**Evolution of the Flower**

Pollination in angiosperms does not involve direct contact between the pollen grain and the ovule. Pollen matures within the anthers and is transported, often by insects, birds, or other animals, to the stigma of another flower. When pollen reaches the stigma, it germinates, and a pollen tube grows down, carrying the sperm nuclei to the embryo sac. After double fertilization takes place, development of the embryo and endosperm begins. The seed matures within the ripening fruit; the germination of the seed initiates another life cycle.

Successful pollination in many angiosperms depends on the regular attraction of pollinators such as insects, birds, and other animals, so that pollen is transferred between plants of the same species. When animals disperse pollen, they perform the same functions for flowering plants that they do for themselves when they actively search out mates. The relationship between plant and pollinator can be quite intricate. Mutations in either partner can block reproduction. If a plant flowers at the "wrong" time, the pollinator may not be available. If the morphology of the flower or pollinator is altered, there may be physical barriers to pollination. Clearly floral morphology has coevolved with pollinators and the result is much more complex and diverse than the initiation of four distinct whorls of organs described in chapter 41.

**Characteristics of Floral Evolution**

The evolution of the angiosperms is a focus of chapter 37. Here we need to keep in mind that the diversity of angiosperms is partly due to the evolution of a great variety of floral phenotypes that may enhance the effectiveness of pollination. All floral organs are thought to have evolved from leaves. In some early angiosperms, these organs maintain the spiral phyllotaxy often found in leaves. The trend has been toward four distinct whorls. A complete flower has four whorls of parts (calyx, corolla, androecium, and gynoecium), while an incomplete flower lacks one or more of the whorls (figure 42.4).

In both complete and incomplete flowers, the calyx usually constitutes the outermost whorl; it consists of flattened appendages, called sepals, which protect the flower in the bud. The petals collectively make up the corolla and may be fused. Petals function to attract pollinators. While these two outer whorls of floral organs are sterile, they can enhance reproductive success.

Androecium (from the Greek andros, "man," + oikos, "house") is a collective term for all the stamens (male structures) of a flower. Stamens are specialized structures that bear the angiosperm microsporangia. There are similar structures bearing the microsporangia in the pollen cones of gymnosperms. Most living angiosperms have stamens whose filaments ("stalks") are slender and often threadlike, and whose four microsporangia are evident at the apex in a swollen portion, the anther. Some of the more primitive angiosperms have stamens that are flattened and leaflike, with the sporangia produced from the upper or lower surface.

The gynoecium (from the Greek gyne, "woman," + oikos, "house") is a collective term for all the female parts of a flower. In most flowers, the gynoecium, which is unique to angiosperms, consists of a single carpel or two or more fused carpels. Single or fused carpels are often referred to as simple or compound pistils, respectively. Most flowers with which we are familiar—for example, those of tomatoes and oranges—have a compound pistil. In other less specialized flowers—for example, buttercups and stonecups—there may be several to many separate, simple pistils, each formed from a single carpel. Ovules (which develop into seeds) are produced in the pistil’s swollen lower portion, the ovary, which usually narrows at the top into a slender, necklike style with a pollen-receptive stigma at its apex. Sometimes the stigma is divided, with the number of stigma branches indicating how many carpels are in the particular pistil. Carpels are essentially inrolled floral leaves with ovules along the margins. It is possible that the first carpels were leaf blades that folded longitudinally; the margins, which had hairs, did not actually fuse until the fruit developed, but the hairs interlocked and were receptive to pollen. In the course of evolution, there is evidence the hairs became localized into a stigma, a style was formed, and the fusing of the carpel margins ultimately resulted in a pistil. In many modern flowering plants, the carpels have become highly modified and are not visually distinguishable from one another unless the pistil is cut open.

**Trends of Floral Specialization**

Two major evolutionary trends led to the wide diversity of modern flowering plants: (1) separate floral parts have
grouped together, or fused, and (2) floral parts have been lost or reduced (figure 42.5). In the more advanced angiosperms, the number of parts in each whorl has often been reduced from many to few. The spiral patterns of attachment of all floral parts in primitive angiosperms have, in the course of evolution, given way to a single whorl at each level. The central axis of many flowers has shortened, and the whorls are close to one another. In some evolutionary lines, the members of one or more whorls have fused with one another, sometimes joining into a tube. In other kinds of flowering plants, different whorls may be fused together. Whole whorls may even be lost from the flower, which may lack sepals, petals, stamens, carpels, or various combinations of these structures. Modifications often relate to pollination mechanisms and, in some cases like the grasses, wind has replaced animals for pollen dispersal.

While much floral diversity is the result of natural selection related to pollination, it is important to recognize the impact breeding (artificial selection) has had on flower morphology. Humans have selected for practical or aesthetic traits that may have little adaptive value to species in the wild. Maize (corn), for example, has been selected to satisfy the human palate. Human intervention ensures the reproductive success of each generation; while in a natural setting modern corn would not have the same protection from herbivores as its ancestors, and the fruit dispersal mechanism would be quite different (see figure 21.13). Floral shops sell heavily bred species with modified petals, often due to polyploidy, that enhance their economic value, but not their ability to attract pollinators. In making inferences about symbioses between flowers and pollinators, be sure to look at native plants that have not been genetically altered by human intervention.

Trends in Floral Symmetry

Other trends in floral evolution have affected the symmetry of the flower (figure 42.6). Primitive flowers such as those of buttercups are radially symmetrical; that is, one could draw a line anywhere through the center and have two roughly equal halves. Flowers of many advanced groups are bilaterally symmetrical; that is, they are divisible into two equal parts along only a single plane. Examples of such flowers are snapdragons, mints, and orchids. Such bilaterally symmetrical flowers are also common among violets and peas. In these groups, they are often associated with advanced and highly precise pollination systems. Bilateral symmetry has arisen independently many times. In snapdragons, the cycloidia gene regulates floral symmetry, and in its absence flowers are more radial (figure 42.7). Here the experimental alteration of a single gene is sufficient to cause a dramatic change in morphology. Whether the same gene or functionally similar genes arose naturally in parallel in other species is an open question.