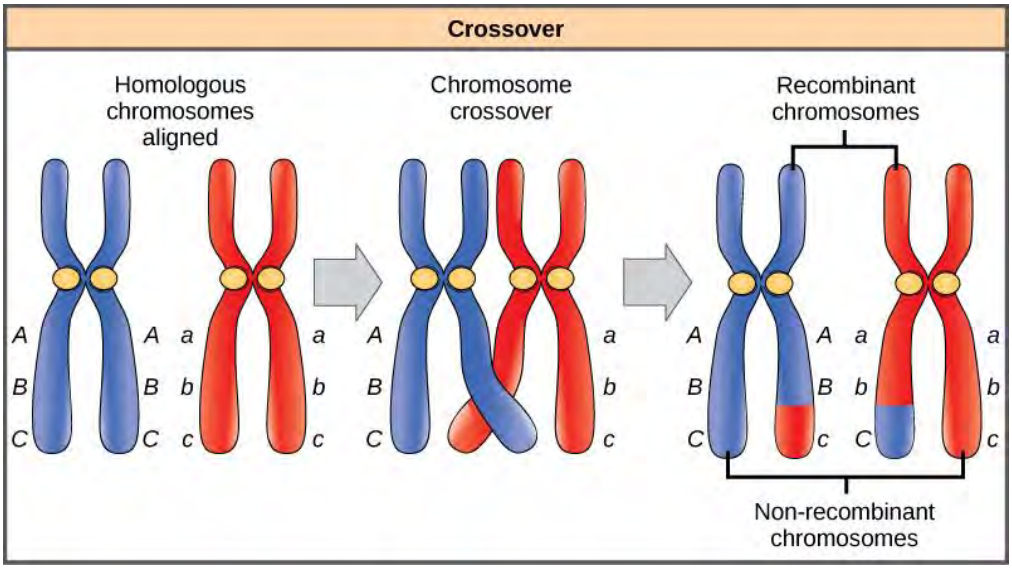

Figure 9.18 The process of crossover, or recombination, occurs when two homologous chromosomes align during meiosis and exchange a segment of genetic material. Here, the alleles for gene C were exchanged. The result is two recombinant and two non-recombinant chromosomes. (credit: Clark et al. / Biology 2E OpenStax)

When two genes are located in close proximity on the same chromosome, they are considered linked, and their alleles tend to be passed through meiosis together. To demonstrate this, imagine a dihybrid cross involving flower color and plant height in which the genes are next to each other on the chromosome. If one homologous chromosome has alleles for tall plants and red flowers, and the other chromosome has genes for short plants and yellow flowers, then when the gametes are formed, the tall and red alleles will go together into gametes, and the short and yellow alleles will go into other gametes. However, because the genes are linked, there will be no gametes with tall and yellow alleles and no gametes with short and red alleles. If you create the Punnett square with these gametes, you will see that the classical Mendelian prediction of a 9:3:3:1 outcome of a dihybrid cross would not apply. As the distance between two genes increases, the probability of one or more crossovers between them increases, and the genes behave more like they are on separate chromosomes. Geneticists have used the proportion of recombinant gametes, the ones not like the parents, as a measure of how far apart genes are on a chromosome. Using this information, they have constructed elaborate maps of genes on chromosomes for well-studied organisms, including humans. Mendel's publication makes no mention of linkage, and many researchers have questioned whether he encountered linkage but chose not to publish those crosses out of concern that they would invalidate his independent assortment hypothesis. The garden pea has seven chromosomes, and some have suggested that his choice of seven characteristics was not a coincidence. However, even if the genes he examined were not located on separate chromosomes, it is possible that he simply did not observe linkage because of the extensive shuffling effects of recombination.

Multiple Alleles

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. We now know that this is an oversimplification. For any given gene, multiple alleles may exist at the population level. Different combinations of alleles lead to different observed phenotypes. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among wild organisms as the **wild type**, often abbreviated "+"; this is considered the standard or norm. All other phenotypes or genotypes are considered **variants** of this standard, meaning that they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele.

An example of multiple alleles is coat color in rabbits (Figure 9.19). Here, four alleles exist for the *c* gene. The wild-type version, C^+C^+, is expressed as brown fur. The chinchilla phenotype, $c^{ch}c^{ch}$, is expressed as black-tipped white fur. The Himalayan phenotype, c^hc^h, has black fur on the extremities and white fur elsewhere. Finally, the albino, or "colorless" phenotype, *cc*, is expressed as white fur. In cases of multiple alleles, dominance hierarchies can exist. In this case, the wild-type allele is dominant over all the others, chinchilla is incompletely dominant over Himalayan and albino, and Himalayan is dominant over albino. This hierarchy, or allelic series, was revealed by observing the phenotypes of each possible heterozygote offspring.

The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of "dosage" of a specific gene product. The wild-type allele supplies the correct amount of gene product, whereas the mutant alleles cannot. For the allelic series in rabbits, the wild-type allele may supply a given dosage of fur pigment, whereas the mutants supply a lesser dosage or none at all. Interestingly, the Himalayan phenotype is the result of an allele that produces a temperature-sensitive gene product that only produces pigment in the cooler extremities of the rabbit's body.

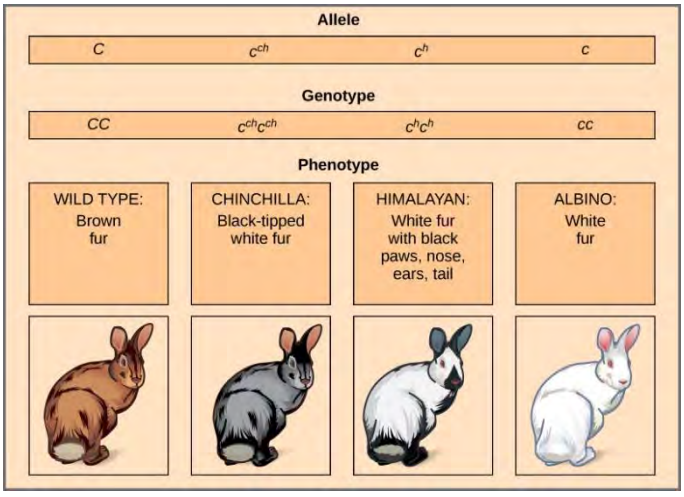

Figure 9.19 Four different alleles exist for the rabbit coat color (C) gene. (credit: Clark et al. / Biology 2E OpenStax)

Mendel's work identified the fundamental principles of heredity; however, as you have now learned, genetics are much more complicated. Had he used a different model organism or investigated both linked and unlinked genes, it would have been much more difficult for him to create a unified model of his data based on probability. Researchers who have since mapped the traits that Mendel investigated have confirmed that all the genes he examined are either on separate chromosomes or are sufficiently far apart as to be statistically unlinked. Some have suggested that Mendel was enormously lucky in both his choice of model organism and that he selected only unlinked genes. Others question whether Mendel discarded any data suggesting linkage. Regardless, Mendel and his data helped build the foundation for modern genetics.

Section Summary

Sutton and Boveri's Chromosomal Theory of Inheritance states that chromosomes are the vehicles of genetic heredity. Neither Mendelian genetics nor gene linkage apply to inheritance of all characteristics. Instead, chromosome behavior involves segregation, independent assortment, and occasionally, linkage. Sturtevant devised a method to assess recombination frequency and infer linked genes' relative positions and distances on a chromosome based on the average number of crossovers in the intervening region between the genes. Sturtevant correctly presumed that genes are arranged in serial order on chromosomes and that recombination between homologs can occur anywhere on a chromosome with equal likelihood. Whereas linkage causes alleles on the same chromosome to be inherited together, homologous recombination biases alleles toward an independent inheritance pattern.

Exercises

1. The Chromosomal Theory of Inheritance was consistent with Mendel's laws. Provide two observations that supported the connection between the two.
2. When many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among individuals as the:
    a. variant
    b. wild type
    c. dosage
    d. none of the above
3. When two genes are located in close proximity on the same chromosome, they are considered linked, and their alleles tend to be passed through meiosis together.
    a. TRUE
    b. FALSE

Answers

1. (1) During meiosis, homologous chromosome pairs migrate as discrete structures that are independent of other chromosome pairs. (2) Chromosome sorting from each homologous pair into gametes appears to be random. (3) Each parent synthesizes gametes that contain only half their chromosomal number. (4) Even though male and female gametes, sperm and egg, differ in size and morphology, they have the same number of chromosomes, suggesting equal genetic contributions from each parent. (5) The chromosomes found in each gamete come together during fertilization to produce offspring with the same chromosome number as their parents.
2. (b)
3. (a)