involve the entire DNA molecule or segments of varying sizes. Here we focus on two types of chromosome alterations that are particularly important in evolution.

Inversions

Chromosome **inversions** often result from a multistep process that starts when radiation causes two double-strand breaks in a chromosome. After breakage, a chromosome segment can detach, flip, and reanneal in its original location. As Figure 5.30 shows, gene order along the chromosome is now inverted.

In addition to involving much larger stretches of DNA than point mutations and gene duplications, inversions have different consequences. Inversions affect a phenomenon known as genetic **linkage**. Linkage is the tendency for alleles of different genes to assort together at meiosis. Genes on the same chromosome tend to be more tightly linked (that is, more likely to be inherited together) than genes on nonhomologous chromosomes. Similarly, the closer together genes are on a chromosome, the tighter the linkage. Crossing over at meiosis, on the other hand, breaks up allele combinations and reduces linkage (see Chapter 8).

When inversions are heterozygous, meaning that one chromosome copy contains an inversion and the other does not, the inverted sequences cannot align properly when homologs synapse during prophase of meiosis I. Successful crossing-over events are rare. The result is that alleles inside the inversion are locked so tightly together that they are inherited as a single "supergene."

Inversions are common in *Drosophila*. Are they important in evolution? To answer this question, consider a series of inversions found in populations of *Drosophila subobscura*. This fruit fly is native to western Europe, North Africa, and the Middle East, and has six chromosomes. Five of these chromosomes are **polymorphic** for at least one inversion (Prevosti et al. 1988), meaning that chromosomes with and without the inversions exist. Biologists have known since the 1960s that the frequencies of these inversions vary regularly with latitude and climate. This type of regular change in the frequency of an allele or an inversion over a geographic area is called a **cline**. Several authors have argued that different inversions must contain specific combinations of alleles that function well together in cold, wet weather or hot, dry conditions. But is the cline really the result of natural selection on the supergenes? Or could it be a historical accident, caused by differences in the founding populations long ago?

A natural experiment has settled the issue. In 1978 *D. subobscura* showed up in the New World for the first time, initially in Puerto Montt, Chile, and then four years later in Port Townsend, Washington, USA. Several lines of evidence argue that the North American population is derived from the South American one. For example, of the 80 inversions present in Old World populations, precisely the same subset of 19 is found in both Chile and Washington State. Within a few years of their arrival on each continent, the *D. subobscura* populations had expanded extensively along each coast and developed the same clines in inversion frequencies found in the Old World (Figure 5.31). The clines are even correlated with the same general changes in climate type: from wet marine environments to mediterranean climates to desert and dry steppe habitats (Prevosti et al. 1988; Ayala et al. 1989). This is strong evidence that the clines result from natural selection and are not due to historical accident.

Which genes are locked in the inversions, and how do they affect adaptation to changes in climate? In the lab, *D. subobscura* lines bred for small body size tend to become homozygous for the inversions found in the dryer, hotter part of the

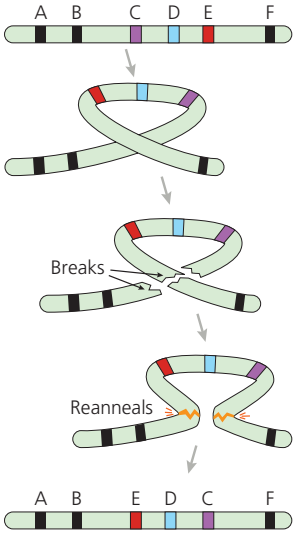

Figure 5.30 Chromosome inversion Inversions result when a chromosome segment breaks in two places and reanneals with the internal segment reversed. Note the order, before and after, of the genes labeled C, D, and E.

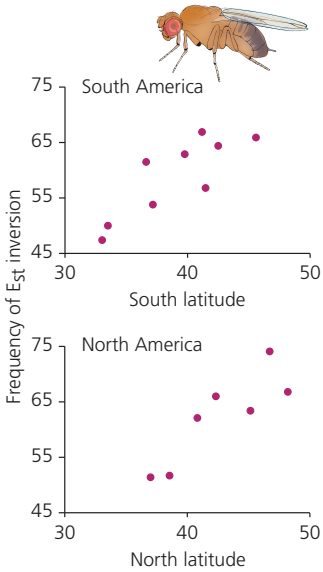

Figure 5.31 Inversion frequencies form clines in *Drosophila subobscura* From data in Prevosti et al. (1988); see also Balanyà et al. (2003).

range (Prevosti 1967). Research by George Gilchrist and colleagues (2004) has confirmed that pronounced and parallel clines in body size exist in fly populations from North America, South America, and Europe. These results hint that alleles in the inversions affect body size, and that natural selection favors large flies in cold, wet climates and small flies in hot, dry areas. The fly study illustrates a key point about inversions: They are an important class of mutations because they affect selection on groups of alleles.

Chromosomal inversions suppress recombination and thus help maintain combinations of alleles across nearby loci.

Genome Duplication

The final type of mutation we will consider occurs at the largest scale possible: entire sets of chromosomes. For example, if homologous chromosomes fail to segregate during meiosis I or if sister chromatids do not separate properly during meiosis II, the resulting cells may have double the number of chromosomes of the parent cell. In plants, because the germ line is not segregated, similar mutations can occur during the mitotic cell divisions that lead up to gamete formation. Mutations like these can lead to the formation of a diploid gamete in species where gametes are normally haploid.

Figure 5.32 shows one possible outcome of a chromosome-doubling mutation. In the diagram, the individual that produces diploid gametes contains both male and female reproductive structures and can self-fertilize. When it does so, a tetraploid ($4n$) offspring results. If this offspring self-fertilizes when it matures, or if it mates with its parent or a tetraploid sibling that also produces diploid gametes, then a population of tetraploids can become established.

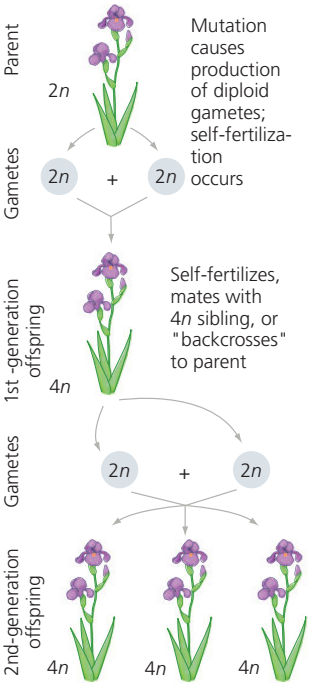

Figure 5.32 How tetraploid plants are produced

Organisms with more than two chromosome sets are said to be **polyploid**. Polyploid organisms can be tetraploid ($4n$), hexaploid ($6n$), octoploid ($8n$), or more. Polyploidy is common in plants and rare in animals—probably because self-fertilization is more common in plants than animals. Nearly half of all flowering plant species and the vast majority of the ferns are descended from ancestors where polyploidization occurred. In animals, polyploidy occurs in taxa like earthworms and some flatworms where individuals contain both male and female gonads and can self-fertilize. It is also present in animal groups that are capable of producing offspring without fertilization, through a process called parthenogenesis. In some species of beetles, sow bugs, moths, shrimp, goldfish, and salamanders, a type of parthenogenesis occurs that can lead to chromosomal doubling.

There are at least two reasons that polyploidy is an important type of mutation in evolution. First, it can lead to new species being formed. Second, it alters cell size, cell geometry, and gene dosage, and thus may endow individuals with new phenotypes that allow them to colonize and adapt to new environments.

Polyploidy and Speciation

To see why genome duplication can lead to speciation, imagine the outcome of matings between individuals in a tetraploid population and the most closely related diploid population. If individuals from the two populations mate, they produce triploid offspring. When these individuals mature and meiosis occurs, the homologous chromosomes cannot synapse correctly, because they are present in an odd number. As a result, the vast majority of the gametes produced by triploids end up with the wrong number of chromosomes and fail to survive. Triploid individuals have extremely low fertility.

Duplications of the entire genome are an important mechanism of speciation—particularly in plants.

In contrast, when tetraploid individuals continue to self-fertilize or mate among themselves, then fully fertile tetraploid offspring will result. In this way,