 percent value can be used to calculate the distance between the gene and the centromere. That distance is ½ the percentage of second-division segregation, or 4 percent.

36. From the fungal cross arg-6 ⊕ al-2 × arg-6+ ⊕ al-2+, what will the spore genotypes be in unordered tetrads that are (a) parental ditypes? (b) tetratypes? (c) nonparental ditypes?

Answer:
a. arg-6 · al-2, arg-6 · al-2, arg-6+ · al-2+, arg-6+ · al-2+

b. arg-6+ · al-2+, arg-6+ · al-2, arg-6 · al-2+, arg-6 · al-2
c. \( \text{arg-6}^+ \cdot \text{al-2}, \text{arg-6}^+ \cdot \text{al-2}, \text{arg-6} \cdot \text{al-2}^+, \text{arg-6} \cdot \text{al-2}^+ \)

37. For a certain chromosomal region, the mean number of crossovers at meiosis is calculated to be two per meiosis. In that region, what proportion of meioses are predicted to have (a) no crossovers? (b) one crossover? (c) two crossovers?

Answer: The formula for this problem is \( f(i) = e^{-mi/i!} \) where \( m = 2 \) and \( i = 0, 1, \) or 2.

a. \( f(0) = e^{-2^0/0!} = e^{-2} = 0.135 \) or 13.5%

b. \( f(1) = e^{-2^1/1!} = e^{-3}(2) = 0.27 \) or 27%

c. \( f(2) = e^{-2^2/2!} = e^{-3}(2) = 0.27 \) or 27%

38. A Neurospora cross was made between a strain that carried the mating-type allele \( A \) and the mutant allele \( \text{arg-1} \) and another strain that carried the mating-type allele \( a \) and the wild-type allele for \( \text{arg-1} (+) \). Four hundred linear octads were isolated, and they fell into the seven classes given in the table below. (For simplicity, they are shown as tetrads.)

a. Deduce the linkage arrangement of the mating-type locus and the \( \text{arg-1} \) locus. Include the centromere or centromeres on any map that you draw. Label all intervals in map units.

b. Diagram the meiotic divisions that led to class 6. Label clearly.

<table>
<thead>
<tr>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>( A \cdot \text{arg} )</td>
<td>( A \cdot + )</td>
<td>( A \cdot \text{arg} )</td>
<td>( A \cdot \text{arg} )</td>
<td>( A \cdot + )</td>
<td>( A \cdot + )</td>
<td></td>
</tr>
<tr>
<td>( A \cdot \text{arg} )</td>
<td>( A \cdot + )</td>
<td>( a \cdot \text{arg} )</td>
<td>( a \cdot + )</td>
<td>( a \cdot \text{arg} )</td>
<td>( a \cdot \text{arg} )</td>
<td></td>
</tr>
<tr>
<td>( a \cdot + )</td>
<td>( a \cdot \text{arg} )</td>
<td>( a \cdot \text{arg} )</td>
<td>( A \cdot + )</td>
<td>( A \cdot \text{arg} )</td>
<td>( A \cdot + )</td>
<td>( A \cdot \text{arg} )</td>
</tr>
<tr>
<td>( a \cdot + )</td>
<td>( a \cdot \text{arg} )</td>
<td>( a \cdot + )</td>
<td>( a \cdot + )</td>
<td>( a \cdot \text{arg} )</td>
<td>( a \cdot \text{arg} )</td>
<td></td>
</tr>
<tr>
<td>127</td>
<td>125</td>
<td>100</td>
<td>36</td>
<td>2</td>
<td>4</td>
<td>6</td>
</tr>
</tbody>
</table>

Unpacking Problem 38

1. Are fungi generally haploid or diploid?

Answer: Fungi are generally haploid.

2. How many ascospores are in the ascus of Neurospora? Does your answer match the number presented in this problem? Explain any discrepancy.

Answer: There are four pairs, or eight ascospores, in each ascus. One member of each pair is presented in the data.
3. What is mating type in fungi? How do you think it is determined experimentally?

Answer: A mating type in fungi is analogous to gender in humans, in that the mating types of two organisms must differ in order to have a mating that produces progeny. Mating type is determined experimentally simply by seeing if progeny result from specific crosses.

4. Do the symbols $A$ and $a$ have anything to do with dominance and recessiveness?

Answer: The mating types $A$ and $a$ do not indicate dominance and recessiveness. They simply symbolize the mating-type difference.

5. What does the symbol $arg-1$ mean? How would you test for this genotype?

Answer: $arg-1$ indicates that the organism requires arginine for growth. Testing for the genotype involves isolating nutritional mutants and then seeing if arginine supplementation will allow for growth.

6. How does the $arg-1$ symbol relate to the symbol $+$?

Answer: $arg-1^+$ indicates that the organism is wild type and does not require supplemental arginine for growth.

7. What does the expression wild type mean?

Answer: Wild type refers to the common form of an organism in its natural population.

8. What does the word mutant mean?

Answer: Mutant means that, for the trait being studied, an organism differs from the wild type.

9. Does the biological function of the alleles shown have anything to do with the solution of this problem?

Answer: The actual function of the alleles in this problem does not matter in solving the problem.
10. What does the expression *linear octad analysis* mean?

Answer: *Linear octad analysis* refers to the fact that the ascospores in each ascus are in a linear arrangement that reflects the order in which the two meiotic divisions and a subsequent mitotic division occurred to produce them. By tracking traits and correlating them with position, it is possible to detect crossing-over events that occurred at the tetrad (four-strand, homologous pairing) stage prior to the two meiotic divisions. Since the mitotic division occurs last, and mitotic sister spores are typically identical, the mitotic sisters may be treated as a pair of identical twins and are listed only once in the diagram, so the octad is treated as a tetrad.

11. In general, what more can be learned from linear tetrad analysis that cannot be learned from unordered tetrad analysis?

Answer: Linear tetrad analysis allows for the mapping of centromeres in relation to genes, which cannot be done with unordered tetrad analysis.

12. How is a cross made in a fungus such as *Neurospora*? Explain how to isolate asci and individual ascospores. How does the term *tetrad* relate to the terms *ascus* and *octad*?

Answer: A cross is made in *Neurospora* by placing the two organisms in the same test tube or Petri dish and allowing them to grow. Gametes develop and fertilization, followed by meiosis, mitosis, and ascus formation, occurs. The asci are isolated, and the ascospores are dissected out of them with the aid of a microscope. The ascus has an octad, or eight spores, within it, and the spores are arranged in four (tetrad) pairs.

13. Where does meiosis take place in the *Neurospora* life cycle? (Show it on a diagram of the life cycle.)

Answer: Meiosis occurs immediately following fertilization in *Neurospora.*
14. What does Problem 38 have to do with meiosis?

Answer: Meiosis produced the ascospores that were analyzed.

15. Can you write out the genotypes of the two parental strains?

Answer: The cross is $A \cdot \text{arg-1} \times a \cdot \text{arg-1}^+$. 

16. Why are only four genotypes shown in each class?

Answer: Although there are eight ascospores, they occur in pairs. Each pair represents one chromatid of the originally paired chromosomes. By convention, both members of a pair are represented by a single genotype.

17. Why are there only seven classes? How many ways have you learned for classifying tetrads generally? Which of these classifications can be applied to both linear and unordered tetrads? Can you apply these classifications to the tetrads in this problem? (Classify each class in as many ways as possible.) Can you think of more possibilities in this cross? If so, why are they not shown?

Answer: The seven classes represent the seven types of outcomes. The specific outcomes can be classified as follows:

<table>
<thead>
<tr>
<th>Class</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>outcome</td>
<td>PD</td>
<td>NPD</td>
<td>T</td>
<td>T</td>
<td>PD</td>
<td>NPD</td>
<td>T</td>
</tr>
<tr>
<td>$A/a$</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>II</td>
<td>II</td>
<td>II</td>
</tr>
<tr>
<td>$\text{arg-1}^+/\text{arg-1}$</td>
<td>I</td>
<td>I</td>
<td>II</td>
<td>I</td>
<td>I</td>
<td>II</td>
<td>II</td>
</tr>
</tbody>
</table>
where PD = parental ditype, NPD = nonparental ditype, T = tetratype, I = first-division segregation, and II = second-division segregation.

Other classes can be detected, but they indicate the same underlying process. For example, the following three asci are equivalent:

```
1     2     3
A arg A arg A arg
A arg A arg A arg
a arg a arg a arg
a arg a arg a arg
```

In the first ascus, a crossover occurred between chromatids 2 and 3, while in the second ascus it occurred between chromatids 1 and 3, and in the third ascus the crossover was between chromatids 1 and 4. A fourth equivalent ascus would contain a crossover between chromatids 2 and 3. All four indicate a crossover between the second gene and its centromere and all are tetratypes.

18. Do you think there are several different spore orders within each class? Why would these different spore orders not change the class?

Answer: This is exemplified in the answer to (17) above.

19. Why is the following class not listed?

```
a +
a +
A · arg
A · arg
```

Answer: The class is identical with class 1 in the problem, but inverted. These are included in class 1 in the table.

20. What does the expression linkage arrangement mean?

Answer: Linkage arrangement refers to the relative positions of the two genes and the centromere along the length of the chromosome.

21. What is a genetic interval?

Answer: A genetic interval refers to the region between two loci, whose size is measured in map units.
22. Why does the problem state “centromere or centromeres” and not just “centromere”? What is the general method for mapping centromeres in tetrad analysis?

Answer: The problem does not specify whether the two loci are on separate chromosomes or are on the same chromosome. The general formula for calculating the distance of a locus to its centromere is to measure the percentage of tetrads that show second-division segregation patterns for that locus and divide by two. You are supposed to determine whether the genes share a common centromere or are associated with different centromeres.

23. What is the total frequency of $A^\oplus +$ ascospores? (Did you calculate this frequency by using a formula or by inspection? Is this a recombinant genotype? If so, is it the only recombinant genotype?)

Answer: Recall that there are eight ascospores per ascus. By inspection, the frequency of recombinant $A \, arg-1^+$ ascospores is $4(125) + 2(100) + 2(36) + 4(4) + 2(6) = 800$. There is also the reciprocal recombinant genotype $a \, arg-1$.

24. The first two classes are the most common and are approximately equal in frequency. What does this information tell you? What is their content of parental and recombinant genotypes?

Answer: Class 1 is parental; class 2 is nonparental ditype. Because they occur at equal frequencies, the two genes are not linked.

**Solution to the Problem**

a. The cross is $A \cdot arg-1 \times a \cdot arg-1^+$. Use the classification of asc in part (17) above. First, decide if the two genes are linked by using the formula $PD >> NPD$, when the genes are linked, while $PD = NPD$ when they are not linked. $PD = 127 + 2 = 129$ and $NPD = 125 + 4 = 129$, which means that the two genes are not linked. Alternatively,

$$RF = 100\% \frac{(1/2T + NPD)}{total \, asci}$$

$$= 100\% \left[\frac{(1/2)(100 + 36 + 6) + (125 + 4)}{400}\right] = 50\%.$$

Next, calculate the distance between each gene and its centromere using the formula $RF = 100\%(1/2 \, number \, of \, tetrads \, exhibiting \, MII \, segregation)/(total \, number \, of \, asci)$:

$$A-cenotromere = 100\% \frac{(1/2)(36 + 2 + 4 + 6)}{400}$$
= 100%(24/400) = 6 m.u.

\[ \text{arg}^+ - \text{centromere} = 100\% \left( \frac{1}{2} \left( 100 + 2 + 4 + 6 \right) \right) / 400 \]

= 100%(56/400) = 14 m.u.

b. Class 6 can be obtained if a single crossover occurred between chromatids 2 and 3 between each gene and its centromere.

39. A geneticist studies 11 different pairs of *Neurospora* loci by making crosses of the type \( a \cdot b \times a^+ \cdot b^+ \) and then analyzing 100 linear asci from each cross. For the convenience of making a table, the geneticist organizes the data as if all 11 pairs of genes had the same designation—\( a \) and \( b \)—as shown below. For each cross, map the loci in relation to each other and to centromeres.

<table>
<thead>
<tr>
<th>Cross</th>
<th>( a \cdot b )</th>
<th>( a \cdot b^+ )</th>
<th>( a^+ \cdot b )</th>
<th>( a^+ \cdot b^+ )</th>
<th>( a \cdot b )</th>
<th>( a^+ \cdot b )</th>
<th>( a \cdot b^+ )</th>
<th>( a^+ \cdot b^+ )</th>
<th>( a \cdot b )</th>
<th>( a^+ \cdot b )</th>
<th>( a \cdot b^+ )</th>
<th>( a^+ \cdot b^+ )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>34</td>
<td>34</td>
<td>32</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>84</td>
<td>1</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>55</td>
<td>3</td>
<td>40</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>71</td>
<td>1</td>
<td>18</td>
<td>1</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>9</td>
<td>6</td>
<td>24</td>
<td>22</td>
<td>8</td>
<td>10</td>
<td>20</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>31</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>61</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>95</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>6</td>
<td>7</td>
<td>20</td>
<td>22</td>
<td>12</td>
<td>11</td>
<td>22</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>69</td>
<td>0</td>
<td>10</td>
<td>18</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>16</td>
<td>14</td>
<td>2</td>
<td>60</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td>51</td>
<td>49</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Answer: Before beginning this problem, classify all asci as PD, NPD, or T and determine whether there is M_I or M_{II} segregation for each gene:

<table>
<thead>
<tr>
<th>Asci type</th>
<th>type</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>gene a</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>II</td>
<td>II</td>
<td>PD</td>
<td>NPD</td>
</tr>
<tr>
<td>gene b</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>II</td>
<td>II</td>
<td>II</td>
<td>II</td>
<td>II</td>
</tr>
</tbody>
</table>

If PD >> NPD, linkage is indicated. The distance between a gene and its centromere = 100% (1/2)(MII)/total. The distance between two genes = 100% (1/2T + NPD)/total.

Cross 1: PD = NPD and RF = 50%; the genes are not linked.
- \(a\)-centromere: 100% \((1/2)(0)/100 = 0\) m.u. Gene \(a\) is close to the centromere.
- \(b\)-centromere: 100% \((1/2)(32)/100 = 16\) m.u.

Cross 2: PD >> NPD; the genes are linked.
- \(a\)-\(b\): 100% \([1/2(15) + 1]/100 = 8.5\) m.u.
- \(a\)-centromere: 100% \((1/2)(0)/100 = 0\) m.u. Gene \(a\) is close to the centromere.
- \(b\)-centromere: 100% \((1/2)(15)/100 = 7.5\) m.u.

Cross 3: PD >> NPD; the genes are linked.
- \(a\)-\(b\): 100% \([1/2(40) + 3]/100 = 23\) m.u.
- \(a\)-centromere: 100% \((1/2)(2)/100 = 1\) m.u.
- \(b\)-centromere: 100% \((1/2)(40 + 2)/100 = 21\) m.u.

Cross 4: PD >> NPD; the genes are linked.
- \(a\)-\(b\): 100% \([1/2(20) + 1]/100 = 11\) m.u.
- \(a\)-centromere: 100% \((1/2)(10)/100 = 5\) m.u.
- \(b\)-centromere: 100% \((1/2)(18 + 8 + 1)/100 = 13.5\) m.u.

Cross 5: PD = NPD (and RF = 49%); the genes are not linked.
- \(a\)-centromere: 100% \((1/2)(22 + 8 + 10 + 20)/99 = 30.3\) m.u.
- \(b\)-centromere: 100% \((1/2)(24 + 8 + 10 + 20)/99 = 31.3\) m.u.

These values are approaching the 67 percent theoretical limit of loci exhibiting M_{II} patterns of segregation and should be considered cautiously.

Cross 6: PD >> NPD; the genes are linked.
- \(a\)-\(b\): 100% \([1/2(1 + 3 + 4) + 0]/100 = 4\) m.u.
- \(a\)-centromere: 100% \((1/2)(3 + 61 + 4)/100 = 34\) m.u.
- \(b\)-centromere: 100% \((1/2)(1 + 61 + 4)/100 = 33\) m.u.
These values are at the 67 percent theoretical limit of loci exhibiting $M_2$ patterns of segregation, and therefore, both loci can be considered unlinked to the centromere.

Cross 7: PD >> NPD; the genes are linked.
\[
a–b: 100% \left\{ \frac{1}{2}(3 + 2) + 0 \right\}/100 = 2.5 \text{ m.u.}
\]
\[
a–\text{centromere}: 100% \left\{ \frac{1}{2}(2) \right\}/100 = 1 \text{ m.u.}
\]
\[
b–\text{centromere}: 100% \left\{ \frac{1}{2}(3) \right\}/100 = 1.5 \text{ m.u.}
\]

Cross 8: PD = NPD; the genes are not linked.
\[
a–\text{centromere}: 100% \left\{ \frac{1}{2}(22 + 12 + 11 + 22) \right\}/100 = 33.5 \text{ m.u.}
\]
\[
b–\text{centromere}: 100% \left\{ \frac{1}{2}(20 + 12 + 11 + 22) \right\}/100 = 32.5 \text{ m.u.}
\]
Same as cross 5.

Cross 9: PD >> NPD; the genes are linked.
\[
a–b: 100% \left\{ \frac{1}{2}(10 + 18 + 2) + 1 \right\}/100 = 16 \text{ m.u.}
\]
\[
a–\text{centromere}: 100% \left\{ \frac{1}{2}(18 + 1 + 2) \right\}/100 = 10.5 \text{ m.u.}
\]
\[
b–\text{centromere}: 100% \left\{ \frac{1}{2}(10 + 1 + 2) \right\}/100 = 6.5 \text{ m.u.}
\]

Cross 10: PD = NPD; the genes are not linked.
\[
a–\text{centromere}: 100% \left\{ \frac{1}{2}(60 + 1 + 2 + 5) \right\}/100 = 34 \text{ m.u.}
\]
\[
b–\text{centromere}: 100% \left\{ \frac{1}{2}(2 + 1 + 2 + 5) \right\}/100 = 5 \text{ m.u.}
\]

Cross 11: PD = NPD; the genes are not linked.
\[
a–\text{centromere}: 100% \left\{ \frac{1}{2}(0) \right\}/100 = 0 \text{ m.u.}
\]
\[
b–\text{centromere}: 100% \left\{ \frac{1}{2}(0) \right\}/100 = 0 \text{ m.u.}
\]

40. Three different crosses in *Neurospora* are analyzed on the basis of unordered tetrads. Each cross combines a different pair of linked genes. The results are shown in the following table:

<table>
<thead>
<tr>
<th>Cross</th>
<th>Parents (%)</th>
<th>Parental ditypes (%)</th>
<th>Tetra- types (%)</th>
<th>Non-parental ditypes (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>a · b⁺ × a⁺ · b</td>
<td>51</td>
<td>45</td>
<td>4</td>
</tr>
<tr>
<td>2</td>
<td>c⁺ · d⁺ × c⁺⁺ · d⁺</td>
<td>64</td>
<td>34</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>e⁺ · f⁺ × e⁺⁺ · f⁺</td>
<td>45</td>
<td>50</td>
<td>5</td>
</tr>
</tbody>
</table>
For each cross, calculate:

a. the frequency of recombinants (RF).
b. the uncorrected map distance, based on RF.
c. the corrected map distance, based on tetrad frequencies.
d. the corrected map distance, based on the mapping function.

Answer: The number of recombinants is equal to NPD + 1/2T. The uncorrected map distance is based on RF = (NPD + ½T)/total. The corrected map distance, based on the Perkins formula, is RF = 50(T + 6NPD)/total. The formula for the Haldane mapping function is RF = ½(1 – e⁻ᵐ). To convert to map distance, m, the measure of crossover frequency is multiplied by 50 percent to give the corrected map distance.

Cross 1:
recombinant frequency  = 4% + ½ (45%) = 26.5%
uncorrected map distance  = [4% + ½ (45%)]/100% = 26.5 m.u.
corrected map distance, Perkins’ formula = 50[45% + 6(4%)]/100% = 34.5 m.u.

The formula for the Haldane mapping function is RF = ½(1 – e⁻ᵐ). Solving for this situation, e⁻ᵐ = 1 – (2 × 0.265) = 0.47 so m = 0.755. To convert to map distance, m, the measure of crossover frequency is multiplied by 50 percent to give a corrected map distance of 37.8%.

Cross 2:
recombinant frequency  = 2% + 1/2(34%) = 19%
uncorrected map distance  = [2% + 1/2(34%)]/100% = 19 m.u.
corrected map distance, using mapping function = 23 m.u.

Cross 3:
recombinant frequency  = 5% + ½ (50%) = 30%
uncorrected map distance  = [5% + ½ (50%)]/100% = 30 m.u.
corrected map distance, using mapping function = 45.8 m.u.

41. On Neurospora chromosome 4, the leu3 gene is just to the left of the centromere and always segregates at the first division, whereas the cys2 gene is to the right of the centromere and shows a second-division segregation frequency of 16 percent. In a cross between a leu3 strain and a cys2 strain, calculate the predicted frequencies of the following seven classes of linear tetrads where \( l = \text{leu3} \) and \( c = \text{cys2} \). (Ignore double and other multiple crossovers.)
Answer: The *leu3* gene is centromere-linked and always segregates at the first division (M₁ patterns). The *cys2* gene is at a distance from its centromere and recombination between these respective locations will result in a second-division segregation (M₂) pattern. For this, there are four patterns of spores, all equally likely:

<table>
<thead>
<tr>
<th>(i) l +</th>
<th>(ii) l +</th>
<th>(iii) l c</th>
<th>(iv) l c</th>
<th>(v) l c</th>
<th>(vi) l +</th>
<th>(vii) l +</th>
</tr>
</thead>
<tbody>
<tr>
<td>l c</td>
<td>l +</td>
<td>l +</td>
<td>+ c</td>
<td>+ +</td>
<td>+ c</td>
<td>+ c</td>
</tr>
<tr>
<td>+ +</td>
<td>+ c</td>
<td>+ +</td>
<td>++</td>
<td>+ c</td>
<td>+ +</td>
<td></td>
</tr>
<tr>
<td>+ +</td>
<td>+ c</td>
<td>++</td>
<td>+ c</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+ c</td>
<td>l +</td>
<td>l c</td>
<td>l +</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

If recombination between the centromere and *cys2* does not occur, then the alleles will show first-division segregation (M₁).

i. Given the cross *leu3 + × + cys2*, this tetrad is classified as a nonparental ditype. For linked genes, NPDs are the result of double crossover events, and since you are told to ignore multiple crossovers, the expected frequency for this would be 0 percent.

ii. This tetrad is a parental ditype (PD). Due to random alignment and segregation during meiosis I, two linear tetrads, both classified as PD, are equally likely:

\[
\begin{array}{ccc}
\text{cys} & \text{cys} & + \\
+ & + & \text{cys} & \text{cys} \\
\text{cys} & + & + & \text{cys} \\
+ & \text{cys} & \text{cys} & +
\end{array}
\]

Therefore, you would expect 100 percent (M₁ segregation of *leu3*) × 84 percent (M₁ segregation of *cys2* `½) = 42 percent of this class of tetrad.

iii. This tetrad is a tetratype (T). It shows one of the two M₁ patterns for *leu3* and one of the four M₂ patterns for *cys2*. You expect 50 percent × 16/4 percent = 2 percent of this class of tetrad.

iv. – vii. 0 percent. In all these tetrads, *leu3* is shown to have a second-division segregation pattern, and you are told that it always segregates at the first division.

42. A rice breeder obtained a triple heterozygote carrying the three recessive alleles for albino flowers (*al*), brown awns (*b*), and fuzzy leaves (*fu*), all paired with
their normal wild-type alleles. This triple heterozygote was testcrossed. The progeny phenotypes were

170 wild type
150 albino, brown, fuzzy
5 brown
3 albino, fuzzy
710 albino
698 brown, fuzzy
42 fuzzy
38 albino, brown

a. Are any of the genes linked? If so, draw a map labeled with map distances. (Don’t bother with a correction for multiple crossovers.)
b. The triple heterozygote was originally made by crossing two pure lines. What were their genotypes?

Answer:
a. Yes, the data indicate that the three genes are linked. The most common classes of progeny, albino \((al^+ fu^+ b^+\) and brown, fuzzy \((al^+ b fu^+)\) represent the “parental” chromosomes. (Gene order is not specified.) The least common classes of progeny, brown \((al^+ b fu^+)\) and albino, fuzzy \((al^+ b fu^+)\) represent the outcomes of double crossover events and can be used to deduce gene order. In comparing the most common to the least common, the gene “in the middle” can be determined to be \(fu^+\). (Compare \(al^+ b fu^+\) to \(al^+ b fu^+\) and \(al^+ b fu^+\) to \(al^+ b fu^+\).) To calculate map distances, you must now determine the various recombinant classes.

<table>
<thead>
<tr>
<th>Progeny</th>
<th>(al^- fu^-)</th>
<th>(fu^- b^-)</th>
</tr>
</thead>
<tbody>
<tr>
<td>710</td>
<td>(al fu^+ b^+)</td>
<td>P P</td>
</tr>
<tr>
<td>698</td>
<td>(al^- fu b)</td>
<td>P P</td>
</tr>
<tr>
<td>170</td>
<td>(al^- fu^+ b^+)</td>
<td>R P</td>
</tr>
<tr>
<td>150</td>
<td>(al fu b)</td>
<td>R P</td>
</tr>
<tr>
<td>42</td>
<td>(al^- fu b^+)</td>
<td>P R</td>
</tr>
<tr>
<td>38</td>
<td>(al^- fu^+ b)</td>
<td>R R</td>
</tr>
<tr>
<td>5</td>
<td>(al^- fu b^+)</td>
<td>R R</td>
</tr>
<tr>
<td>3</td>
<td>(al^- fu b^+)</td>
<td>R R</td>
</tr>
</tbody>
</table>

So there are \(170 + 150 + 5 + 3 = 328\) recombinants between \(al\) and \(fu\) for a map distance of \((328/progeny) \times 100\% = 18.1\) m.u. and \(42 + 38 + 5 + 3 = 88\) recombinants between \(fu\) and \(b\) for a map distance of \(4.8\) m.u.

\[
\begin{array}{ccc}
\text{al} & \text{fu} & \text{b} \\
\hline
& & \\
18.1 \text{ cM} & 4.8 \text{ cM} &
\end{array}
\]

The most common classes of progeny (the parentals) tell you the original genotypes:
43. In a fungus, a proline mutant (pro) was crossed with a histidine mutant (his). A nonlinear tetrad analysis gave the following results:

\[
\begin{array}{cccc}
+ & + & + & + \\
+ & + & + & \text{his} \\
\text{pro} & \text{his} & \text{pro} & + \\
\text{pro} & \text{his} & \text{pro} & \text{his} \\
6 & 82 & 112
\end{array}
\]

\( al \text{ fu}^+ \text{ b}^+ / al \text{ fu}^+ \text{ b}^+ \times al^- \text{ fu} \text{ b} / al^- \text{ fu} \text{ b} \)

\( a. \) Are the genes linked or not?

\( b. \) Draw a map (if linked) or two maps (if not linked), showing map distances based on straightforward recombinant frequency where appropriate.

\( c. \) If there is linkage, correct the map distances for multiple crossovers (choose one approach only).

Answer:

\( a. \) The cross was \( \text{pro} + \times + \text{his} \). This makes the first tetrad class NPD (6 of these), the second tetrad class T (82 of these) and the third tetrad class PD (112 of these). When PD >> NPD, you know the two genes are linked.

\( b. \) Map distance can be calculated using the formula \( RF = (\text{NPD} + 1/2 \text{ T})100\% \). In this case, the frequency of NPD is 6/200 or 3 percent, and the frequency of T is 82/200 or 41 percent. Map distance is therefore 23.5 m.u. between these two loci.

\( pro \) \hspace{1cm} 23.5 \text{ cM} \hspace{1cm} \text{his} \)

\( c. \) To correct for multiple crossovers, the Perkins formula may be used. Thus, map distance = \(( \text{T} + 6\text{NPD})50\% \) or \((0.41 + 0.18)50\% = 29.5 \text{ m.u.} \)

44. In the fungus \( \text{Neurospora} \), a strain that is auxotrophic for thiamine (mutant allele \( t \)) was crossed with a strain that is auxotrophic for methionine (mutant allele \( m \)). Linear asci were isolated and classified into the following groups.

<table>
<thead>
<tr>
<th>Spore pair</th>
<th>Ascus types</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 and 2</td>
<td>( t^+ ) \hspace{1cm} ( t^+ ) \hspace{1cm} ( t^+ ) \hspace{1cm} ( t^+ ) \hspace{1cm} ( t^+ m ) \hspace{1cm} ( t^+ m )</td>
</tr>
<tr>
<td>3 and 4</td>
<td>( t^+ ) \hspace{1cm} ( t^+ m ) \hspace{1cm} ( t^+ m ) \hspace{1cm} ( t^+ m ) \hspace{1cm} ( t^+ m ) \hspace{1cm} ( t^+ m )</td>
</tr>
<tr>
<td>5 and 6</td>
<td>( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m )</td>
</tr>
<tr>
<td>7 and 8</td>
<td>( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m ) \hspace{1cm} ( +^+ m )</td>
</tr>
<tr>
<td>Number</td>
<td>260 \hspace{1cm} 76 \hspace{1cm} 4 \hspace{1cm} 54 \hspace{1cm} 1 \hspace{1cm} 5</td>
</tr>
</tbody>
</table>
a. Determine the linkage relations of these two genes to their centromere(s) and to each other. Specify distances in map units.

b. Draw a diagram to show the origin of the ascus type with only one single representative (second from right).

Answer:

a. The cross is $t^+ \times +m$. Knowing this, you can then determine that column one (260) is PD, column two (76) is T, column three (4) is PD, column four (54) is T, column five (1) is NPD, and column six (5) is T. Given that PD >> NPD, you know the two genes are linked. For determining the distance of a gene from its centromere, you need to determine what percentage of asci show MII segregation for that gene and then divide that in half to find map distance. For gene $t$, columns three, four, and six show MII segregation (63/400) and for gene $m$, columns two, three, and six show MII segregation (85/400). Therefore, gene $t$ is 7.88 m.u. and gene $m$ is 10.63 m.u. from their centromere. What remains to be determined is whether the two genes reside on the same side of their centromere or on opposite sides. The map distance between the two genes will determine which option is correct. For simple map distance, the formula to use is $RF = 1/2 \cdot T + NPD$, so $(1/2(135) + 1)/400$ or 17.13 m.u.. This best fits the following map:

```
+---------+   +---------+
<table>
<thead>
<tr>
<th>t</th>
<th>8</th>
<th>m</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.88 cM</td>
<td></td>
<td>10.63 cM</td>
</tr>
</tbody>
</table>
```

b. When two genes are linked, it requires a four-stranded double crossover to generate an NPD type ascus. Also, since neither gene shows MII segregation, both crossovers must have occurred on the same side of the centromere.

```
+   +   +   +   +   +   +   +
|   |   |   |   |   |   |   |
|   |   |   |   |   |   |   |
+   +   +---+   +   +   +   +
```

45. A corn geneticist wants to obtain a corn plant that has the three dominant phenotypes: anthocyanin (A), long tassels (L), and dwarf plant (D). In her collection of pure lines, the only lines that bear these alleles are $AA LL dd$ and $aa ll DD$. She also has the fully recessive line $aa ll dd$. She decides to intercross the first two and testcross the resulting hybrid to obtain in the progeny 0 plant of the desired phenotype (which would have to be $Aa Ll Dd$ in this case). She knows that the three genes are linked in the order written and that the distance between the $A/a$ and the $L/l$ loci is 16 map units and that the distance between the $L/l$ and the $D/d$ loci is 24 map units.
a. Draw a diagram of the chromosomes of the parents, the hybrid, and the tester.
b. Draw a diagram of the crossover(s) necessary to produce the desired genotype.
c. What percentage of the testcross progeny will be of the phenotype that she needs?
d. What assumptions did you make (if any)?

Answer:

a. A diagram of the $AA LL dd$ parent’s chromosomes would be

```
A           L           d
```

A diagram of the $aa ll dd$ parent’s chromosomes would be

```
          
  a         l         D
          
```

A diagram of the hybrid’s chromosomes would be

```
A           L           d
```

```
  a         l         D
```

A diagram of the tester’s chromosomes would be

```
          
  a         l         D
          
```

b. A diagram of the crossover(s) necessary to produce the desired genotype would be

```
A           L           d
```

```
  a         l
     X
```

Please note, this diagram shows a location of crossover that would give the desired genotype but does not take into consideration that each chromosome would actually consist of two chromatids.
c. The genotype of the desired crossover product is $A L D$. This is a result of a single crossover event between the $L$ and $D$ genes. The map distance between these genes includes both these single crossover events and also any double crossover events (simultaneous events between genes $A$ and $L$ and between genes $L$ and $D$). The double crossovers will not give the desired outcome and therefore must be subtracted to calculate the percentage of test-cross progeny with the desired phenotype. The expected double crossover is simply the chance of recombination in one interval multiplied by the chance of recombination in another interval, or in this case $0.16 \times 0.24 = 0.038$. Therefore, the 24 percent recombination between genes $L$ and $D$ is the sum of 3.8 percent double crossover events and 20.2 percent single crossover events. Thus, the percentage of $A L D/a l d$ progeny from this testcross should be $1/2 \times 20.2 = 10.1$ percent of the total.

d. To calculate the frequency of double crossovers, we assumed that the two recombinations were independent and that there was no interference.

46. In the model plant *Arabidopsis thaliana* the following alleles were used in a cross:

- $T =$ presence of trichomes
- $t =$ absence of trichomes
- $D =$ tall plants
- $d =$ dwarf plants
- $W =$ waxy cuticle
- $w =$ nonwaxy
- $A =$ presence of purple anthocyanin pigment
- $a =$ absence (white)

The $T/t$ and $D/d$ loci are linked 26 m.u. apart on chromosome 1, whereas the $W/w$ and $A/a$ loci are linked 8 m.u. apart on chromosome 2.

A pure-breeding double-homozygous recessive trichome less nonwaxy plant is crossed with another pure-breeding double-homozygous recessive dwarf white plant.

- **a.** What will be the appearance of the $F_1$?
- **b.** Sketch the chromosomes 1 and 2 of the parents and the $F_1$, showing the arrangement of the alleles.
- **c.** If the $F_1$ is testcrossed, what proportion of the progeny will have all four recessive phenotypes?

**Answer:**

- **a.** The $F_1$ would have all the dominant phenotypes: presence of trichomes, tall, waxy cuticle, and presence of purple pigment.
- **b.** A sketch of the parents’ chromosomes would be
For the progeny of a test cross to have all four recessive phenotypes, it must inherit a recombinant $t d$ chromosome 1 and a $w a$ recombinant chromosome 2 from its $F_1$ parent. Since the $T/t$ and $D/d$ loci are 26 m.u. apart, 26 percent of the progeny are expected to be recombinant for these genes and of these, half, or 13 percent, will be $t d$. Similarly, 8 percent of the progeny are expected to be recombinant for the $W/w$ and $A/a$ loci and half of these, or 4 percent, will be $w a$. Since these are independent events, $13\% \times 4\% = 0.52\%$ of the total progeny will have all four recessive phenotypes.

In corn, the cross $WW ee FF \times ww EE ff$ is made. The three loci are linked as follows:

Assume no interference.

a. If the $F_1$ is testcrossed, what proportion of progeny will be $ww ee ff$?
b. If the $F_1$ is selfed, what proportion of progeny will be $ww ee ff$?

Answer:

a. The cross is $W e F \times W e F \times w E f / w E f$ and the $F_1$ are $W e F / w E f$. Progeny that are $ww ee ff$ from a testcross of this $F_1$ must have inherited one of the double crossover recombinant chromosomes ($w e f$). Assuming no interference, the expected percentage of double crossovers is $8\% \times 24\% = 1.92\%$, and half of this is 0.96 percent.

b. To obtain a $ww ee ff$ progeny from a self cross of this $F_1$ requires the independent inheritance of two doubly recombinant $w e f$ chromosomes. The
chance of this, based on the answer to part (a) of this question would be \(0.96 \times 0.96 = 0.009\) percent.

48. The fungal cross \(+ \cdot + \times c \cdot m\) was made, and nonlinear (unordered) tetrads were collected. The results were

\[
\begin{array}{ccc}
+ + & + + & + m \\
+ + & + m & + m \\
\text{c m} & c + & c + \\
\text{c m} & \text{c m} & c + \\
\hline
\text{Total} & 112 & 82 & 6
\end{array}
\]

a. From these results, calculate a simple recombinant frequency.

b. Compare the Haldane mapping function and the Perkins formula in their conversions of the RF value into a “corrected” map distance.

c. In the derivation of the Perkins formula, only the possibility of meioses with zero, one, and two crossovers was considered. Could this limit explain any discrepancy in your calculated values? Explain briefly (no calculation needed).

Answer: Since the cross is \(+ + \times c m\), the first class of tetrad is PD, the second class is T, and the third class is NPD. That PD >> NPD tells you the genes are linked.

a. \(RF = (1/2T + NPD)100\% = (0.205 + 0.03)100\% = 23.5\%\)

b. The Perkins formula is \(RF = (T + 6 NPD)50\% = 29.5\%\)

The formula for the Haldane mapping function is \(RF = 1/2(1 – e^{-m})\). Solving for this situation, \(e^{-m} = 1 – (2 \times 0.235) = 0.53\) so \(m = 0.635\).

To convert to map distance, \(m\), the measure of crossover frequency is multiplied by 50 percent, to give a corrected map distance of 31.74%.

c. Yes. The Perkins formula only takes into account 0, 1, and 2 crossovers while the Haldane mapping formula has no limitations on the number of crossover events. It predicts the chance of any nonzero number of crossovers.

49. In mice, the following alleles were used in a cross:

- \(W\) = waltzing gait
- \(w\) = nonwaltzing gait
- \(G\) = normal gray color
- \(g\) = albino
- \(B\) = bent tail
- \(b\) = straight tail
A waltzing gray bent-tailed mouse is crossed with a nonwaltzing albino straight-tailed mouse and, over several years, the following progeny totals are obtained:

<table>
<thead>
<tr>
<th>Trait</th>
<th>Color</th>
<th>Tail</th>
<th>Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Waltzing</td>
<td>Gray</td>
<td>Bent</td>
<td>18</td>
</tr>
<tr>
<td>Waltzing</td>
<td>Albino</td>
<td>Bent</td>
<td>21</td>
</tr>
<tr>
<td>Nonwaltzing</td>
<td>Gray</td>
<td>Straight</td>
<td>19</td>
</tr>
<tr>
<td>Nonwaltzing</td>
<td>Albino</td>
<td>Straight</td>
<td>22</td>
</tr>
<tr>
<td>Waltzing</td>
<td>Gray</td>
<td>Straight</td>
<td>4</td>
</tr>
<tr>
<td>Waltzing</td>
<td>Albino</td>
<td>Straight</td>
<td>5</td>
</tr>
<tr>
<td>Nonwaltzing</td>
<td>Gray</td>
<td>Bent</td>
<td>5</td>
</tr>
<tr>
<td>Nonwaltzing</td>
<td>Albino</td>
<td>Bent</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>100</td>
</tr>
</tbody>
</table>

a. What were the genotypes of the two parental mice in the cross?

b. Draw the chromosomes of the parents.

c. If you deduced linkage, state the map unit value or values and show how they were obtained.

Answer: There are three patterns of possible outcomes from a testcross of a triply heterozygous parent. If all genes are linked, you expect pairs of roughly equal numbers of progeny in four different frequencies (for example, see problem 20 of this chapter). If all genes are unlinked, the expectation is eight classes of progeny in roughly equal numbers due to the independent assortment of all genes. The last possibility is that two of the genes are linked, but the third is unlinked. In that case, the expectation is two groups of four of two different frequencies. This final pattern is observed in the data of this problem.

In reviewing the data, the four most common classes are either waltzing bent or nonwaltzing straight with gray or albino segregating equally among those two groups. This observation tells you that the \( W/w \) and \( B/b \) genes are linked and both are unlinked to the \( G/g \) gene.

a. \( W/w \cdot G/G \cdot A/A \times w/w \cdot g/g \cdot a/a \)

b. \( W \quad B \quad G \quad w \quad b \quad g \)

c. For this cross, \( W \) \( B \) and \( w \) \( b \) begin linked to each other so any progeny of the testcross that are \( W \) \( b \) or \( w \) \( B \) are recombinant.

\[
\text{map distance} = \frac{(4 + 5 + 5 + 6)}{100} \times 100\% = 20 \text{ map units}
\]

50. Consider the \textit{Neurospora} cross \(+ \quad + \times f \quad p \)
It is known that the \(+/f\) locus is very close to the centromere on chromosome 7—in fact, so close that there are never any second-division segregations. It is also known that the \(+/p\) locus is on chromosome 5, at such a distance that there is usually an average of 12 percent second-division segregations. With this information, what will be the proportion of octads that are

a. parental ditypes showing \(M_I\) patterns for both loci?

b. nonparental ditypes showing \(M_I\) patterns for both loci?

c. tetratypes showing an \(M_I\) pattern for \(+/f\) and an \(M_{II}\) pattern for \(+/p\)?

d. tetratypes showing an \(M_{II}\) pattern for \(+/f\) and an \(M_I\) pattern for \(+/p\)?

Answer: The cross is \(+ ; + \times f ; p\) and you know that \(f\) is linked to its centromere and only segregates at the first division (\(M_I\)). The \(p\) gene, on average, segregates at the second divisions (\(M_{II}\)) 12 percent of the time (and therefore segregates at the first division 88 percent of the time).

a. All octads will show \(M_I\) segregation for the \(+/f\) gene and 88 percent will show \(M_I\) segregation for the \(+/p\) gene. Since the genes are unlinked, PD = NPD so half of all octads that meet these conditions will be PD, or in this case, 44 percent.

b. 44 percent (see part (a)).

c. Since all octads will show \(M_I\) segregation for \(+/f\); all \(M_{II}\) patterns for \(+/p\) will be tetratypes or, in this case, 12 percent.

d. 0 percent. \(+/f\) does not segregate at the second division.

51. In a haploid fungus, the genes \(al-2\) and \(arg-6\) are 30 map units apart on chromosome 1, and the genes \(lys-5\) and \(met-1\) are 20 map units apart on chromosome 6. In a cross

\[
al-2 + ; + met-1 \times + arg-6 ; lys-5 +
\]

what proportion of progeny would be prototrophic \(++ ; + +\)?

Answer: The cross is \(al-2 + ; + met-1 \times + arg-6 ; lys-5 +\). The transient diploid will be \(al-2 +/+ arg-6 ; + met-1/lys-5 +\). From this, one-half of the recombinant chromosomes 1 will be \(+ +\) and one-half of the recombinant chromosomes 6 will be \(+ +\). Since these are independent events, \(1/2(30\%) \times 1/2(20\%) = 1.5\%\) of the progeny will be \(+ + ; + +\).

52. The recessive alleles \(k\) (kidney-shaped eyes instead of wild-type round), \(c\) (cardinal-colored eyes instead of wild-type red), and \(e\) (ebony body instead of wild-type gray) identify three genes on chromosome 3 of \(Drosophila\). Females
with kidney-shaped, cardinal-colored eyes were mated with ebony males. The F₁ was wild type. When F₁ females were testcrossed with kk cc ee males, the following progeny phenotypes were obtained:

<table>
<thead>
<tr>
<th></th>
<th>k</th>
<th>c</th>
<th>e</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>k  c</td>
<td>+</td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>k  +</td>
<td></td>
<td>e</td>
<td></td>
<td>67</td>
</tr>
<tr>
<td>k  +</td>
<td></td>
<td></td>
<td></td>
<td>49</td>
</tr>
<tr>
<td>+</td>
<td>c</td>
<td>e</td>
<td></td>
<td>44</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td></td>
<td>e</td>
<td>58</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>899</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>2000</td>
</tr>
</tbody>
</table>

a. Determine the order of the genes and the map distances between them.
b. Draw the chromosomes of the parents and the F₁.
c. Calculate interference and say what you think of its significance.

Answer:

a. The data include that the three genes are linked. The most common classes of progeny, k c + and + + e represent the “parental” chromosomes. (Gene order is not specified.) The least common classes of progeny, k c e and + + + represent the outcomes of double crossover events and can be used to deduce gene order. In comparing the most common to the least common, the gene “in the middle” can be determined to be e. (Compare k c + to k c e and + + e to + + +.) To calculate map distances, you must now determine the various recombinant classes.

```
899  + + e  P  P
876  k c +  P  P
  67  k + e  R  P
  58  + c +  R  P
  49  k + +  P  R
  44  + c e  P  R
   4  + + +  R  R
   3  k c e  R  R
```

So there are 67 + 58 + 4 + 3 = 132 recombinants between k and e for a map distance of (132/total progeny) \( \times 100\% = 6.6 \text{ m.u.} \) and 49 + 44 + 4 + 3 = 100 recombinants between e and c for a map distance of 5 m.u.
b.

\[
\begin{align*}
&k + c \times + e + \\
&\downarrow \\
&k + c + e +
\end{align*}
\]

c. The expected frequency of double crossovers is 6.6 percent \times 5 percent = 0.33 percent. The actual frequency of double crossovers is \((4 + 3)/2000 \times 100\% = 0.35\%\). To calculate interference, the formula is \(I = 1 - \text{(observed DCO/expected DCO)}\) = -0.06. In this case, the interference is “negative.” The occurrence of one recombination event appears to slightly increase the chances of another. Of course, the difference between observed (7) and expected (6.6) is not statistically meaningful. While there are observed instances of negative interference, generally, interference values are between 0 (no interference) and 1 (complete interference).

53. From parents of genotypes \(A/A \cdot B/B\) and \(a/a \cdot B/b\), a dihybrid was produced. In a testcross of the dihybrid, the following seven progeny were obtained:

\[
A/a \cdot B/b, a/a \cdot b/b, A/a \cdot B/b, A/a \cdot b/b, a/a \cdot b/b, A/a \cdot B/b, \text{and } a/a \cdot B/b
\]

Do these results provide convincing evidence of linkage?

Answer: The results tell us little about linkage. Although the number of recombinants (3) is less than the number of parentals (5), one can have no confidence in the fact that the RF is <50%. The main problem is that the sample size is small, so just one individual more or less in a genotypic class can dramatically affect the ratios. Even the Chi-square test is unreliable at such small sample sizes. It is probably safe to say that there is not tight linkage because several recombinants were found in a relatively small sample. However, one cannot distinguish between more distant linkage and independent assortment. A larger sample size is required.

CHALLENGING PROBLEMS

54. Use the Haldane map function to calculate the corrected map distance in cases where the measured RF = 5%, 10%, 20%, 30%, and 40%. Sketch a graph of RF against corrected map distance and use it to answer the question, When should one use a map function?
Answer: The formula for the Haldane mapping function is \( RF = \frac{1}{2}(1 - e^{-m}) \).
Solving for a measured \( RF = 5\% \), \( e^{-m} = 1 - (2 \times 0.05) = 0.90 \), so \( m = 0.105 \). To convert to map distance, \( m \), the measure of crossover frequency is multiplied by 50 percent, to give a corrected map distance of 5.27%. Similarly, an \( RF = 10\% \) would be corrected to 11.2%, \( RF = 20\% \) to 25.5%, \( RF = 30\% \) to 46% and \( RF = 40\% \) to 80%! A graph of this data is presented below.

As can be observed, when map distances are small, the observed and corrected recombination frequencies are much the same. So the larger the RF, the more important it is to correct for underestimation of map distance by use of the mapping function.

Unpacking the Problem
55. An individual heterozygous for four genes, \( A/a \cdot B/b \cdot C/c \cdot D/d \), is testcrossed with \( a/a \cdot B/b \cdot c/c \cdot d/d \), and 1000 progeny are classified by the gametic contribution of the heterozygous parent as follows:

\[
\begin{align*}
  a \cdot B \cdot C \cdot D & \quad 42 \\
  A \cdot b \cdot c \cdot d & \quad 43 \\
  A \cdot B \cdot C \cdot d & \quad 140 \\
  a \cdot b \cdot c \cdot D & \quad 145 \\
  a \cdot B \cdot c \cdot D & \quad 6 \\
  A \cdot b \cdot C \cdot d & \quad 9 \\
  A \cdot B \cdot c \cdot d & \quad 305
\end{align*}
\]
a · b · C · D 310

a. Which genes are linked?
b. If two pure-breeding lines had been crossed to produce the heterozygous individual, what would their genotypes have been?
c. Draw a linkage map of the linked genes, showing the order and the distances in map units.
d. Calculate an interference value, if appropriate.

Answer:
a. All of these genes are linked. To determine this, each gene pair is examined separately. For example, are \( A \) and \( B \) linked?

\[
\begin{align*}
A \times B &= 140 + 305 = 445 \\
a \times b &= 145 + 310 = 455 \\
a \times B &= 42 + 6 = 48 \\
A \times b &= 43 + 9 = 52
\end{align*}
\]

Conclusion: the two genes are linked and 10 m.u. apart.

Are \( A \) and \( D \) linked?

\[
\begin{align*}
A \times D &= 0 \\
a \times d &= 0 \\
A \times d &= 43 + 140 + 9 + 305 = 497 \\
a \times D &= 42 + 145 + 6 + 310 = 503
\end{align*}
\]

Conclusion: the two genes show no recombination, and at this resolution are 0 m.u. apart.

Are \( B \) and \( C \) linked?

\[
\begin{align*}
B \times C &= 42 + 140 = 182 \\
b \times c &= 43 + 145 = 188 \\
B \times c &= 6 + 305 = 311 \\
b \times C &= 9 + 310 = 319
\end{align*}
\]

Conclusion: the two genes are linked and 37 m.u. apart.

Are \( C \) and \( D \) linked?

\[
\begin{align*}
C \times D &= 42 + 310 = 350 \\
c \times d &= 43 + 305 = 348 \\
C \times d &= 140 + 9 = 149 \\
c \times D &= 145 + 6 = 151
\end{align*}
\]
Conclusion: the two genes are linked and 30 m.u. apart. Therefore, all four genes are linked.

b. and c. Because $A$ and $D$ show no recombination, first rewrite the progeny omitting $D$ and $d$ (or omitting $A$ and $a$).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>$aBc$</td>
<td>42</td>
</tr>
<tr>
<td>$Abc$</td>
<td>43</td>
</tr>
<tr>
<td>$ABc$</td>
<td>140</td>
</tr>
<tr>
<td>$abc$</td>
<td>145</td>
</tr>
<tr>
<td>$ABc$</td>
<td>6</td>
</tr>
<tr>
<td>$Abc$</td>
<td>9</td>
</tr>
<tr>
<td>$ABC$</td>
<td>305</td>
</tr>
<tr>
<td>$aBC$</td>
<td>310</td>
</tr>
</tbody>
</table>

Note that the progeny now look like those of a typical three-point testcross, with $ABc$ and $abc$ the parental types (most frequent) and $aBc$ and $Abc$ the double recombinants (least frequent). The gene order is $BAC$. This is determined either by the map distances or by comparing double recombinants with the parentals; the gene that switches in reference with the other two is the gene in the center ($BAc \rightarrow BaC$, $baC \rightarrow bAC$).

Next, rewrite the progeny again, this time putting the genes in the proper order, and classify the progeny.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Count</th>
<th>Classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>$BaC$</td>
<td>42</td>
<td>CO $A-B$</td>
</tr>
<tr>
<td>$bAc$</td>
<td>43</td>
<td>CO $A-B$</td>
</tr>
<tr>
<td>$BAC$</td>
<td>140</td>
<td>CO $A-C$</td>
</tr>
<tr>
<td>$bac$</td>
<td>145</td>
<td>CO $A-C$</td>
</tr>
<tr>
<td>$Bac$</td>
<td>6</td>
<td>DCO</td>
</tr>
<tr>
<td>$bAC$</td>
<td>9</td>
<td>DCO</td>
</tr>
<tr>
<td>$Bac$</td>
<td>305</td>
<td>parental</td>
</tr>
<tr>
<td>$baC$</td>
<td>310</td>
<td>parental</td>
</tr>
</tbody>
</table>

To construct the map of these genes, use the following formula:

\[
\text{distance between two genes} = \frac{(100\%) \times (\text{number of single CO} \times \text{number of DCO})}{\text{total number of progeny}}
\]

For the $A$ to $B$ distance

\[
= \frac{(100\%)(42 + 43 + 6 + 9)}{1000} = 10 \text{ m.u.}
\]

For the $A$ to $C$ distance

\[
= \frac{(100\%)(140 + 145 + 6 + 9)}{1000} = 30 \text{ m.u.}
\]
The parental chromosomes actually were $B (A,d) c/b (a,D) C$, where the parentheses indicate that the order of the genes within is unknown.

d. Interference = 1 – (observed DCO/expected DCO)

$$= 1 - \frac{6 + 9}{(0.10)(0.30)(1000)}$$

$$= 1 - \frac{15}{30} = 0.5$$

56. An autosomal allele $N$ in humans causes abnormalities in nails and patellae (kneecaps) called the nail–patella syndrome. Consider marriages in which one partner has the nail–patella syndrome and blood type A and the other partner has normal nails and patellae and blood type O. These marriages produce some children who have both the nail–patella syndrome and blood type A. Assume that unrelated children from this phenotypic group mature, intermarry, and have children. Four phenotypes are observed in the following percentages in this second generation:

- Nail–patella syndrome, blood type A: 66%
- Normal nails and patellae, blood type O: 16%
- Normal nails and patellae, blood type A: 9%
- Nail–patella syndrome, blood type O: 9%

Fully analyze these data, explaining the relative frequencies of the four phenotypes. (See page 214-215 for the genetic basis of these blood types.)

Answer: The verbal description indicates the following cross and result:

P $N/– \times A/– \times O/O$

F$_1$ $N/n \times A/O \times N/n \times A/O$

The results indicate linkage, so the cross and results can be rewritten:

P $N \times A/n \times A/n \times O/n O$

F$_1$ $N \times N / A/n \times N A/n O$

F$_2$ 66% $N A/– – \times O/n O$

16% $N A/– – \times A/n O/n O$
9%  n A/n –
9%  N O/O

Only one genotype is fully known: 16 percent n O/n O, a combination of two parental gametes. The frequency of two parental gametes coming together is the frequency of the first times the frequency of the second. Therefore, the frequency of each n O gamete is the square root of 0.16, or 0.4. Within an organism the two parental gametes occur in equal frequency. Therefore, the frequency of N A is also 0.4. The parental total is 0.8, leaving 0.2 for all recombinants. Therefore, N O and n A occur at a frequency of 0.1 each. The two genes are 20 m.u. apart. Complete frequencies for all genotypes contributing to the four phenotypes can be obtained from a Punnett square using the gamete frequencies provided above.

57. Assume that three pairs of alleles are found in Drosophila: x+ and x, y+ and y, and z+ and z. As shown by the symbols, each non-wild-type allele is recessive to its wild-type allele. A cross between females heterozygous at these three loci and wild-type males yields progeny having the following genotypes: 1010 x+ · y+ · z+ females, 430 x · y+ · z males, 441 x+ · y · z+ males, 39 x · y · z males, 32 x+ · y+ · z males, 30 x+ · y+ · z+ males, 27 x · y · z+ males, 1 x+ · y · z male, and 0 x · y+ · z+ males.

a. On what chromosome of Drosophila are the genes carried?
b. Draw the relevant chromosomes in the heterozygous female parent, showing the arrangement of the alleles.
c. Calculate the map distances between the genes and the coefficient of coincidence.

Answer:
a. and b. The data indicate that the progeny males have a different phenotype than the females. Therefore, all the genes are on the X chromosome. The two most frequent phenotypes in the males indicate the genotypes of the X chromosomes in the female, and the two least frequent phenotypes in the males indicate the gene order. Gene z is in the middle. Data from only the males are used to determine map distances. The cross is:

P  

x z y+/x+ z+ y · x+ z+ y+/Y

X1 males  
430  x z y+/Y  parental
441  x+ z+ y/Y  parental
39  x z y/ Y  CO z-y
30  x+ z+ y+/Y  CO z-y
32  x+ z y+/Y  CO x-z
27  x z+ y/Y  CO x-z
1  x+ z y/ Y  DCO
0  x z+ y+/Y  DCO
c. \( z\rightarrow y \): 
\[
100\% \frac{(39 + 30 + 1)}{1000} = 7.0 \text{ m.u.}
\]
\( x\rightarrow z \): 
\[
100\% \frac{(32 + 27 + 1)}{1000} = 6.0 \text{ m.u.}
\]

\[c.c. = \frac{\text{observed DCO}}{\text{expected DCO}}\]
\[= \frac{1}{[(0.06)(0.07)(1000)]} = 0.238\]

58. From the five sets of data given in the following table, determine the order of genes by inspection—that is, without calculating recombination values. Recessive phenotypes are symbolized by lowercase letters and dominant phenotypes by pluses.

<table>
<thead>
<tr>
<th>Phenotypes observed in 3-point testcross</th>
<th>Data sets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>+ + +</td>
<td>317</td>
</tr>
<tr>
<td>+ + c</td>
<td>58</td>
</tr>
<tr>
<td>+ b +</td>
<td>10</td>
</tr>
<tr>
<td>+ b c</td>
<td>2</td>
</tr>
<tr>
<td>a + +</td>
<td>0</td>
</tr>
<tr>
<td>a + c</td>
<td>21</td>
</tr>
<tr>
<td>a b +</td>
<td>72</td>
</tr>
<tr>
<td>a b c</td>
<td>203</td>
</tr>
</tbody>
</table>

Answer: The data given for each of the three-point testcrosses can be used to determine the gene order by realizing that the rarest recombinant classes are the result of double crossover events. By comparing these chromosomes to the “parental” types, the alleles that have switched represent the gene in the middle.

For example, in (1), the most common phenotypes (+ + + and a b c) represent the parental allele combinations. Comparing these to the rarest phenotypes of this data set (+ b c and a + +) indicates that the \( a \) gene is recombinant and must be in the middle. The gene order is \( b a c \).

For (2), + b c and a + + (the parentals) should be compared to + + + and a b c (the rarest recombinants) to indicate that the \( a \) gene is in the middle. The gene order is \( b a c \).

For (3), compare + b + and a + c with a b + and + + c, which gives the gene order \( b a c \).

For (4), compare + + c and a b + with + + + and a b c, which gives the gene order \( a c b \).

For (5), compare + + + and a b c with + + c and a b +, which gives the gene order \( a c b \).
59. From the phenotype data given in the following table for two three-point testcrosses for (1) \(a, b, \) and \(c\) and (2) \(b, c, \) and \(d\), determine the sequence of the four genes \(a, b, c,\) and \(d\) and the three map distances between them. Recessive phenotypes are symbolized by lowercase letters and dominant phenotypes by pluses.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>+++</td>
<td>b c d</td>
</tr>
<tr>
<td>+++</td>
<td>669</td>
<td>8</td>
</tr>
<tr>
<td>a b +</td>
<td>139</td>
<td>b ++</td>
</tr>
<tr>
<td>a ++</td>
<td>3</td>
<td>b + d</td>
</tr>
<tr>
<td>+ + c</td>
<td>121</td>
<td>+ c d</td>
</tr>
<tr>
<td>+ b c</td>
<td>2</td>
<td>+ ++</td>
</tr>
<tr>
<td>a + c</td>
<td>2280</td>
<td>+ + d</td>
</tr>
<tr>
<td>a b c</td>
<td>653</td>
<td>+ c +</td>
</tr>
<tr>
<td>+ b +</td>
<td>2215</td>
<td>b c +</td>
</tr>
</tbody>
</table>

Answer: The gene order is \(a c b d\).

Recombination between \(a\) and \(c\) occurred at a frequency of:

\[
100\% \frac{(139 + 3 + 121 + 2)}{(669 + 139 + 3 + 121 + 2 + 2280 + 653 + 2215)} = 100\% \left( \frac{265}{6082} \right) = 4.36\%
\]

Recombination between \(b\) and \(c\) in cross 1 occurred at a frequency of:

\[
100\% \frac{(669 + 3 + 2 + 653)}{(669 + 139 + 3 + 121 + 2 + 2280 + 653 + 2215)} = 100\% \left( \frac{1327}{6082} \right) = 21.82\%
\]

Recombination between \(b\) and \(c\) in cross 2 occurred at a frequency of:

\[
100\% \frac{(8 + 14 + 153 + 141)}{(8 + 441 + 90 + 376 + 14 + 153 + 65 + 141)} = 100\% \left( \frac{316}{1288} \right) = 24.55\%
\]

The difference between the two calculated distances between \(b\) and \(c\) is not surprising because each set of data would not be expected to yield exactly identical results. Also, many more offspring were analyzed in cross 1. Combined, the distance would be:

\[
100\% \frac{(316 + 1327)}{(1288 + 6082)} = 22.3\%
\]

Recombination between \(b\) and \(d\) occurred at a frequency of:

\[
100\% \frac{(8 + 90 + 14 + 65)}{(8 + 441 + 90 + 376 + 14 + 153 + 65 + 141)} = 100\% \left( \frac{177}{1288} \right) = 13.68\%
\]
60. The father of Mr. Spock, first officer of the starship Enterprise, came from planet Vulcan; Spock’s mother came from Earth. A Vulcan has pointed ears (determined by allele $P$), adrenals absent (determined by $A$), and a right-sided heart (determined by $R$). All these alleles are dominant to normal Earth alleles. The three loci are autosomal, and they are linked as shown in this linkage map:

```
   P   A   R
```

\[ \text{15 m.u.} \quad \text{20 m.u.} \]

If Mr. Spock marries an Earth woman and there is no (genetic) interference, what proportion of their children will have

a. Vulcan phenotypes for all three characters?
b. Earth phenotypes for all three characters?
c. Vulcan ears and heart but Earth adrenals?
d. Vulcan ears but Earth heart and adrenals?

(Problem 60 is from D. Harrison, Problems in Genetics. Addison-Wesley, 1970.)

Answer: Part (a) of this problem is solved two ways, once in the standard way, once in a way that emphasizes a more mathematical approach.

The cross is:

\[
P \quad P \ A \ R/ \ P \ A \ R \times \ p \ a \ r/ \ p \ a \ r
\]

\[
F_1 \quad P \ A \ R/ \ p \ a \ r \times \ p \ a \ r/ \ p \ a \ r, \ a \ three-point \ test \ cross
\]

a. In order to find what proportion will have the Vulcan phenotype for all three characteristics, we must determine the frequency of parentals. Crossing over occurs 15 percent of the time between $P$ and $A$, which means it does not occur 85 percent of the time. Crossing over occurs 20 percent of the time between $A$ and $R$, which means that it does not occur 80 percent of the time.

\[
p \text{ (no crossover between either gene)} = p \text{ (no crossover between } P \text{ and } A) \times p \text{ (no crossover between } A \text{ and } R)
\]

\[
= (0.85)(0.80) = 0.68
\]

Half the parentals are Vulcan, so the proportion that are completely Vulcan is $1/2(0.68) = 0.34$

*Mathematical method:*

Number of parentals \[= 1 - \{ \text{single CO individuals} - \text{DCO individuals} \} \]
\[= 1 - \{ [0.15 + 0.20 - 2(0.15)(0.20)] - (0.15)(0.20) \} \]
\[= 0.68 \]
Because half the parentals are Earth alleles and half are Vulcan, the frequency of children with all three Vulcan characteristics is \( 1/2(0.68) = 0.34 \)

b. Same as above, 0.34

c. To yield Vulcan ears and hearts and Earth adrenals, a crossover must occur in both regions, producing double crossovers. The frequency of Vulcan ears and hearts and Earth adrenals will be half the DCOs, or \( 1/2(0.15)(0.20) = 0.015 \)

d. To yield Vulcan ears and an Earth heart and adrenals, a single crossover must occur between \( P \) and \( A \), and no crossover can occur between \( A \) and \( R \). The frequency will be:

\[
p(CO P–A) \times p(\text{no CO} A–R) = (0.15)(0.80) = 0.12
\]

Of these, 1/2 are \( P a r \) and 1/2 are \( p A R \). Therefore, the proportion with Vulcan ears and an Earth heart and adrenals is 0.06

61. In a certain diploid plant, the three loci \( A, B, \) and \( C \) are linked as follows:

\[
\begin{array}{c}
A \\
\hline
\text{20 m.u.} \\
\hline
B \\
\hline
\text{30 m.u.} \\
C \\
\end{array}
\]

One plant is available to you (call it the parental plant). It has the constitution \( A b c/a B C \).

a. With the assumption of no interference, if the plant is selfed, what proportion of the progeny will be of the genotype \( a b c/a b c \)?

b. Again, with the assumption of no interference, if the parental plant is crossed with the \( a b c/a b c \) plant, what genotypic classes will be found in the progeny? What will be their frequencies if there are 1000 progeny?

c. Repeat part b, this time assuming 20 percent interference between the regions.

Answer:

a. To obtain a plant that is \( a b c/a b c \) from selfing of \( A b c/a B C \), both gametes must be derived from a crossover between \( A \) and \( B \). The frequency of the \( a b c \) gamete is:

\[
1/2 \times p(CO A–B) \times p(\text{no CO} B–C) = 1/2(0.20)(0.70) = 0.07
\]

Therefore, the frequency of the homozygous plant will be \((0.07)^2 = 0.0049\)
b. The cross is $A \, b \, c / a \, B \, C \times a \, b \, c / a \, b \, c$.

To calculate the progeny frequencies, note that the parentals are equal to all those that did not experience a crossover. Mathematically this can be stated as:

$$\text{parentals} = p(\text{no CO} \, A–B) \times p(\text{no CO} \, B–C) = (0.80)(0.70) = 0.56$$

Because each parental should be represented equally:

$$A \, b \, c = 1/2(0.56) = 0.28$$
$$a \, B \, C = 1/2(0.56) = 0.28$$

As calculated above, the frequency of the $a \, b \, c$ gamete is:

$$1/2 \, p(\text{CO} \, A–B) \times p(\text{no CO} \, B–C) = 1/2(0.20)(0.70) = 0.07$$

as is the frequency of $A \, B \, C$.

The frequency of the $A \, b \, C$ gamete is:

$$1/2 \, p(\text{CO} \, B–C) \times p(\text{no CO} \, A–B) = 1/2(0.30)(0.80) = 0.12$$

as is the frequency of $a \, B \, c$.

Finally, the frequency of the $A \, B \, c$ gamete is:

$$1/2 \, p(\text{CO} \, A–B) \times p(\text{CO} \, B–C) = 1/2(0.20)(0.30) = 0.03$$

as is the frequency of $a \, b \, C$.

So for 1,000 progeny, the expected results are

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A , b , c$</td>
<td>280</td>
</tr>
<tr>
<td>$a , B , C$</td>
<td>280</td>
</tr>
<tr>
<td>$A , B , C$</td>
<td>70</td>
</tr>
<tr>
<td>$a , b , c$</td>
<td>70</td>
</tr>
<tr>
<td>$A , b , C$</td>
<td>120</td>
</tr>
<tr>
<td>$a , B , c$</td>
<td>120</td>
</tr>
<tr>
<td>$A , B , c$</td>
<td>30</td>
</tr>
<tr>
<td>$a , b , C$</td>
<td>30</td>
</tr>
</tbody>
</table>

c. Interference = 1 – observed DCO/expected DCO

$$0.2 = 1 – \frac{\text{observed DCO}}{(0.20)(0.30)}$$

observed DCO = $(0.20)(0.30) – (0.20)(0.20)(0.30) = 0.048$
The \( A-B \) distance = 20\% = 100\% \[ p(CO A-B) + p(DCO) \]
Therefore, \( p(CO A-B) = 0.20 - 0.048 = 0.152 \)

Similarly, the \( B-C \) distance = 30\% = 100\% \[ p(CO B-C) + p(DCO) \]
Therefore, \( p(CO B-C) = 0.30 - 0.048 = 0.252 \)

The \( p(\text{parental}) = 1 - p(CO A-B) - p(CO B-C) - p(\text{observed DCO}) \)
\[ = 1 - 0.152 - 0.252 - 0.048 = 0.548 \]

So for 1,000 progeny, the expected results are:

\[
\begin{array}{|c|c|}
\hline
A b c & 274 \\
a B C & 274 \\
A B C & 76 \\
\hline
a b c & 76 \\
A b C & 126 \\
a B c & 126 \\
A B c & 24 \\
a b C & 24 \\
\hline
\end{array}
\]

62. The following pedigree shows a family with two rare abnormal phenotypes: blue sclerotic (a brittle-bone defect), represented by a black-bordered symbol, and hemophilia, represented by a black center in a symbol. Members represented by completely black symbols have both disorders. The numbers in some symbols are the numbers of those types.

a. What pattern of inheritance is shown by each condition in this pedigree?
b. Provide the genotypes of as many family members as possible.
c. Is there evidence of linkage?
d. Is there evidence of independent assortment?

e. Can any of the members be judged as recombinants (that is, formed from at least one recombinant gamete)?

Answer:

a. Blue sclerotic \((B)\) appears to be an autosomal dominant disorder. Hemophilia \((h)\) appears to be an X-linked recessive disorder.

b. If the individuals in the pedigree are numbered as generations I through IV and the individuals in each generation are numbered clockwise, starting from the top right-hand portion of the pedigree, their genotypes are:

I: \(b/b; H/h, B/b; H/Y\)

II: \(B/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/h, b/b; H/Y, B/b; H/h, B/b; H/h, B/b; H/Y, b/b; H/Y, B/b\)

III: \(b/b; H/Y, B/b; H/Y, b/b; h/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b\)

IV: \(H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, b/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b; H/Y, b/b; H/Y, B/b\)


c. There is no evidence of linkage between these two disorders. Because of the modes of inheritance for these two genes, no linkage would be expected.

d. The two genes exhibit independent assortment.

e. No individual could be considered intrachromosomally recombinant. However, a number show interchromosomal recombination, for example, all individuals in generation III that have both disorders.

63. The human genes for color blindness and for hemophilia are both on the X chromosome, and they show a recombinant frequency of about 10 percent. The linkage of a pathological gene to a relatively harmless one can be used for genetic prognosis. Shown here is part of a bigger pedigree. Blackened symbols indicate that the subjects had hemophilia, and crosses indicate color blindness. What information could be given to women III-4 and III-5 about the likelihood of their having sons with hemophilia?
(Problem 63 is adapted from J. F. Crow, *Genetics Notes: An Introduction to Genetics.* Burgess, 1983.)

Answer: If \( h = \) hemophilia and \( b = \) colorblindness, the genotypes for individuals in the pedigree can be written as:

The mother of the two women in question would produce the following gametes:

- 0.45 \( H B \)
- 0.45 \( h b \)
- 0.05 \( H b \)
- 0.05 \( h B \)

Woman III-4 can be either \( H b/H B \) (0.45 chance) or \( H b/h B \) (0.05 chance) because she received \( B \) from her mother. If she is \( H b/h B \) \([0.05/(0.45 + 0.05) = 0.10 \text{ chance}]\), she will produce the parental and recombinant gametes with the same probabilities as her mother. Thus, her child has a 45 percent chance of receiving \( h B \), a 5 percent chance of receiving \( h b \), and a 50 percent chance of receiving a \( Y \) from his father. The probability that her child will be a hemophiliac son is \((0.1)(0.5)(0.5) = 0.025 = 2.5 \text{ percent}.\)

Woman III-5 can be either \( H b/H b \) (0.05 chance) or \( H b/h b \) (0.45 chance), because she received \( b \) from her mother. If she is \( H b/h b \) \([0.45/(0.45 + 0.05) = 0.90 \text{ chance}]\), she has a 50 percent chance of passing \( h \) to her child, and there is
a 50 percent chance that the child will be male. The probability that she will have a son with hemophilia is \((0.9)(0.5)(0.5) = 0.225 = 22.5\) percent.

64. A geneticist mapping the genes \(A, B, C, D,\) and \(E\) makes two 3-point testcrosses. The first cross of pure lines is

\[
A/A \cdot B/B \cdot C/C \cdot D/D \cdot E/E \times a/a \cdot b/b \cdot C/C \cdot d/d \cdot E/E
\]

The geneticist crosses the F1 with a recessive tester and classifies the progeny by the gametic contribution of the F1:

\[
\begin{align*}
A \cdot B \cdot C \cdot D \cdot E & \quad 316 \\
a \cdot b \cdot C \cdot d \cdot E & \quad 314 \\
A \cdot B \cdot C \cdot d \cdot E & \quad 31 \\
a \cdot b \cdot C \cdot D \cdot E & \quad 39 \\
A \cdot b \cdot C \cdot d \cdot E & \quad 130 \\
a \cdot B \cdot C \cdot D \cdot E & \quad 140 \\
A \cdot b \cdot C \cdot D \cdot E & \quad 17 \\
a \cdot B \cdot C \cdot d \cdot E & \quad 13 \\
\end{align*}
\]

The second cross of pure lines is \(A/A \cdot B/B \cdot C/C \cdot D/D \cdot E/E \times a/a \cdot B/B \cdot c/c \cdot D/D \cdot e/e.\)

The geneticist crosses the F1 from this cross with a recessive tester and obtains

\[
\begin{align*}
A \cdot B \cdot C \cdot D \cdot E & \quad 243 \\
a \cdot B \cdot c \cdot D \cdot e & \quad 237 \\
A \cdot B \cdot c \cdot D \cdot e & \quad 62 \\
a \cdot B \cdot C \cdot D \cdot E & \quad 58 \\
A \cdot B \cdot C \cdot D \cdot e & \quad 155 \\
a \cdot B \cdot c \cdot D \cdot E & \quad 165 \\
a \cdot B \cdot C \cdot D \cdot e & \quad 46 \\
A \cdot B \cdot c \cdot D \cdot E & \quad 34 \\
\end{align*}
\]

The geneticist also knows that genes \(D\) and \(E\) assort independently.

a. Draw a map of these genes, showing distances in map units wherever possible.

b. Is there any evidence of interference?

Answer:

a. Cross 1 reduces to:

\[
P \quad A/A \cdot B/B \cdot D/D \times a/a \cdot b/b \cdot d/d
\]
\[ F_1 \quad A/a \cdot B/b \cdot D/d \times a/a \cdot b/b \cdot d/d \]

The testcross progeny indicate these three genes are linked.

<table>
<thead>
<tr>
<th>Testcross</th>
<th>A B D</th>
<th>316</th>
<th>parental</th>
</tr>
</thead>
<tbody>
<tr>
<td>progeny</td>
<td>a b d</td>
<td>314</td>
<td>CO B–D</td>
</tr>
<tr>
<td>A B d</td>
<td>31</td>
<td>CO B–D</td>
<td></td>
</tr>
<tr>
<td>a b D</td>
<td>39</td>
<td>CO B–D</td>
<td></td>
</tr>
<tr>
<td>A b d</td>
<td>130</td>
<td>CO A–B</td>
<td></td>
</tr>
<tr>
<td>a B D</td>
<td>140</td>
<td>CO A–B</td>
<td></td>
</tr>
<tr>
<td>A b D</td>
<td>17</td>
<td>DCO</td>
<td></td>
</tr>
<tr>
<td>a B d</td>
<td>13</td>
<td>DCO</td>
<td></td>
</tr>
</tbody>
</table>

\[ A–B: \frac{100\%(130 + 140 + 17 + 13)}{1000} = 30 \text{ m.u.} \]
\[ B–D: \frac{100\%(31 + 39 + 17 + 13)}{1000} = 10 \text{ m.u.} \]

Cross 2 reduces to:

\[ P \quad A/A \cdot C/C \cdot E/E \times a/a \cdot c/c \cdot e/e \]

\[ F_1 \quad A/a \cdot C/c \cdot E/e \times a/a \cdot c/c \cdot e/e \]

The testcross progeny indicate these three genes are linked.

<table>
<thead>
<tr>
<th>Testcross</th>
<th>A C E</th>
<th>243</th>
<th>parental</th>
</tr>
</thead>
<tbody>
<tr>
<td>progeny</td>
<td>a c e</td>
<td>237</td>
<td>CO A–C</td>
</tr>
<tr>
<td>A c e</td>
<td>62</td>
<td>CO A–C</td>
<td></td>
</tr>
<tr>
<td>a C E</td>
<td>58</td>
<td>CO A–C</td>
<td></td>
</tr>
<tr>
<td>A C e</td>
<td>155</td>
<td>CO C–E</td>
<td></td>
</tr>
<tr>
<td>a c E</td>
<td>165</td>
<td>CO C–E</td>
<td></td>
</tr>
<tr>
<td>a C e</td>
<td>46</td>
<td>DCO</td>
<td></td>
</tr>
<tr>
<td>A c E</td>
<td>34</td>
<td>DCO</td>
<td></td>
</tr>
</tbody>
</table>

\[ A–C: \quad 100\% \frac{(62 + 58 + 46 + 34)}{1000} = 20 \text{ m.u.} \]
\[ C–E: \quad 100\% \frac{(155 + 165 + 46 + 34)}{1000} = 40 \text{ m.u.} \]

The map that accommodates all the data is:

\[ \begin{array}{cccc}
E & & & \\
\hline
40 \text{ m.u.} & & & \\
& C & & A \\
& 20 \text{ m.u.} & & 30 \text{ m.u.}
& & B & D \\
& 10 \text{ m.u.} & & &
\end{array} \]

b. Interference (I) = 1 – [(observed DCO)/(expected DCO)]

For cross 1: I = 1 – \{30/[(0.30)(0.10)(1000)]\} = 1 – 1 = 0, no interference
For cross 2: \[ I = 1 - \frac{80}{(0.20)(0.40)(1000)} = 1 - 1 = 0, \text{ no interference} \]

65. In the plant *Arabidopsis*, the loci for pod length (*L*, long; *l*, short) and fruit hairs (*H*, hairy; *h*, smooth) are linked 16 map units apart on the same chromosome. The following crosses were made:

(i) \[ L H/L H \times l h/l h \rightarrow F_1 \]
(ii) \[ L h/L h \times l H/l H \rightarrow F_1 \]

If the F₁’s from cross i and cross ii are crossed,

a. what proportion of the progeny are expected to be \( l h/l h \)?

b. what proportion of the progeny are expected to be \( L h/l h \)?

Answer:

a. The first F₁ is \( L H/l h \), and the second is \( l H/L h \). For progeny that are \( l h/l h \), they have received a “parental” chromosome from the first F₁ and a “recombinant” chromosome from the second F₁. The genes are 16 percent apart so the chance of a parental chromosome is \( \frac{1}{2}(100 - 16\%) = 42\% \), and the chance of a recombinant chromosome is \( \frac{1}{2}(16\%) = 8\% \).

The chance of both events = \( 42\% \times 8\% = 3.36\% \)

b. To obtain \( L h/l h \) progeny, either a parental chromosome from each parent was inherited or a recombinant chromosome from each parent was inherited. The total probability will therefore be:

\[(42\% \times 42\%) + (8\% \times 8\%) = (17.6\% + 0.6\%) = 18.2\% \]

66. In corn (*Zea mays*), the genetic map of part of chromosome 4 is as follows, where *w*, *s*, and *e* represent recessive mutant alleles affecting the color and shape of the pollen:

\[ \text{8 m.u.} \quad \text{14 m.u.} \]

If the following cross is made

\[ +++/+++ \times w s e/w s e \]

and the F₁ is testcrossed with \( w s e/w s e \), and if it is assumed that there is no interference on this region of the chromosome, what proportion of progeny will be of genotypes?

a. +++

e. ++ e
b. \( w s e \)  \hspace{1cm} f. \( w s + \)
c. \( + s e \)  \hspace{1cm} g. \( w + e \)
d. \( w + + \)  \hspace{1cm} h. \( + s + \)

Answer: Crossing over occurs 8 percent of the time between \( w \) and \( s \), which means it does not occur 92 percent of the time. Crossing over occurs 14 percent of the time between \( s \) and \( e \), which means that it does not occur 86 percent of the time.

a. and b. The frequency of parentals = \( p \) (no crossover between either gene)

\[
= p(\text{no CO } w–s) \times p(\text{no CO } s–e) = (0.92)(0.86) = 0.791
\]

or

\[
1/2(0.791) = 0.396 \text{ each}
\]

c. and d. The frequency that will show recombination between \( w \) and \( s \) only

\[
= p(\text{CO } w–s) \times p(\text{no CO } s–e) = (0.08)(0.86) = 0.069
\]

or

\[
1/2(0.069) = 0.035 \text{ each}
\]

e. and f. The frequency that will show recombination between \( s \) and \( e \) only

\[
= p(\text{CO } s–e) \times p(\text{no CO } w–s) = (0.14)(0.92) = 0.128
\]

or

\[
1/2(0.128) = 0.064 \text{ each}
\]

g. and h. The frequency that will show recombination between \( w \) and \( s \) and \( s \) and \( e \)

\[
= p(\text{CO } w–s) \times p(\text{CO } s–e) = (0.08)(0.14) = 0.011
\]

or

\[
1/2(0.011) = 0.006 \text{ each}
\]

67. Every Friday night, genetics student Jean Allele, exhausted by her studies, goes to the student union’s bowling lane to relax. But, even there, she is haunted by her genetic studies. The rather modest bowling lane has only four bowling balls: two red and two blue. They are bowled at the pins and are then collected and returned down the chute in random order, coming to rest at the end stop. As the evening passes, Jean notices familiar patterns of the four balls as they come to rest at the stop. Compulsively, she counts the different patterns. What patterns did she see, what were their frequencies, and what is the relevance of this matter to genetics?
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Answer: This problem is analogous to meiosis in organisms that form linear tetrads. Let red = \( R \) and blue = \( r \). This can now be compared to meiosis in an organism that is \( R/r \). The patterns, their frequencies, and the division of segregation are given below. Notice that the probabilities change as each ball/allele is selected. This occurs when there is sampling without replacement.

\[
\begin{align*}
1/2 \ R & \quad \times 1/3 \ R \times 1/1 \ r \times 1/1 \ r = 1/6 \ RRrr \\
1/2 \ R & \quad \times 1/2 \ R \times 1/1 \ r = 1/6 \ RrrR \\
& \quad \text{second division}
\end{align*}
\]

These results indicate one-third first-division segregation and two-thirds second-division segregation.

68. In a tetrad analysis, the linkage arrangement of the \( p \) and \( q \) loci is as follows:

Assume that

- in region i, there is no crossover in 88 percent of meioses and there is a single crossover in 12 percent of meioses;
- in region ii, there is no crossover in 80 percent of meioses and there is a single crossover in 20 percent of meioses; and
- there is no interference (in other words, the situation in one region does not affect what is going on in the other region).

What proportions of tetrads will be of the following types? (a) \( M_I M_{II} \), PD; (b) \( M_I M_{II} \), NPD; (c) \( M_I M_{II} \), T; (d) \( M_{II} M_I \), T; (e) \( M_{II} M_{II} \), PD; (f) \( M_{II} M_{II} \), NPD; (g) \( M_{II} M_{II} \), T. (Note: Here the \( M \) pattern written first is the one that pertains to the \( p \) locus.) Hint: The easiest way to do this problem is to start by calculating the frequencies of asci with crossovers in both regions, region i, region ii, and neither region. Then determine what \( M_I \) and \( M_{II} \) patterns result.

Answer: As the problem suggests, calculate the frequencies of the various possibilities. The percentage of tetrads without crossing over is 88% × 80% =
70.4%. The percentage of tetrads with a single crossover in region (i) and none in region (ii) is 12% \times 80% = 9.6%. The percentage of tetrads with a single crossover in region (ii) and none in region (i) is 20% \times 88% = 17.6%, and the percentage of tetrads with crossovers in both regions is 12% \times 20% = 2.4%.

Now work out the patterns of segregation that result in each case

For no crossovers

For a single crossover in region (i)

For a single crossover in region (ii)

For double crossovers, there are four types, all equally likely

two-strand
four-strand

\[
\begin{array}{c}
p \\
+ \\
+ q \\
+ \\
M_{II} M_{I} T
\end{array}
\]

and two different three-strand

\[
\begin{array}{c}
p \\
+ \\
+ q \\
+ \\
M_{II} M_{II} T
\end{array}
\]

\[
\begin{array}{c}
p \\
+ \\
+ q \\
+ \\
M_{II} M_{II} T
\end{array}
\]

(a) \(M_{I} M_{I} PD\) is the result of no crossovers = 70.4%

(b) \(M_{I} M_{I} NPD\) is not found as a result.

(c) \(M_{I} M_{II} T\) is the result of a single crossover in region (ii) = 17.6%

(d) \(M_{II} M_{I} T\) is the result of the two- and four-strand double crossovers = 1.2%

(e) \(M_{II} M_{II} PD\) is the result of a single crossover in region (i) = 9.6%

(f) \(M_{II} M_{II} NPD\) is not found as a result.

(g) \(MII MII T\) is the result of both three-strand double crossovers = 1.2%

69. For an experiment with haploid yeast, you have two different cultures. Each will grow on minimal medium to which arginine has been added, but neither will grow on minimal medium alone. (Minimal medium is inorganic salts plus sugar.) Using appropriate methods, you induce the two cultures to mate. The diploid cells then divide meiotically and form unordered tetrads. Some of the ascospores will grow on minimal medium. You classify a large number of these
tetrads for the phenotypes ARG\(^-\) (arginine requiring) and ARG\(^+\) (arginine independent) and record the following data:

<table>
<thead>
<tr>
<th>Segregation of ARG(^-) : ARG(^+)</th>
<th>Frequency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 : 0</td>
<td>40</td>
</tr>
<tr>
<td>3 : 1</td>
<td>20</td>
</tr>
<tr>
<td>2 : 2</td>
<td>40</td>
</tr>
</tbody>
</table>

a. Using symbols of your own choosing, assign genotypes to the two parental cultures. For each of the three kinds of segregation, assign genotypes to the segregants.

b. If there is more than one locus governing arginine requirement, are these loci linked?

Answer:

a. and b. The data support the independent assortment of two genes (call them \(\text{arg}1\) and \(\text{arg}2\)). The cross becomes \(\text{arg}1^- \times \text{arg}1^- ; \text{arg}2\) and the resulting tetrads are:

\[
\begin{align*}
4 : 0 (PD) & \quad 3 : 1 (T) & \quad 2 : 2 (NPD) \\
\text{arg}1^- ; \text{arg}2^+ & \quad \text{arg}1^+ ; \text{arg}2^+ & \quad \text{arg}1^- ; \text{arg}2^- \\
\text{arg}1^- ; \text{arg}2^+ & \quad \text{arg}1^+ ; \text{arg}2^- & \quad \text{arg}1^- ; \text{arg}2^- \\
\text{arg}1^+ ; \text{arg}2^- & \quad \text{arg}1^+ ; \text{arg}2^- & \quad \text{arg}1^+ ; \text{arg}2^- \\
\end{align*}
\]

Because PD = NPD, the genes are unlinked.

70. An RFLP analysis of two pure lines \(A/A \cdot B/B\) and \(a/a \cdot B/b\) showed that the former was homozygous for a long RFLP allele (l) and the latter for a short allele (s). The two were crossed to form an F1, which was then backcrossed to the second pure line. A thousand progeny were scored as follows:

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Aa Bb ss)</td>
<td>9</td>
</tr>
<tr>
<td>(Aa Bb ls)</td>
<td>362</td>
</tr>
<tr>
<td>(aa bb ls)</td>
<td>11</td>
</tr>
<tr>
<td>(aa bb ss)</td>
<td>358</td>
</tr>
<tr>
<td>(Aa bb ss)</td>
<td>43</td>
</tr>
<tr>
<td>(Aa bb ls)</td>
<td>93</td>
</tr>
<tr>
<td>(aa Bb ls)</td>
<td>37</td>
</tr>
<tr>
<td>(aa Bb ss)</td>
<td>87</td>
</tr>
</tbody>
</table>

a. What do these results tell us about linkage?

b. Draw a map if appropriate.

c. Incorporate the RFLP fragments into your map.
Answer:

a. The cross is $A/A \cdot B/B \cdot l/l \times a/a \cdot b/b \cdot s/s$. The resulting F$_1$ is backcrossed to the second parent and the backcross progeny indicate that all three markers are linked.

b. and c. By comparing the most common progeny to the least ($A B l/a b s$ to $A B s/a b s$ and $a b s/abs$ to $a b l/a b s$) we can deduce that the RFLP allele is between genes $A/a$ and $B/b$. The distance between these markers is $(43 + 37 + 9 + 11)/1000 = 10$ map units between gene $A/a$ and the RFLP and $(93 + 87 + 9 + 11)/1000 = 20$ map units between the RFLP and gene $B/b$. The restriction sites are not drawn to scale relative to the genetic distances.