Chapter Five: Extensions and Modifications of Basic Principles

COMPREHENSION QUESTIONS

Section 5.1

*1. How do incomplete dominance and codominance differ?
Incomplete dominance means the phenotype of the heterozygote is intermediate to the phenotypes of the homozygotes. Codominance refers to situations in which both alleles are expressed and both phenotypes are manifested simultaneously.

Section 5.2

*2. What is incomplete penetrance and what causes it?
Incomplete penetrance occurs when an individual with a particular genotype does not express the expected phenotype. Environmental factors, as well as the effects of other genes, may alter the phenotypic expression of a particular genotype.

Section 5.5

3. What is gene interaction? What is the difference between an epistatic gene and a hypostatic gene?
Gene interaction is the determination of a single trait or phenotype by genes at more than one locus; the effect of one gene on a trait depends on the effects of a different gene located elsewhere in the genome. One type of gene interaction is epistasis. The alleles at the epistatic gene mask or repress the effects of alleles at another gene. The gene whose alleles are masked or repressed is called the hypostatic gene.

4. What is a recessive epistatic gene?
Recessive epistasis occurs when the epistatic gene in a homozygous recessive state masks the interacting gene or genes. In the example from the text, being homozygous recessive at the locus for deposition of color in hair shafts (ee) *completely masked the effect of the color locus regardless of whether it had the dominant black* (B-) *or recessive brown* (bb) *allele.*

*5. What is a complementation test and what is it used for?
Complementation tests are used to determine whether different recessive mutations affect the same gene or locus (are allelic) or whether they affect different genes. The two mutations are introduced into the same individual by crossing homozygotes for each of the mutants. If the progeny show a mutant phenotype, then the mutations are allelic (in the same gene). If the progeny show a wild-type (dominant) phenotype, then the mutations are in different genes and are said to complement each other because each of the mutant parents can supply a functional copy (or dominant allele) of the gene mutated in the other parent.

Section 5.6

*6. What characteristics are exhibited by a cytoplasmically inherited trait?

Cytoplasmically inherited traits are encoded by genes in the cytoplasm. Because the cytoplasm usually is inherited from a single (most often the female) parent, reciprocal crosses do not show the same results. Cytoplasmically inherited traits often show great variability because different egg cells (female gametes) may have differing proportions of cytoplasmic alleles from random sorting of mitochondria (or plastids in plants).

7. What is genomic imprinting?
Genomic imprinting refers to different expression of a gene depending on whether it was inherited from the male parent or the female parent.

8. What is the difference between genetic maternal effect and genomic imprinting?
In genetic maternal effect, the phenotypes of the progeny are determined by the genotype of the mother only. The genotype of the father and the genotype of the affected individual have no effect. In genomic imprinting, the phenotype of the progeny differs based on whether a particular allele is inherited from the mother or the father. The phenotype is therefore based on both the individual's genotype and the paternal or maternal origins of the genotype.

9. What is the difference between a sex-influenced gene and a gene that exhibits genomic imprinting?
For a sex-influenced gene, the phenotype is influenced by the sex of the individual bearing the genotype. For an imprinted gene, the phenotype is influenced by the sex of the parent *from which each allele was inherited.*

Section 5.7

10. What characteristics do you expect to see in a trait that exhibits anticipation?
Traits that exhibit anticipation become stronger or more pronounced, or are expressed earlier in development, as they are transmitted to each succeeding generation.

Section 5.8

*11. What are continuous characteristics and how do they arise?
Continuous characteristics, also called quantitative characteristics, exhibit many phenotypes with a continuous distribution. They result from the interaction of multiple genes (polygenic traits), the influence of environmental factors on the phenotype, or both.

APPLICATION QUESTIONS AND PROBLEMS

Sections 5.1 through 5.8

12. Match each term with its correct definition.

d phenocopy

h pleiotrophy

e polygenic trait

a penetrance

c sex-limited trait

i genetic maternal effect

f genomic imprinting

b sex-influenced trait

g anticipation

a. the percentage of individuals with a particular genotype that express the expected phenotype

b. a trait determined by an autosomal gene that is more easily expressed in one sex

c. a trait determined by an autosomal gene that is expressed in only one sex

d. a trait that is determined by an environmental effect and has the same phenotype as a genetically determined trait

e. a trait determined by genes at many loci

f. the expression of a trait is affected by the sex of the parent that transmits the gene to the offspring

g. the trait appears earlier or more severely in succeeding generations

h. a gene affects more than one phenotype

i. the genotype of the maternal parent influences the phenotype of the offspring

Section 5.1

*13. Palomino horses have a golden yellow coat, chestnut horses have a brown coat, and cremello horses have a coat that is almost white. A series of crosses between the three different types of horses produced the following offspring:

Cross	**Offspring**
palomino × palomino	13 palomino, 6 chestnut, 5 cremello
chestnut × chestnut	16 chestnut
cremello × cremello	13 cremello
palomino × chestnut	8 palomino, 9 chestnut
palomino × cremello	11 palomino, 11 cremello
chestnut × cremello	23 palomino

a. Explain the inheritance of the palomino, chestnut, and cremello phenotypes in horses.
The results of the crosses indicate that cremello and chestnut are pure-breeding traits (homozygous). Palomino is a hybrid trait (heterozygous) that produces a 2:1:1 ratio when palominos are crossed with each other. The simplest hypothesis consistent with these results is incomplete dominance, with palomino as the phenotype of the heterozygotes resulting from chestnuts crossed with cremellos.

b. Assign symbols for the alleles that determine these phenotypes and list the genotypes of all parents and offspring given in the preceding table.
Let C^B = chestnut, C^W = cremello, C^BC^W = palomino.

Cross	**Offspring**		
palomino × palomino	*13 palomino, 6 chestnut, 5 cremello*		
$C^BC^W \times C^BC^W$	C^BC^W	C^BC^B	C^WC^W
chestnut × chestnut	*16 chestnut*		
$C^BC^B \times C^BC^B$	C^BC^B		
cremello × cremello	*13 cremello*		
$C^WC^W \times C^WC^W$	C^WC^W		

palomino × chestnut	*8 palomino, 9 chestnut*
$C^BC^W \times C^BC^B$	C^BC^W C^BC^B
palomino × cremello	*11 palomino, 11 cremello*
$C^BC^W \times C^WC^W$	C^BC^W C^WC^W
chestnut × cremello	*23 palomino*
$C^BC^B \times C^WC^W$	C^BC^W

*14. The L^M and L^N alleles at the MN blood group locus exhibit codominance. Give the expected genotypes and phenotypes and their ratios in progeny resulting from the following crosses:

a. $L^ML^M \times L^ML^N$
½ L^ML^M *(type M), ½* L^ML^N *(type MN)*

b. $L^NL^N \times L^NL^N$
All L^NL^N *(type N)*

c. $L^ML^N \times L^ML^N$
½ L^ML^N *(type MN), ¼* L^ML^M *(type M), ¼* L^NL^N *(type N)*

d. $L^ML^N \times L^NL^N$
½ L^ML^N *(type MN), ½* L^NL^N *(type N)*

e. $L^ML^M \times L^NL^N$
All L^ML^N *(type MN)*

Section 5.2

15. Assume that long ear lobes in humans are an autosomal dominant trait that exhibits 30% penetrance. A person who is heterozygous for long ear lobes mates with a person who is homozygous for normal ear lobes. What is the probability that their first child will have long ear lobes?
To have long ear lobes, the child must inherit the dominant allele and also express it. The probability of inheriting the dominant allele is 50%; the probability of expressing it is 30%. The combined probability of both is 0.5(0.3) = 0.15, or 15%

16. The eastern mosquito fish (*Gambusia affinis holbrooki*) has XX-XY sex determination. Its spotting is inherited as a Y-linked trait. The trait exhibits 100% penetrance when the fish are raised at 22°C, but the penetrance drops to 42% when the fish are raised at 26°C. A male with spots is crossed with a female without spots, and the F_1 are intercrossed to produce the F_2. If all the offspring are raised at 22°C, what proportion of the F_1 and F_2 will have spots? If all the offspring are raised at 26°C, what proportion of the F_1 and F_2 will have spots?
Because spotting is Y-linked, the parental genotypes are: XY^s *and XX, where* Y^s *denotes the spotted allele on the Y chromosome. The* F_1 *genotypes will be: ½* XY^s *and ½ XX, like the parents. The* F_2 *genotypes will also be ½* XY^s *and ½ XX. Note that incomplete penetrance and expressivity do not affect genotypic ratios. At 22°C, where penetrance is 100%, the phenotypic ratios will be all spotted males and all unspotted females in both the* F_1 *and* F_2 *progeny. At 26°C, where penetrance is only 42%, then 42% of the* XY^s *males will be spotted, in the* F_1 *and* F_2*.*

Section 5.3

*17. When a Chinese hamster with white spots is crossed with another hamster that has no spots, approximately ½ of the offspring have white spots and ½ have no spots. When two hamsters with white spots are crossed, 2/3 of the offspring possess white spots and 1/3 have no spots.

a. What is the genetic basis of white spotting in Chinese hamsters?
The 2:1 ratio when two spotted hamsters are mated suggests lethality, and the 1:1 ratio when spotted hamsters are mated to hamsters without spots indicates that spotted is a heterozygous phenotype. Using S *and* s *to symbolize the locus responsible for white spotting, spotted hamsters are* Ss and *solid-colored hamsters are* ss. *One-quarter of the progeny expected from a mating of two spotted hamsters is* SS, *embryonic lethal, and missing from those progeny, resulting in the 2:1 ratio of spotted to solid progeny.*

b. How might you go about producing Chinese hamsters that breed true for white spotting?
Because spotting is a heterozygous phenotype, it should not be possible to obtain Chinese hamsters that breed true for spotting, unless the locus that produces spotting can somehow be separated from the lethality.

18. As discussed in the introduction to this chapter, Cuénot studied the genetic basis of yellow coat color in mice. He carried out a number of crosses between two yellow mice and obtained what he thought was a 3:1 ratio of yellow to gray mice in the progeny. The following table gives Cuénot's actual results, along with the results of a much larger series of crosses carried out by Castle and Little (Castle, W.E., and C. C. Little. 1910. *Science* 32:868–870).

Progeny resulting from crosses of yellow ´ yellow mice

Investigators	**yellow progeny**	**Non-yellow progeny**	**Total progeny**
Cuénot	263	100	363
Castle and Little	800	435	1,235
Both combined	1,063	535	1,598

a. Using a chi-square test, determine whether Cuénot's results are significantly different from the 3:1 ratio that he thought he observed. Are they different from a 2:1 ratio?

Testing Cuénot's data for a 3:1 ratio -

	Obs	*Expected (3:1)*	*O – E*	*(O – E)^2/E*
Yellow	*263*	*272.25*	*–9.25*	*0.314*
Non-yellow	*100*	*90.75*	*9.25*	*0.943*
Total	*363*	*363*		*1.257 = χ^2*

d.f. = 2 – 1 = 1
0.1 < p < .5
Cannot reject hypothesis of 3:1 ratio

Now test for 2:1 ratio -

	Obs	*Expected (2:1)*	*O – E*	*(O – E)^2/E*
Yellow	*263*	*242*	*21*	*1.82*
Non-yellow	*100*	*121*	*–21*	*3.64*

Total	*363*	*363*		*5.46 =* χ^2

d.f. = 1; $p < .025$

The observations are inconsistent with a 2:1 ratio.

b. Determine whether Castle and Little's results are significantly different from a 3:1 ratio. Are they different from a 2:1 ratio?

	Obs	*Expected (3:1)*	*O – E*	$(O - E)^2/E$
Yellow	*800*	*926.25*	*–126.25*	*17.2*
Non-yellow	*435*	*308.75*	*126.25*	*51.6*
Total	*1,235*	*1,235*		*68.8 =* χ^2

d.f. = 1; $p << .005$

Reject 3:1 ratio

	Obs	*Expected (2:1)*	*O – E*	$(O - E)^2/E$
Yellow	*800*	*823.3*	*–23.3*	*0.66*
Non-yellow	*435*	*411.7*	*23.3*	*1.32*
Total	*1,235*	*1,235*		*1.98 =* χ^2

d.f. = 1; $0.1 < p < 0.5$

Cannot reject 2:1 ratio

c. Combine the results of Castle and Cuénot and determine whether they are significantly different from a 3:1 ratio and a 2:1 ratio.

	Obs	*Expected (3:1)*	*O – E*	$(O - E)^2/E$
Yellow	*1,063*	*1,198.5*	*–135.5*	*15.3*
Non-yellow	*535*	*399.5*	*135.5*	*46.0*
Total	*1,598*	*1,598*		*61.3 =* χ^2

d.f. = 1; $p << .005$

Reject 3:1 ratio

	Obs	*Expected (2:1)*	*O – E*	$(O - E)^2/E$
Yellow	*1,063*	*1,065.3*	*–2.3*	*0.005*
Non-yellow	*535*	*532.7*	*2.3*	*0.010*
Total	*1,598*	*1,598*		*0.015 =* χ^2

d.f. = 1; $0.9 < p < 0.975$

Cannot reject 2:1 ratio

d. Offer an explanation for the different ratios that Cuénot and Castle obtained.
Cuénot had far smaller numbers of progeny, so his ratios are more susceptible to error from chance deviation. Indeed, only a slight shift in numbers of progeny would make Cuénot's data compatible with a 2:1 ratio as well as a 3:1 ratio. Investigator bias may also have played a role, based on the expectation of a 3:1 ratio.

Section 5.4

19. In the pearl millet plant, color is determined by three alleles at a single locus: Rp^1 (red), Rp^2 (purple), and *rp* (green). Red is dominant over purple and green, and purple is dominant over green ($Rp^1 > Rp^2 > rp$). Give the expected phenotypes and ratios of offspring produced by the following crosses:

    a. $Rp^1/Rp^2 \times Rp^1/rp$
    We expect ¼ $\mathrm{Rp}^1/\mathrm{Rp}^1$ *(red), ¼* $\mathrm{Rp}^1/\mathrm{rp}$ *(red), ¼* $\mathrm{Rp}^2/\mathrm{Rp}^1$ *(red), ¼* $\mathrm{Rp}^2/\mathrm{rp}$ *(purple), for overall phenotypic ratio of ¾ red, ¼ purple.*

    b. $Rp^1/rp \times Rp^2/rp$
    ¼ $\mathrm{Rp}^1/\mathrm{Rp}^2$ *(red), ¼* $\mathrm{Rp}^1/\mathrm{rp}$ *(red), ¼* $\mathrm{Rp}^2/\mathrm{rp}$ *(purple), ¼* rp/rp *(green), for overall phenotypic ratio of ½ red, ¼ purple, ¼ green.*

    c. $Rp^1/Rp^2 \times Rp^1/Rp^2$
    This cross is equivalent to a two-allele cross of heterozygotes, so the expected phenotypic ratio is ¾ red, ¼ purple.

    d. $Rp^2/rp \times rp/rp$
    Another two-allele cross of a heterozygote with a homozygous recessive. Phenotypic ratio is ½ purple, ½ green.

    e. $rp/rp \times Rp^1/Rp^2$
    ½ $\mathrm{Rp}^1/\mathrm{rp}$ *(red), ½* $\mathrm{Rp}^2/\mathrm{rp}$ *(purple)*

20. If there are five alleles at a locus, how many genotypes may there be at this locus? How many different kinds of homozygotes will there be? How many genotypes and homozygotes would there be with eight alleles?

    Mathematically, this question is the same as asking how many different groups of two (diploid genotypes have two alleles for each locus) are possible from n *objects (alleles). Assign numbers 1, 2, 3, 4, and 5 to each of the five alleles and group the possible genotypes according to the following table:*

1,1					
1,2	*2,2*				
1,3	*2,3*	*3,3*			
1,4	*2,4*	*3,4*	*4,4*		
1,5	*2,5*	*3,5*	*4,5*	*5,5*	

Such an arrangement allows us to easily see that the number of genotypes for any n *number of alleles is simply* □ *(1, 2, 3 …* n*)* = n(n+1)/2*. Looking at the table, we see that the number of filled boxes (genotypes) is equal to half the number of boxes in a rectangle of dimensions* n × (n+1)*. So, the number of genotypes =* n(n+1)/2*. For five alleles (*n = 5*), we get 15 possible genotypes and five homozygotes. For eight alleles, there are 8(8+1)/2 = 36 possible genotypes.*

21. Turkeys have black, bronze, or black-bronze plumage. Examine the results of the following crosses:

Parents	**Offspring**
Cross 1: black and bronze	All black
Cross 2: black and black	¾ black, ¼ bronze
Cross 3: black-bronze and black-bronze	All black-bronze
Cross 4: black and bronze	½ black, ¼ bronze, ¼ black-bronze
Cross 5: bronze and black-bronze	½ bronze, ½ black-bronze
Cross 6: bronze and bronze	¾ bronze, ¼ black-bronze

Do you think these differences in plumage arise from incomplete dominance between two alleles at a single locus? If yes, support your conclusion by assigning symbols to each allele and providing genotypes for all turkeys in the crosses. If your answer is no, provide an alternative explanation and assign genotypes to all turkeys in the crosses.

The results of Cross 2 tell us that black is dominant to bronze. Similarly, the results of Cross 6 tell us that bronze is dominant to black-bronze. We can use B^L *for black,* B^R *for bronze, and* b *for black-bronze.*

Parents	***Offspring***
Cross 1: black (B^LB^L) × *bronze* (B^RB^R)	*All black* (B^LB^R)
Cross 2: black (B^LB^R) × *black* (B^LB^R)	*¾ black* (B^L--), *¼ bronze* (B^RB^R)
Cross 3: black-bronze (bb) × *black-bronze* (bb)	*All black-bronze* (bb)
Cross 4: black (B^Lb) × *bronze* (B^Rb)	*½ black* (B^L--), *¼ bronze* (B^Rb), *¼ black-bronze* (bb)
Cross 5: bronze (B^Rb) × *black-bronze* (bb)	*½ bronze* (B^Rb), *½ black-bronze* (bb)
Cross 6: bronze (B^Rb) × *bronze* (B^Rb)	*¾ bronze* (B^R--), *¼ black-bronze* (bb)

22. In rabbits, an allelic series helps to determine coat color: C (full color), c^{ch} (chinchilla, gray color), c^h (Himalayan, white with black extremities), and c (albino, all white). The C allele is dominant over all others, c^{ch} is dominant over c^h and c, c^h is dominant over c, and c is recessive to all the other alleles. This dominance hierarchy can be summarized as $C > c^{ch} > c^h > c$. The rabbits in the following list are crossed and produce the progeny shown. Give the genotypes of the parents for each cross.

a. full color × albino ▯ ½ full color, ½ albino
   Cc × cc. *1:1 phenotypic ratios in the progeny result from a cross of a heterozygote with a homozygous recessive. Because albino is recessive to all other alleles, the full-color parent must have an albino allele, and the albino parent must be homozygous for the albino allele.*

b. himalayan × albino ▯ ½ himalayan, ½ albino
   c^hc × cc. *Again, the 1:1 ratio of the progeny indicate the parents must be a heterozygote and a homozygous recessive.*

c. full color × albino ▯ ½ full color, ½ chinchilla

Cc^{ch} × cc. *This time, we get a 1:1 ratio, but we have chinchilla progeny instead of albino. Therefore, the heterozygous full-color parent must have a chinchilla allele as well as a dominant full-color allele. The albino parent has to be homozygous albino because albino is recessive to all other alleles.*

d. full color × himalayan ½ full color, ¼ himalayan, ¼ albino
Cc × c^hc. *The 1:2:1 ratio in the progeny indicates that both parents are heterozygotes. Both must have an albino allele because the albino progeny must have inherited an albino allele from each parent.*

e. full color × full color ¾ full color, ¼ albino
Cc × Cc. *The 3:1 ratio indicates that both parents are heterozygous. Both parents must have an albino allele for albino progeny to result.*

23. In this chapter, we discussed Joan Barry's paternity suit against Charlie Chaplin and how, on the basis of blood types, Chaplin could not have been the father of her child.

a. What blood types are possible for the father of Barry's child?
Because Barry's child inherited an I^B *allele from the father, the father could have been B or AB.*

b. If Chaplin had possessed one of these blood types, would that prove that he fathered Barry's child?

No. Many other men have these blood types. The results would have meant only that Chaplin cannot be eliminated as a possible father of the child.

*24. A woman has blood type A MM. She has a child with blood type AB MN. Which of the following blood types could *not* be that of the child's father? Explain your reasoning.

George	O	NN
Tom	AB	MN
Bill	B	MN
Claude	A	NN
Henry	AB	MM

The child's blood type has a B allele and an N allele that could not have come from the mother and must have come from the father. Therefore, the child's father must have a B and an N. George, Claude, and Henry are eliminated as possible fathers because they lack either a B or an N.

Section 5.5

*25. In chickens, comb shape is determined by alleles at two loci (*R*, *r* and *P*, *p*). A walnut comb is produced when at least one dominant allele *R* is present at one locus and at least one dominant allele *P* is present at a second locus (genotype *R_ P_*). A rose comb is produced when at least one dominant allele is present at the first locus and two recessive alleles are present at the second locus (genotype *R_ pp*). A pea comb is produced when two recessive alleles are present at the first locus and at least one dominant allele is present at the second (genotype *rr P_*). If two recessive alleles are present at the first and at the second locus (*rr pp*), a single comb is produced. Progeny with what types of combs and in what proportions will result from the following crosses?

a. *RR PP* × rr pp
All walnut (Rr Pp)
b. *Rr Pp* × *rr pp*
¼ walnut (Rr Pp), *¼ rose* (Rr pp), *¼ pea* (rr Pp), *¼ single* (rr pp)
c. *Rr Pp* × *Rr Pp*
9/16 walnut (R_ P_), *3/16 rose* (R_ pp), *3/16 pea* (rr P_), *1/16 single* (rr pp)
d. *Rr pp* × *Rr pp*
¾ rose (R_ pp), *¼ single* (rr pp)
e. *Rr pp* × *rr Pp*
¼ walnut (Rr Pp), *¼ rose* (Rr pp), *¼ pea* (rr Pp), *¼ single* (rr pp)
f. *Rr pp* × *rr pp*
½ rose (Rr pp), *½ single* (rr pp)

*26. Tatuo Aida investigated the genetic basis of color variation in the Medaka *(Aplocheilus latipes),* a small fish that occurs naturally in Japan (T. Aida. 1921. *Genetics* 6:554–573). Aida found that genes at two loci (*B, b* and *R, r*) determine the color of the fish: fish with a dominant allele at both loci (*B_ R_*) are brown, fish with a dominant allele at the *B* locus only (*B_ rr*) are blue, fish with a dominant allele at the *R* locus only (*bb R_*) are red, and fish with recessive alleles at both loci (*bb rr*) are white. Aida crossed a homozygous brown fish with a homozygous white fish. He then backcrossed the F_1 with the homozygous white parent and obtained 228 brown fish, 230 blue fish, 237 red fish, and 222 white fish.

a. Give the genotypes of the backcross progeny.
Each of the backcross progeny received recessive alleles b *and* r. *Their phenotype is therefore determined by the alleles received from the other parent:*
Brown fish are Bb Rr*; blue fish are* Bb rr*; red fish are* bb Rr*; and white fish are* bb rr.
b. Use a chi-square test to compare the observed numbers of backcross progeny with the number expected. What conclusion can you make from your chi-square results?
We expect a 1:1:1:1 ratio of the four phenotypes.

	Observed	*Expected*	*O – E*	*(O – E)²/E*
Brown	*228*	*229.25*	*–1.25*	*.007*
Blue	*230*	*229.25*	*0.75*	*.002*
Red	*237*	*229.25*	*7.75*	*.262*
White	*222*	*229.25*	*–7.25*	*.229*
Total	*917*	*917*		*.5 =* χ^2

d.f. = 4 – 1 = 3; .9 < p < .975; we cannot reject the hypothesis.

c. What results would you expect for a cross between a homozygous red fish and a white fish?
The homozygous red fish would be bb RR, *crossed to* bb rr. *All progeny would be* bb Rr, *or red fish.*
d. What results would you expect if you crossed a homozygous red fish with a homozygous blue fish and then backcrossed the F_1 with a homozygous red parental fish?

Homozygous red fish bb RR × *homozygous blue fish* BB rr
F_1 *will be all brown:* Bb Rr *backcrossed to* bb RR *(homozygous red parent)*
Backcross progeny will be in equal proportions Bb RR *(brown);* Bb Rr *(brown);* bb RR *(red); and* bb Rr *(red). Overall, ½ brown and ½ red.*

27. A variety of opium poppy (*Papaver somniferum L.*) having lacerate leaves was crossed with a variety that has normal leaves. All the F_1 had lacerate leaves. Two F_1 plants were interbred to produce the F_2. Of the F_2, 249 had lacerate leaves and 16 had normal leaves. Give genotypes for all the plants in the P, F_1, and F_2 generations. Explain how lacerate leaves are determined in the opium poppy.
The F_1 *progeny tell us that lacerate is dominant over normal leaves. In the* F_2*, 249:16 does not come close to a 3:1 ratio. Let's see if these numbers fit a dihybrid ratio. Dividing 265 total progeny by 16 (because dihybrid ratios are based on 16ths), we see that 1/16 of 265 is 16.56. Therefore, the* F_2 *progeny are very close to 15/16 lacerate, 1/16 normal, a modified dihybrid ratio. If we symbolize the two genes as* A *and* B, *then:*
F_1 Aa Bb × Aa Bb *all lacerate*
F_2 *9/16* A- B- *lacerate (like* F_1*)*
3/16 A- bb *lacerate*
3/16 aa B- *lacerate*
1/16 aa bb *normal*
A dominant allele at either gene A *or gene* B, *or both, results in lacerate leaves. Finally, the parents must have been* AA BB *lacerate* × aa bb *normal. Note that only* AA BB *for the lacerate parent would result in* F_1 *that are* Aa Bb.

28. E. W. Lindstrom crossed two corn plants with green seedlings and obtained the following progeny: 3583 green seedlings, 853 virescent-white seedlings, and 260 yellow seedlings. (E. W. Lindstrom. 1921. *Genetics* 6:91–110).

    a. Give the genotypes for the green, virescent-white, and yellow progeny.
    There are 4,696 total progeny. Green appears dominant. The ratios at first glance don't fit any type of incomplete dominance for a single locus, so we hypothesize multiple loci with gene interactions. The simplest case is two loci, so we look for a fit to a ratio based on 1/16 of the total: 293.5. Quick computation with a calculator shows that these numbers are close to a 12:3:1 ratio of green:virescent-white:yellow, a modified 9:3:3:1 ratio. Let's define G *and* g *for one locus, and* Y *and* y *for the other locus.*
    9 G_ Y_ *+ 3* G_ yy *= 12 green*
    3 gg Y_ *= 3 virescent-white*
    1 gg yy *= 1 yellow*

    b. Provide an explanation for how color is determined in these seedlings.
    The green arises when the G *locus is dominant, regardless of the alleles at the other* Y *locus. Yellow requires that both loci be recessive, and virescent-white arises when the* G *locus is homozygous recessive, and the* Y *locus has a dominant allele.*
    c. Does epistasis occur among the genes that determine color in the maize seedlings? If so, which gene is epistatic and which is hypostatic?
    As defined above, the G *locus is the epistatic locus. It is an example of dominant epistatis, because a dominant allele at this locus masks the effect of the* Y *locus. The*

Y *locus is hypostatic, and its effect revealed only when the epistatic locus is homozygous recessive.*

*29. A dog breeder liked yellow and brown Labrador retrievers. In an attempt to produce yellow and brown puppies, he bought a yellow Labrador male and a brown Labrador female and mated them. Unfortunately, all the puppies produced in this cross were black. (See pp. 113–114 for a discussion of the genetic basis of coat color in Labrador retrievers.)

a. Explain this result.
Labrador retrievers vary in two loci, B *and* E. *Black dogs have dominant alleles at both loci* (B- E-), *brown dogs have* bb E-, *and yellow dogs have* B- ee *or* bb ee. *Because all the puppies were black, they must all have inherited a dominant* B *allele from the yellow parent, and a dominant* E *allele from the brown parent. The brown female parent must have been* bb EE, *and the yellow male must have been* BB ee. *The black puppies were all* Bb Ee.

b. How might the breeder go about producing yellow and brown Labradors?
Simply mating yellow with yellow will produce all yellow Labrador puppies. Mating two brown Labradors will produce either all brown puppies, if at least one of the parents is homozygous EE, *or ¾ brown and ¼ yellow if both parents are heterozygous* Ee.

30. When a yellow female Labrador retriever was mated with a brown male, half of the puppies were brown and half were yellow. The same female, when mated to a different brown male, produced all brown males. Explain these results.
The first brown male was heterozygous for the E *locus, hence he was* bb Ee. *The yellow female has to be* bb ee. *The puppies from this first mating were therefore ½* bb Ee *(brown) and ½* bb ee *(yellow). The second brown male was homozygous* bb EE. *Thus, all the puppies from the second mating were* bb Ee *(brown).*

*31. A summer squash plant that produces disc-shaped fruit is crossed with a plant that produces long fruit. All the F_1 have disc-shaped fruit. When the F_1 are intercrossed, F_2 progeny are produced in the following ratio: 9/16 disc-shaped fruit: 6/16 spherical fruit: 1/16 long fruit. Give the genotypes of the F_2 progeny.
The modified dihybrid ratio in the F_2 *indicates that two genes interact to determine fruit shape. Using generic gene symbols* A *and* B *for the two loci, the* F_1 *heterozygotes are* Aa Bb.

The F_2 *are:*
9/16 A- B- *disc-shaped (like* F_1*)*
3/16 A- bb *spherical*
3/16 aa B- *spherical*
1/16 aa bb *long*

32. Some sweet-pea plants have purple flowers and other plants have white flowers. A homozygous variety of pea that has purple flowers is crossed with a homozygous variety that has white flowers. All the F_1 have purple flowers. When these F_1 are self-fertilized, the F_2 appear in a ratio of 9/16 purple to 7/16 white.

a. Give genotypes for the purple and white flowers in these crosses.
The F_2 *ratio of 9:7 is a modified dihybrid ratio, indicating two genes interacting. Using* A *and* B *as generic gene symbols, we can start with the* F_1 *heterozygotes:*

F_1 AaBb *purple self-fertilized*
F_2 *9/16* A- B- *purple (like* F_1*)*
3/16 A- bb *white*
3/16 aa B- *white*
1/16 aa bb *white*

Now we see that purple requires dominant alleles for both genes, so the purple parent must have been AA BB, *and the white parent must have been* aa bb *to give all purple* F_1.

b. Draw a hypothetical biochemical pathway to explain the production of purple and white flowers in sweet peas.

$$\textit{White precursor 1} \xrightarrow[\textit{Enzyme A}]{} \textit{white intermediate 2} \xrightarrow[\textit{Enzyme B}]{} \textit{purple pigment}$$

33. For the following questions, refer to pages 113–114 for a discussion of how coat color and pattern are determined in dogs.

a. Why are Irish setters reddish in color?
According to the information in Table 5.3, Irish setters are BBeeSS, *and* A *or* a^t. *The* B *permits expression of black pigment, but the* ee *genotype prevents black color on the body coat,resulting in a reddish color except on the nose and in the eyes. The* S *prevents spotting, resulting in a uniform coat color.*

b. Can a poodle crossed with any other breed produce spotted puppies? Why or why not?
Poodles are SS. *Because the dominant* S *allele prevents spotting, no puppies from matings with poodles will have spotting.*

c. If a St. Bernard is crossed with a Doberman, will the offspring have solid, yellow, saddle, or bicolor coats?
St. Bernards are a^ya^yBB, *and Dobermans are* a^ta^tEESS. *The offspring will be of genotype* a^ya^tB-E-S-. *Because* a^y *specifying yellow is dominant over* a^t, *and the* E *allele allows expression of the* A *genotype throughout, the offspring will have yellow coats.*

d. If a Rottweiler is crossed with a Labrador Retriever, will the offspring have solid, yellow, saddle, or bicolor coats?
Rottweilers are a^ta^tBBEESS, *and Labrador Retrievers are* A^sA^sSS. *The offspring will be* A^sa^tB-E-SS. *The combination of the dominant* A^s *and* E *alleles should create solid coats.*

Section 5.6

34. Male-limited precocious puberty results from a rare, sex-limited autosomal allele (*P*) that is dominant over the allele for normal puberty (*p*) and is expressed only in males. Bill undergoes precocious puberty, but his brother Jack and his sister Beth underwent puberty at the usual time, between the ages of 10 and 14. Although Bill's mother and father underwent normal puberty, two of his maternal uncles (his mother's brothers) underwent precocious puberty. All of Bill's grandparents underwent normal puberty. Give the most likely genotypes for all the relatives mentioned in this family.

Since precocious puberty is dominant, all the males who experienced normal puberty, such as Jack, Bill's father, and Bill's grandfathers, must be pp. *Bill and his two maternal uncles, who all experienced precocious puberty, are* Pp. *We know they are heterozygotes not only because* P *is a rare allele but also because these individuals all had fathers that are* pp. *This means Bill inherited* P *from his mother, who must have been* Pp. *Bill's sister Beth could be either* Pp *or* pp.

35. In some goats, the presence of horns is produced by an autosomal gene that is dominant in males and recessive in females. A horned female is crossed with a hornless male. The F_1 offspring are intercrossed to produce the F_2. What proportion of the F_2 females will have horns?
Let H^+ *represent the allele for the presence of horns and* H^- *represent the allele for hornlessness. Since* H^+ *is recessive in females, the horned female parent must be* H^+H^+. *The hornless male is* H^-H^- *because the absence of horns is recessive in males. Then their* F_1 *progeny must be all heterozygous* H^+H^-. *An intercross of the* F_1 *would produce both male and female progeny in the ratio of 1* H^+H^+, *2* H^+H^-, *and 1* H^-H^-. *Again, remembering that* H^+ *is recessive in females, we would expect a ratio of 3:1 hornless to horned females.*

36. In goats, a beard is produced by an autosomal allele that is dominant in males and recessive in females. We'll use the symbol B^b for the beard allele and B^+ for the beardless allele. Another independently assorting autosomal allele that produces a black coat (W) is dominant over the allele for white coat (w). Give the phenotypes and their proportions expected for the following crosses:

a. B^+B^b Ww male × B^+B^b Ww female
Because beardedness and coat color independently assort, we can treat them independently. The difference between this cross and a dihybrid cross is that the bearded allele B^b *is dominant in males and recessive in females. So we deal with male and female progeny separately. For each sex, then, we should get a typical dihybrid ratio. In males, the dominant phenotype is bearded, so we should get ¾ bearded, ¼ beardless. In females the dominant phenotype is beardless, so we should get ¾ beardless and ¼ bearded. Each sex will have ¾ black and ¼ white coats.*

Males:	*9/16 bearded, black*	*Females:*	*9/16 beardless, black*
	3/16 bearded, white		*3/16 beardless, white*
	3/16 beardless, black		*3/16 bearded, black*
	1/16 beardless, white		*1/16 bearded, white*

b. B^+B^b Ww male × B^+B^b ww female
Here the males will again be ¾ bearded and ¼ beardless, and the females will be ¾ beardless and ¼ bearded. This time half the progeny of either sex will be black, and half will be white.

Males:	*3/8 bearded, black*	*Females:*	*3/8 beardless, black*
	3/8 bearded, white		*3/8 beardless, white*
	1/8 beardless, black		*1/8 bearded, black*
	1/8 beardless, white		*1/8 bearded, white*

c. B^+B^+ Ww male × B^bB^b Ww female
In this cross, all of the male progeny will be bearded, and all of the female progeny will be beardless. All will be ¾ black, ¼ white.

Males:	*¾ bearded, black*	*Females:*	*¾ beardless, black*
	¼ bearded, white		*¼ beardless, white*

d. B^+B^b *Ww* male × B^bB^b *ww* female
Males will be all bearded, and females will be ½ bearded, ½ beardless. Both males and females will be ½ black, ½ white.

Males:	*½ bearded, black*	*Females:*	*¼ beardless, black*
	½ bearded, white		*¼ beardless, white*
			¼ bearded, black
			¼ bearded, white

37. J. K. Breitenbecher (1921. *Genetics* 6:65–86) investigated the genetic basis of color variation in the four-spotted cowpea weevil *(Bruchus quadrimaculatus).* The weevils were red, black, white, or tan. Breitenbecher found that four alleles (R, R^b, R^w, and r) at a single locus determine color. The alleles exhibit a dominance hierarchy, with red (R) dominant over all other alleles, black (R^b) dominant over white (R^w) and tan (r), white dominant over tan, and tan recessive to all others ($R > R^b > R^w > r$). The following genotypes encode each of the colors:

RR, RR^b, RR^w, Rr red
R^bR^b, R^bR^w, R^br black
R^wR^w, R^wr white
rr tan

Color variation in this species is sex-limited to females: males carry color genes but are always tan regardless of their genotype. For each of the following crosses carried out by Breitenbecher, give all possible genotypes of the parents.

Parents **Progeny**

a. tan ´ tan 78 red , 70 white , 184 tan
rr □RR^w*; the tan female has only one possible genotype. We ignore the male progeny, and see that the female progeny are 1:1 red white, so the tan male parent must have been heterozygous with both red and white alleles.*

b. black ´ tan 151 red , 49 black , 61 tan , 249 tan
The black female is R^{b}r*, the male is* Rr*. The tan female progeny indicates that both parents had a tan allele. The black female must then have a black allele, and the red progeny can arise only if the male has a red allele.*

c. white ´ tan 32 red , 31 tan
The white female could be either R^{w}R^w *or* R^{w}r*. The male parent must be* RR*, to produce all red female progeny.*

d. black ´ tan 3586 black , 1282 tan , 4791 tan
Black female is R^{b}r*, and the male is* R^{b}r*, to produce a 3:1 ratio of black to tan.*

e. white ´ tan 594 white , 189 tan , 862 tan
R^{w}r *female and* R^{w}r *male, to produce 3:1 white to tan.*

f. black ´ tan 88 black , 88 tan , 186 tan
Black female is R^{b}r*, the male is* rr*, to produce a 1:1 ratio of black to tan.*

g. tan ´ tan 47 white , 51 tan , 100 tan
Tan female can be only rr*; male must be* R^wr.

h. red ´ tan 1932 red , 592 tan , 2587 tan
Red female is Rr*; male is also* Rr.

i. white ´ tan 13 red , 6 white , 5 tan , 19 tan
White female is R^wr*; male is* Rr.

j. red ´ tan 190 red , 196 black , 311 tan
RR^b *female and* R^bR^b *male. The 1:1 ratio is produced by a heterozygote crossed with a homozygous recessive.*

k. black ´ tan 1412 black , 502 white , 1766 tan
R^bR^w *female and* R^bR^w *male, to produce 3:1 black to white progeny. Additionally, either one of the parents, but not both, could be* R^br.

38. Shell coiling of the snail *Limnaea peregra* results from a genetic maternal effect. An autosomal allele for a right-handed shell (s^+), called dextral, is dominant over the allele for a left-handed shell (*s*), called sinistral. A pet snail called Martha is sinistral and reproduces only as a female (the snails are hermaphroditic). Indicate which of the following statements are true and which are false. Explain your reasoning in each case.

a. Martha's genotype *must* be *ss.*
False. For maternal effect genes, the phenotype of the individual is determined solely by the genotype of the individual's mother. So we know Martha's mother must have been ss *because Martha is sinistral. If Martha was produced as a result of self-fertilization, then Martha must indeed be* ss. *But if Martha was produced by cross-fertilization, then we cannot know Martha's genotype without more information.*

b. Martha's genotype cannot be s^+s^+.
True. As explained in the answer to part (a), Martha's mother is ss, *so Martha must be either* s^+s *or* ss.

c. All the offspring produced by Martha *must* be sinistral.
False. Because we do not know Martha's genotype, we cannot yet predict the phenotype of her offspring.

d. At least some of the offspring produced by Martha *must* be sinistral.
False. If Martha is s^+s, *then all her children will be dextral. If Martha is* ss, *then all her children will be sinistral.*

e. Martha's mother *must* have been sinistral.
False. Martha's mother's phenotype is determined by the genotype of her *mother (Martha's maternal grandmother). We know Martha's mother's genotype must have been* ss, *so her mother's mother had at least one* s *allele. But we cannot know if she was a heterozygote or homozygous* ss.

f. All Martha's brothers *must* be sinistral.
True. Because Martha's mother must have been ss, *all her progeny must be sinistral.*

39. Hypospadias, a birth defect in male humans in which the urethra opens on the shaft instead of the tip of the penis, results from an autosomal dominant gene in some families. Females who carry the gene show no effects. This is an example of: (a) an X-linked trait, (b) a Y-linked trait, (c) a sex-limited trait, (d) a sex influenced trait, or (e) genetic maternal effect? Explain your answer.
Knowing that the condition arises from an autosomal gene, we can eliminate either (a) an X-linked trait or (b) a Y-linked trait. Dominant inheritance also eliminates (e) maternal

effect. If it were (d) a sex influenced trait, females would be affected to a lesser degree or differently than males. Because females who carry the gene show no effects, this condition is (c) a sex-limited trait.

40. In unicorns, two autosomal loci interact to determine the type of tail. One locus controls whether a tail is present at all; the allele for a tail (*T*) is dominant over the allele for tailless (*t*). If a unicorn has a tail, then alleles at a second locus determine whether the tail is curly or straight. Farmer Baldridge has two unicorns with curly tails. When he crosses these two unicorns, ½ of the progeny have curly tails, ¼ have straight tails, and ¼ do not have a tail. Give the genotypes of the parents and progeny in Farmer Baldridge's cross. Explain how he obtained the 2:1:1 phenotypic ratio in his cross.
We are given the symbols T *for dominant tailed and* t *for recessive tailless. We are not given any information about dominance or recessiveness for the second locus. We will use* S *and* s *for the second locus that determines whether the tail is curly or straight. Although two genes are interacting, we can analyze one locus at a time. Farmer Baldridge crossed two unicorns with tails and got a 3:1 ratio of tailed to tailless. Therefore, the two unicorns were heterozygous for the tail locus:* Tt. *The parents were both curly, and the progeny were both curly and straight, in a 2:1 ratio of curly:straight. The fact that he got straight-tailed progeny indicates that the curly tailed parents were heterozygous* Ss. *The fact that he got a 2:1 ratio instead of a 3:1 ratio indicates that this locus may not have a dominant:recessive relationship. A 2:1 ratio may be obtained if ¼ of the progeny, one of the homozygote classes, are missing (because of embryonic lethality).*

Having deduced the genotypes of the parents, we can determine the expected genotypes of the progeny:

P: curly tailed Tt Ss × *curly tailed* Tt Ss
Using a branch diagram:

¼ SS = *3/16 straight-tailed*
¾ T- → ½ Ss = *6/16 curly tailed*
¼ ss = *3/16 lethal*

and

¼ SS = *1/16 tailless*
¼ tt → ½ Ss = *2/16 tailless*
¼ ss = *1/16 lethal*

Because 4/16 of the progeny die, leaving 12/16 viable, the surviving progeny would be 6/12 curly tailed, 3/12 straight-tailed, and 3/12 tailless, which reduces to a 2:1:1 ratio of curly tailed to straight-tailed to tailless.

If S *were dominant over* s *without lethality, we would expect the following* F_1:

9/16 T- S- *curly tailed*
3/16 T- ss *straight-tailed*
3/16 tt S- *tailless*
1/16 tt ss *tailless*

However, these predictions do not fit the observed 2:1:1 ratio.

41. In 1983, a sheep farmer in Oklahoma noticed a ram in his flock that possessed increased muscle mass in his hindquarters. Many of the offspring of this ram possessed the same trait, which became known as the callipyge mutant (*callipyge* is Greek for "beautiful buttocks"). The mutation that caused the callipyge phenotype was eventually mapped to a position on the sheep chromosome 18.

    When the male callipyge offspring of the original mutant ram were crossed with normal females, they produced the following progeny: ¼ male callipyge, ¼ female callipyge, ¼ male normal, and ¼ female normal. When female callipyge offspring of the original mutant ram were crossed with normal males, all of the offspring were normal. Analysis of the chromosomes of these offspring of callipyge females showed that half of them received a chromosome 18 with the callipyge gene from their mother. Propose an explanation for the inheritance of the callipyge gene. How might you test your explanation?
    Here we get different results depending on the sex of the parent with the callipyge mutation. Because we know the gene is on chromosome 18, we can eliminate sex linkage as a possible cause. The phenotype is also not sex-limited because male callipyge sire equal proportions of male and female callipyge offspring. We can further eliminate maternal inheritance for the same reason. That leaves imprinting as a possible explanation. We note that half the progeny are callipyge if the father has the mutation, but none express the callipyge mutation if the mother has the mutation. We can therefore hypothesize that maternal alleles of this gene undergo imprinting and are silenced, so that the embryo expresses only the paternal allele.

    We can test this hypothesis by mating the phenotypically normal male and female progeny that inherited the chromosome 18 with the callipyge gene from their mother. The hypothesis predicts that males will have normal and callipyge progeny if mated to either a normal female or a callipyge female. Conversely, the females will have all normal progeny if mated to a normal male, and both normal and callipyge progeny if mated to a callipyge male. In short, the progeny will reflect the genotype of the father, and the genotype of the mother will not be expressed.

Section 5.8

42. Which of the following statements is an example of a phenocopy? Explain your reasoning.

    a. Phenylketonuria results from a recessive mutation that causes light skin as well as mental retardation.
    Phenocopy is an environmentally induced phenotype that resembles a phenotype produced by a genotype. Since phenylketonuria has a genetic basis, this is not a phenocopy. One genotype affecting multiple traits is called pleitrophy.

    b. Human height is influenced by genes at many different loci.

This is again not an example of phenocopy, but of a continuous characteristic or a quantitative trait.

c. Dwarf plants and mottled leaves in tomatoes are caused by separate genes that are linked.
Linkage of genes is not an example of phenocopy.

d. Vestigial wings in *Drosophila* are produced by a recessive mutation. This trait is also produced by high temperature during development.
This is indeed an example of phenocopy because an environmental factor produces a phenotype that resembles the phenotype generated by a genotype.

e. Intelligence in humans is influenced by both genetic and environmental factors.
As long as there is a significant effect of the underlying genotype, this is not a phenocopy. The expression of many genotypes is indeed influenced by environmental factors.

43. Long ears in some dogs are an autosomal dominant trait. Two dogs mate and produce a litter in which 75% of the puppies have long ears. Of the dogs with long ears in this litter, 1/3 are known to be phenocopies. What are the most likely genotypes of the two parents of this litter?
Accounting for the phenocopies, we have 50% (subtracting 1/3 that are phenocopies from the 75%) of the puppies having the autosomal dominant genotype for long ears, and 50% having the recessive genotype. Therefore, one parent is homozygous recessive, and the other parent is a heterozygote.

CHALLENGE QUESTION

Section 5.1

44. Pigeons have long been the subject of genetic studies. Indeed, Charles Darwin bred pigeons in the hope of unraveling the principles of heredity but was unsuccessful. A series of genetic investigations in the early 1900s worked out the hereditary basis of color variation in these birds. W. R. Horlancher was interested in the genetic basis of kiteness, a color pattern that consists of a mixture of red and black stippling of the feathers. Horlancher knew from earlier experiments that black feather color was dominant over red. He carried out the following crosses to investigate the genetic relationship of kiteness to black and red feather color (W. R. Horlancher. 1930. *Genetics* 15:312–346).

Cross	**Offspring**
kitey ´ kitey	16 kitey, 5 black, 3 red
kitey ´ black	6 kitey, 7 black
red ´ kitey	18 red, 9 kitey, 6 black

a. On the basis of these results and the assumption that black is dominant over red, propose an hypothesis to explain the inheritance of kitey, black, and red feather color in pigeons.
The first cross of kitey kitey indicates that both kitey parents must be heterozygous, to produce black and red progeny in addition to kitey progeny. The second cross, yielding a 1:1 ratio of the two parental phenotypes, is consistent with a mating between a heterozygote and a homozygous recessive. The third cross, also yielding progeny of three different phenotypes, again must be between two

heterozygotes. The challenge is to assign genotypes to the parents and progeny that is consistently explains all three crosses.

Given that black is dominant over red, we have to introduce at least one additional allele to account for kitey. Starting with the simplest possible model, let's define C^B *as the allele for black,* C^R *as the allele for red, and* C^K *as the allele for kitey. Starting with cross 1, if the two kitey parents are heterozygotes, then kitey must be the dominant allele. The recessive alleles must be different in the two kitey parents, or else the progeny would show a 3:1 phenotypic ratio. So we can assign* C^KC^B *and* C^KC^R *for the two parents, and the progeny will be:*

C^KC^B – *kitey, like one parent*
C^KC^R – *kitey, like the other parent*
C^BC^R – *black, because black is dominant over red*
C^KC^K – *red, because all other genotypes are accounted for*

The problem with this scheme is that it cannot account for the third cross of red × kitey. This scheme indicates that red is either homozygous C^RC^R *or* C^KC^K*, and the red parent in the third cross must be heterozygous. In fact, there is no way three alleles can be sufficient to account for all three crosses.*

Let's try accounting for the two kitey parents in cross 1 with different kitey alleles, C^{K1} *and* C^{K2}*:*

P: $C^{K1}C^B$ *(kitey) ×* $C^{K2}C^R$ *(kitey)*
F_1*:* $C^{K2}C^B$ – *kitey?*
$C^{K1}C^R$ – *red?*
C^BC^R – *black*
$C^{K1}C^{K2}$ – *kitey?*

Cross 2 would then be:

$C^{K1}C^B$ *(kitey) ×* C^BC^B *(black) →* $C^{K1}C^B$ *(kitey) +* C^BC^B *(black) in 1:1 ratio*

Cross 3 would then be:

P: $C^{K1}C^R$ *(red) ×* $C^{K1}C^B$ *(black)*
F_1*:* $C^{K1}C^B$ – *kitey*
$C^{K1}C^R$ – *red*
$C^{K1}C^{K1}$ – *red?*
Expected progeny phenotypic ratio: 2 red, 1 kitey, 1 black

In this revised model, C^{K2} *is a kitey allele that is dominant over all other alleles.* C^B *is dominant over* C^R*, as given in the problem, and* C^R *is dominant over* C^{K1}*.* C^{K1}*, however, is dominant over* C^B *– modifies the black allele to produce a kitey phenotype. In the absence of the black allele,* C^{K1} *produces red; hence* C^{K1} *homozygotes or heterozygotes with* C^R *are all red.*

b. For each cross given above, test your hypothesis by using a chi-square test.

Cross 1:

	Observed	*Expected*	*O – E*	$(O - E)^2/E$
Kitey	*16*	*12*	*4*	*1.33*
Black	*5*	*6*	*–1*	*0.17*
Red	*3*	*6*	*–3*	*1.50*
Total	*24*	*24*		$3.0 = \chi^2$

d.f. = 2; .1 < p < .5; do not reject hypothesis.

Cross 2:

	Observed	*Expected*	*O – E*	*(O – E)²/E*
Kitey	*6*	*6.5*	*–0.5*	*.04*
Black	*7*	*6.5*	*0.5*	*.04*
Total	*13*	*13*		*.08 =* χ^2

d.f. = 1; .5 < p < .9; do not reject hypothesis

Cross 3:

	Observed	*Expected*	*O – E*	*(O – E)²/E*
Kitey	*9*	*8.25*	*0.75*	*0.07*
Black	*6*	*8.25*	*–2.25*	*0.61*
Red	*18*	*16.5*	*1.5*	*0.14*
Total	*33*	*33*		*0.82 =* χ^2

d.f. = 2; .5 < p < .9; do not reject hypothesis

Section 5.6

45. Suppose that you are tending a mouse colony at a genetics research institute and one day you discover a mouse with twisted ears. You breed this mouse with twisted ears and find that the trait is inherited. Male and female mice have twisted ears, but when you cross a twisted-eared male with normal-eared female, you obtain different results from those you obtained when you cross a twisted-eared female with normal-eared male—the reciprocal crosses give different results. Describe how you would go about determining whether this trait results from a sex-linked gene, a sex-influenced gene, a genetic maternal effect, a cytoplasmically inherited gene, or genomic imprinting. What crosses would you conduct and what results would be expected with these different types of inheritance?

Each of these is a distinct pattern of inheritance. Because male and females have twisted ears (te)*, Y-linkage is eliminated. X-linked genes are passed from mother to son and from father to daughter. A sex-influenced gene shows a different phenotype depending on the sex but is inherited autosomally. A genetic maternal effect depends only on the genotype of the mother; the genotype of the zygote is immaterial. A cytoplasmically inherited trait is serially perpetuated from mother to all her progeny. Genomic imprinting results in the gene of only one of the parents being expressed.*

To distinguish among these possibilities, you will need pure-breeding lines of mice with twisted ears and normal ears. Perform reciprocal crosses of males with twisted ears to females with normal ears (cross A) and males with normal ears to females with twisted ears (cross B).

	A: te *male × normal female*		*B: normal male ×* te *female*	
	F_1 *males*	F_1 *females*	F_1 *males*	F_1 *females*
Sex-linked	*All normal*	*All dominant*	*All te*	*All dominant*
Sex-influenced	*Het male*	*Het female*	*Het male*	*Het female*
Maternal	*Normal*	*Normal*	*te*	*te*
Cytoplasmic	*Normal*	*Normal*	*te*	*te*
Imprinting pat	*Normal*	*Normal*	*te*	*te*
Imprinting mat	te	te	*Normal*	*Normal*

What we see from the table above is that if the trait is sex-linked, cross A and cross B give different phenotypes for the F_1 males, which match the phenotypes of their mothers. The F_1 females have the same dominant phenotype in either cross. If the trait is sex-influenced (heterozygous males have a different phenotype than heterozygous females), these reciprocal crosses with pure-breeding parents give the same results.

Both of these results are distinct from the results with maternal inheritance, cytoplasmic inheritance, or paternal imprinting, which all give the same results: no difference between male and female F_1 progeny, but the two crosses result in opposite phenotypes.

A further cross is needed to distinguish among maternal effect, cytoplasmic inheritance, and paternal imprinting. For these modes of inheritance, the phenotypes of the progeny depend solely on the maternal contribution, and no phenotypic differences are expected among male and female progeny. The F_1 female progeny from cross A and cross B should have the same genotype (heterozygous), but they have different phenotypes. The three remaining modes of inheritance predict different phenotypes of F_2 progeny from these females, as shown in the table below.

	Phenotypes of progeny of normal male × F_1 female from:	
Mode of inheritance	*Cross A (normal ears)*	*Cross B (twisted ears)*
Maternal	*Dominant phenotype*	*Dominant phenotype*
Cytoplasmic	*Normal ears*	*Twisted ears*
Paternal imprinting	*1:1 normal:twisted*	*1:1 normal:twisted*

In the case of maternal inheritance, the progeny depend on the genotype of the mother, and because the F_1 females from both crosses have the same heterozygous genotype, their progeny will have the same phenotype: normal ears or twisted ears, whichever is dominant.

For cytoplasmic inheritance, the phenotype of the progeny will be the same as the phenotype of the mother. Because the F_1 females have different phenotypes, their progeny will have different phenotypes.

For paternal imprinting, only the maternal genes are expressed in the progeny. Because the mother is heterozygous, the progeny should have 1:1 ratio of normal ears and twisted ears.

Other solutions are possible; this is just one.