Chapter 13

The Flower and Sexual Reproduction

KEY CONCEPTS

1. Sexual reproduction occurs in flowering plants in specialized structures called flowers. They are composed of four whorls of leaflike structures: the calyx (composed of sepals) serves a protective function; the corolla (composed of petals) usually functions to attract insects; the androecium (composed of stamens) is the male part of the flower; and the gynoecium (carpels or pistil) is the female part.

2. Stamens produce pollen. The stamen's female counterpart is the pistil, which is composed of the stigma (collects pollen), the style, and the ovary. The ovary produces eggs.

3. Sexual reproduction in plants involves pollination, which is the transfer of pollen from the anther of one flower to the stigma of the same or a different flower. The pollen lands on the stigma and grows into the style (as the pollen tube) until it penetrates the ovule and releases two sperm.

4. Double fertilization is unique to flowering plants. One sperm fuses to the egg to form the zygote; the other fuses to the polar nuclei to form the primary endosperm nucleus. The zygote forms the embryo, and the primary endosperm nucleus forms the endosperm (a nutritive tissue). The fertilized ovule develops into the seed.

5. There are basically two types of pollination: self-pollination, in which the pollen comes from within the same flower or plant, and cross-pollination, in which the pollen comes from different plants. Pollination strategies involve abiotic factors such as wind and water and interesting relationships between plants and animals, biotic factors.

13.1 THE FLOWER: SITE OF SEXUAL REPRODUCTION

The vivid colors and intricate patterns of flowers have always attracted the notice of humans and captured their imagination. The symmetry and brightness of petals and the interesting scents from flowers are evolutionary designs to attract pollinators (mostly insects and birds) to visit flowers. The result of such visits is often a reward of nectar (sugary water); in exchange, the insect will fly away carrying pollen to a different flower. This fine-tuned relationship between the flower and the animal guarantees that sexual reproduction continues between plants, which are not able to roam about to select a mate. People will always love flowers, but the most important function of the flower is as the site where sexual reproduction occurs, leading to the formation of seeds. Imagine a world without wheat grains to make bread, corn for products we use every day, or barley to make beer; we'd all live very different lives without seeds.

Of all the characteristics of flowering plants, the **angiosperms**, the flower and fruit are the least affected by changes in the environment such as age, light, water, and nutrition. Consequently, the appearance of flowers and fruits is important to understanding evolutionary relationships among angiosperms.

The development of the flower begins the sexual reproductive cycle in all flowering plants. The function of the flower is to facilitate the important events of gamete formation and fusion. The essential steps of sexual reproduction, meiosis, and fertilization, described in Chapter 12, take place in the flower. The complete sexual cycle involves (a) the production of special reproductive cells following meiosis, (b) pollination, (c) fertilization, (d) seed and fruit development, (e) seed and fruit dissemination, and (f) seed germination.

13.2 THE PARTS OF A COMPLETE FLOWER AND THEIR FUNCTIONS

A typical flower is composed of four whorls of modified leaves--(1) sepals, (2) petals, (3) stamens, and (4) carpels--which are all attached to the terminal end of a modified stem, the receptacle (Fig. 13.1).

The **sepals** are generally green and enclose the other flower parts in the bud. All the sepals collectively constitute the **calyx**, and they function to protect the reproductive parts inside the flower. The **petals** are usually the conspicuous, colored, attractive flower parts, which together constitute the **corolla**. Their most important function is to catch the attention of pollinators.

The **stamens** form the whorl just inside the corolla. Each stamen has a slender stalk, or **filament**, at the top of which is an **anther**, the pollen-bearing organ. The whorl or grouping of stamens is called the **androecium**, and this constitutes the male part of the flower (Fig. 13.1).

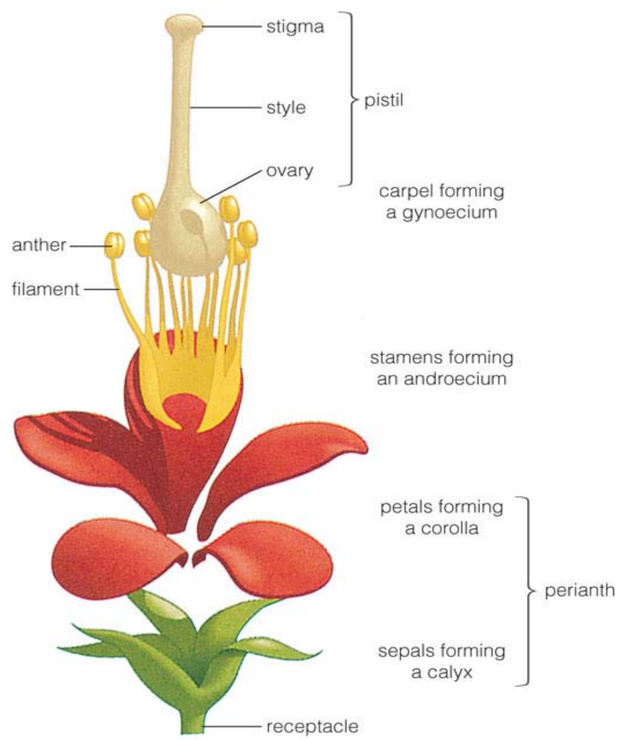


Figure 13.1. A flower, showing the whorls of parts. The perianth consists of two whorls of sepals and petals (calyx and corolla). There is one whorl of stamens (collectively called the *androecium*). A single carpel (a pistil) forms the central whorl of floral parts, the *gynoecium*.

The female part of the flower is called the **gynoecium**. It is composed of one or more **carpels**, which are modified leaves folded over and fused to protect the attached ovules. Sometimes an individual carpel or group of fused carpels is called a **pistil**. The term is used simply because its shape is reminiscent of the pistil (or pestle) used to grind objects in a mortar. There may be more than one pistil in the gynoecium. The carpels are usually located at the center of the flower (Fig. 13.1).

Carpels generally have three distinct parts: (1) an expanded basal portion, the **ovary**, which contains the **ovules**; (2) the **style**, a slender supporting stalk; and (3) the **stigma**, at the very tip (Fig. 13.1).

The term **perianth** is applied to the calyx and corolla collectively. The flower organs necessary for sexual reproduction are the stamens (androecium) and carpels (gynoecium). The perianth, composed of calyx and corolla, protects the stamens and pistil(s), and also attracts and guides the movements of some pollinators.

The Male Organs of the Flower Are the Androecium

As mentioned earlier, the androecium is the whorl of stamens, with each stamen consisting of an anther at the end of a filament. The anther usually is made up of four elongated lobes called **pollen sacs** (Fig. 13.2a). Early in the development of the anther, each pollen sac contains a mass of dividing cells called **microsporocytes** (Fig. 13.2b). Each microsporocyte divides by meiosis to form four haploid (n) microspores (Fig. 13.2c, d). The nucleus of each microspore then divides by mitosis to form a two-celled **pollen grain**, which contains a **tube cell** and a smaller **generative cell** (Fig. 13.2e). The role of this two-celled, haploid, **male gametophyte** (gamete-producing plant) is to produce **sperm cells** for fertilization.

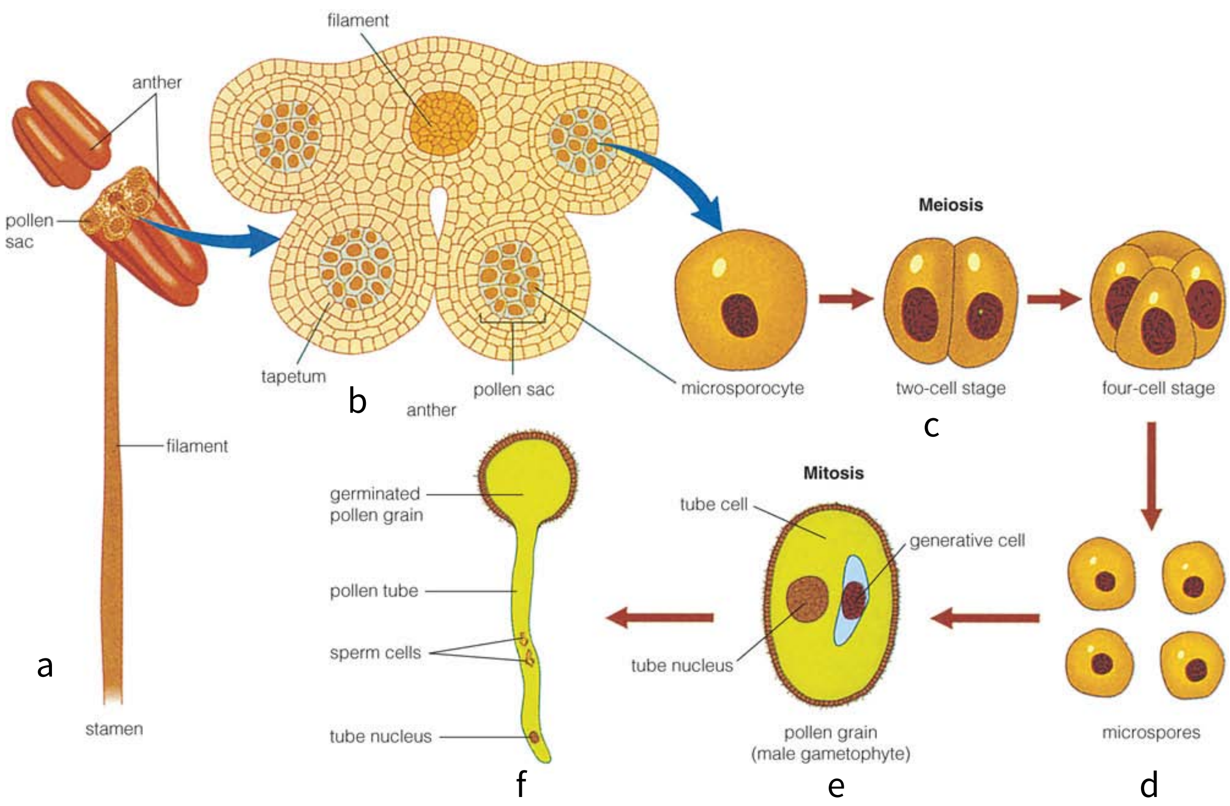


Figure 13.2. Development of pollen from microsporocyte to pollen grain. (a) Stamen. (b) Cross section of anther. The tapetum immediately surrounds the pollen sac. (c) Development of four-cell stage from the microsporocyte by meiosis. (d) Four microspores. (e) Pollen grain. (f) Germination of pollen grain.

The pollen grain is surrounded by an elaborate cell wall. The pattern on this wall is genetically fixed, and it varies widely among major groups of plants (Fig. 13.3). The walls contain *sporopollenin,* a very hard material that resists decay. As a result, pollen grains make good fossils, and botanists have found them very useful in studying the evolutionary history of seed plants.

After the pollen grains are mature, the anther wall splits open and the pollen is shed. In various ways discussed later in this chapter, pollen grains are transported to the stigmas of adjacent or distant flowers. This process is called **pollination**. The dry pollen grain then absorbs water from the stigma and becomes hydrated. It also secretes proteins, including some that are involved in pollen recognition and compatibility reactions with the cells of the stigma. This recognition mechanism is important because it inhibits pollen from germinating and growing on the wrong species. These proteins are the same ones that cause allergies and hay fever.

The pollen grain then germinates to form a **pollen tube**, which grows toward the ovary. The pollen tube grows between cells in the center of the style, a region called the *transmitting tissue* (Fig. 13.4). In some plants, like the lily *(Lilium),* the style is hollow, and the transmitting tissue is reduced to a layer of secretory cells on its inner surface; the cells secrete a special material in which the pollen tube grows. In solid transmitting tissues, the pollen tube secretes digestive enzymes that partially break down the transmitting tissue cells, making it easier for the pollen tube to grow.

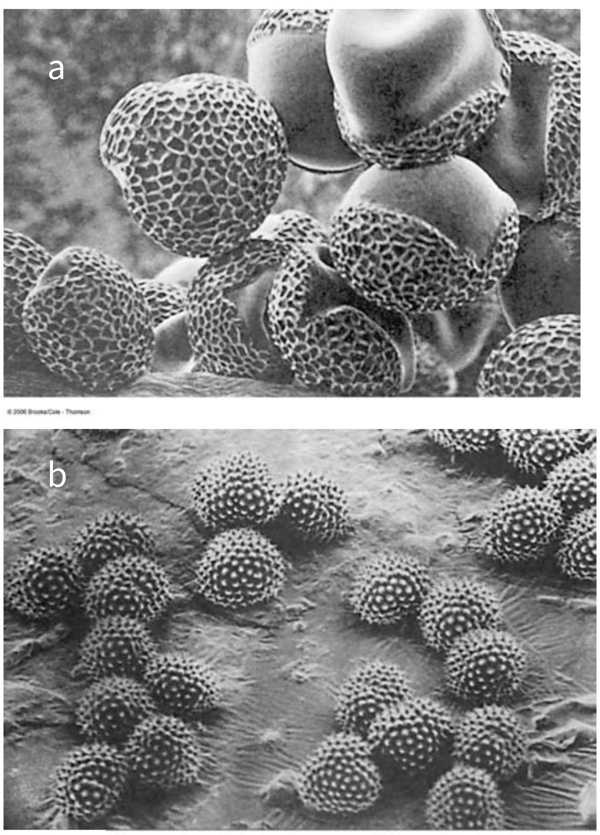


Figure 13.3. Pollen grains as viewed with the scanning electron microscope. (a) *Iris*. X174. (b) ragweed (*Ambrosia*). X700.

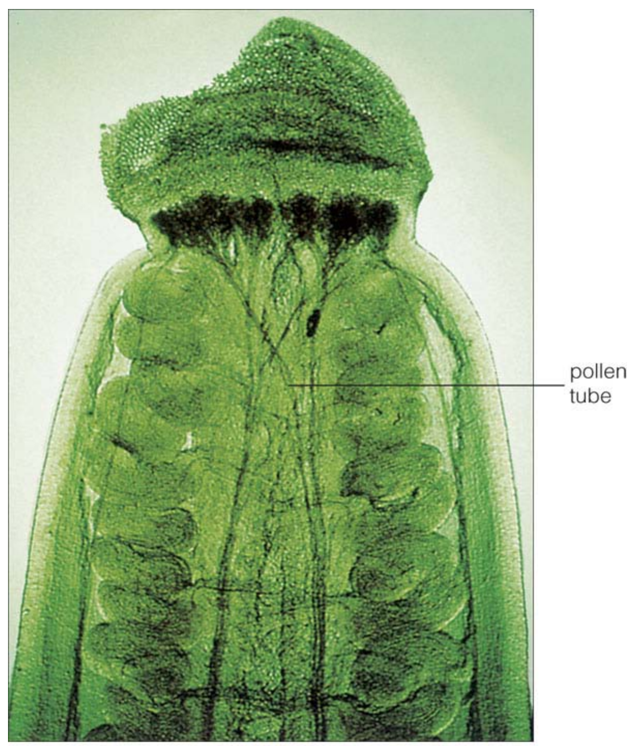


Figure 13.4. Style of jewel plant (*Strepthanthus*) flower with pollen tubes which have grown toward the ovary. X62.

The pollen tube grows by elongation of its cell wall in a region very near its tip. It is filled with many small vesicles containing cell-wall building materials needed for tube growth. Endoplasmic reticulum and other organelles are also present. Very rapid cytoplasmic streaming (see Chapter 3) occurs in pollen tubes.

The Female Organs of the Flower Are the Gynoecium

In its simplest form, the gynoecium consists of a single folded carpel or **simple pistil** (Fig. 13.5a) in which the ovary resides. In more complex flowers, the gynoecium may consist of several separate carpels or several groups of fused carpels. A group of fused carpels is called a **compound pistil** (Fig. 13.5b).

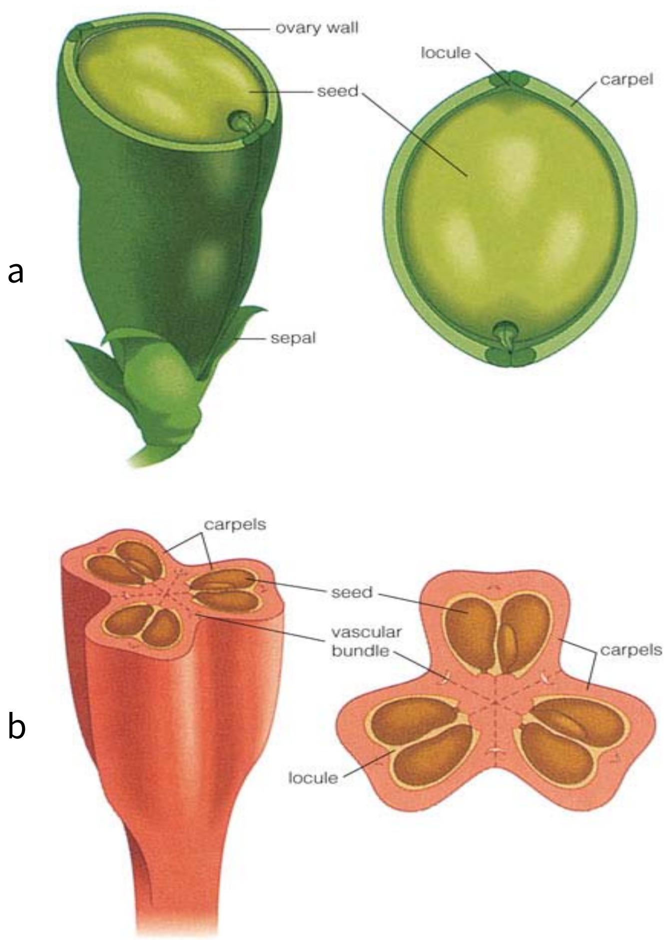


Figure 13.5. Simple and compound pistils compared. (a) A section through the simple pistil of pea (*Pisum*), showing an ovary composed of a single carpel. (b) A section through the compound pistil of tulip (*Tulipa*), showing an ovary with three fused carpels.

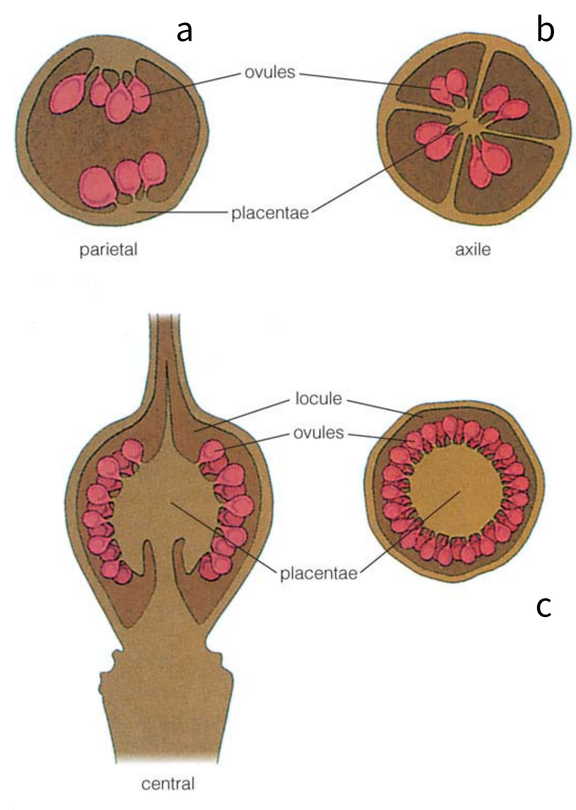


Figure 13.6. Three types of placentation. (a) Parietal (*Dicentra*), (b) Axile (*Fuchsia*), and (c) Free central (*Primula*). (Redrawn from Priestley and Scott. An Introduction to Botany. c 1949 by Longmans Green. Reprinted with permission of the Longmans Group. Ltd.)

The ovary is a hollow structure having from one to several chambers, or **locules** (Fig. 13.5b). The number of carpels in a compound pistil is generally related to the number of stigmas, the number of locules, and the number of sides on the ovary. The pea (*Pisum*) has a single stigma, and its ovary has one locule (Fig. 13.5a). The tulip (*Tulipa*) pistil has three stigmas, its ovary has three sides, and it contains three locules and three carpels (Fig. 13.5b).

The tissue within the ovary to which an ovule is attached is called the **placenta** (Fig. 13.6). The manner in which placentae are distributed in the ovary is termed **placentation**. When the placentae are on the ovary wall, as in bleeding heart *(Dicentra;* Fig. 13.6a), the placentation is **parietal**. When they arise on the axis of an ovary that has several locules, as in *Fuchsia,* the placentation is **axile** (Fig. 13.6b). Less frequently, the ovules form on a central column, which is **central** placentation *(Primula;* Fig. 13.6c).

Emanating from the ovary is the style--a stalk whose length and shape vary by species--with a stigma at its upper end (see Fig. 13.1). It is through stylar tissue that the pollen tube grows (Fig. 13.4). In general, the style withers after pollination. Often, the surface of the stigma is covered with short hairs that aid in holding the pollen grains, and sometimes they secrete a sticky fluid that stimulates pollen tube growth. In many wind-pollinated plants, such as the grasses, the stigma are elaborately branched or featherlike.

Within the ovary is the ovule, the structure that (if fertilized) will eventually become the seed. As the ovule matures (Fig. 13.7), it forms one or two outer protective layers, the **integuments**. The integuments do not fuse, leaving a small opening called the **micropyle** (Fig. 13.7b). At the same time, one of the internal dividing cells of the ovule, the **megasporocyte**, is enlarging in preparation for meiosis (Fig. 13.7c). The megasporocyte is embedded in a tissue called the **nucellus.** The ovule thus is composed of one or two outer protecting integuments, along with the micropyle, megasporoctye, and nucellus.

The Embryo Sac Is the Female Gametophyte Plant

As a result of meiosis of the megasporocyte, a row of four cells called **megaspores** is produced in the nucellus (Fig. 13.7d). Each megaspore is haploid (n). As a rule, the three cells nearest the micropyle disintegrate and disappear, whereas the one farthest from the micropyle enlarges greatly. This megaspore develops into the mature **embryo sac** in several stages: (a) a series of three mitotic divisions occurs to form an eight-nuclei embryo sac (Fig. 13.7e-g), (b) the nuclei migrate, and (c) a cell wall forms around the nuclei.

At the end of this process (Fig. 13.7g), an **egg cell** and two **synergid cells** are positioned at the micropylar end of the embryo sac. Because it is frequently difficult to differentiate the egg cell from the other two cells, all three cells are sometimes referred to as the **egg apparatus**. The two nuclei that migrate toward the center are **polar nuclei**; they lie in the center of the large **central cell**. The three nuclei at the end of the embryo sac opposite the micropyle form three **antipodal cells**. As described in Chapter 12 (see Fig. 12.5), the embryo sac is the **female gametophyte** phase of the flowering plant's life cycle; it is a haploid or *n* plant.

Not every species of flowering plant produces an embryo sac with the same number of cells, nor do they all follow the same developmental sequence. In cotton *(Gossypium hirsutum),* for example, the antipodal cells disintegrate before fertilization (Fig. 13.7h). However, the mature embryo sac must contain, at a minimum, an egg and polar nuclei.

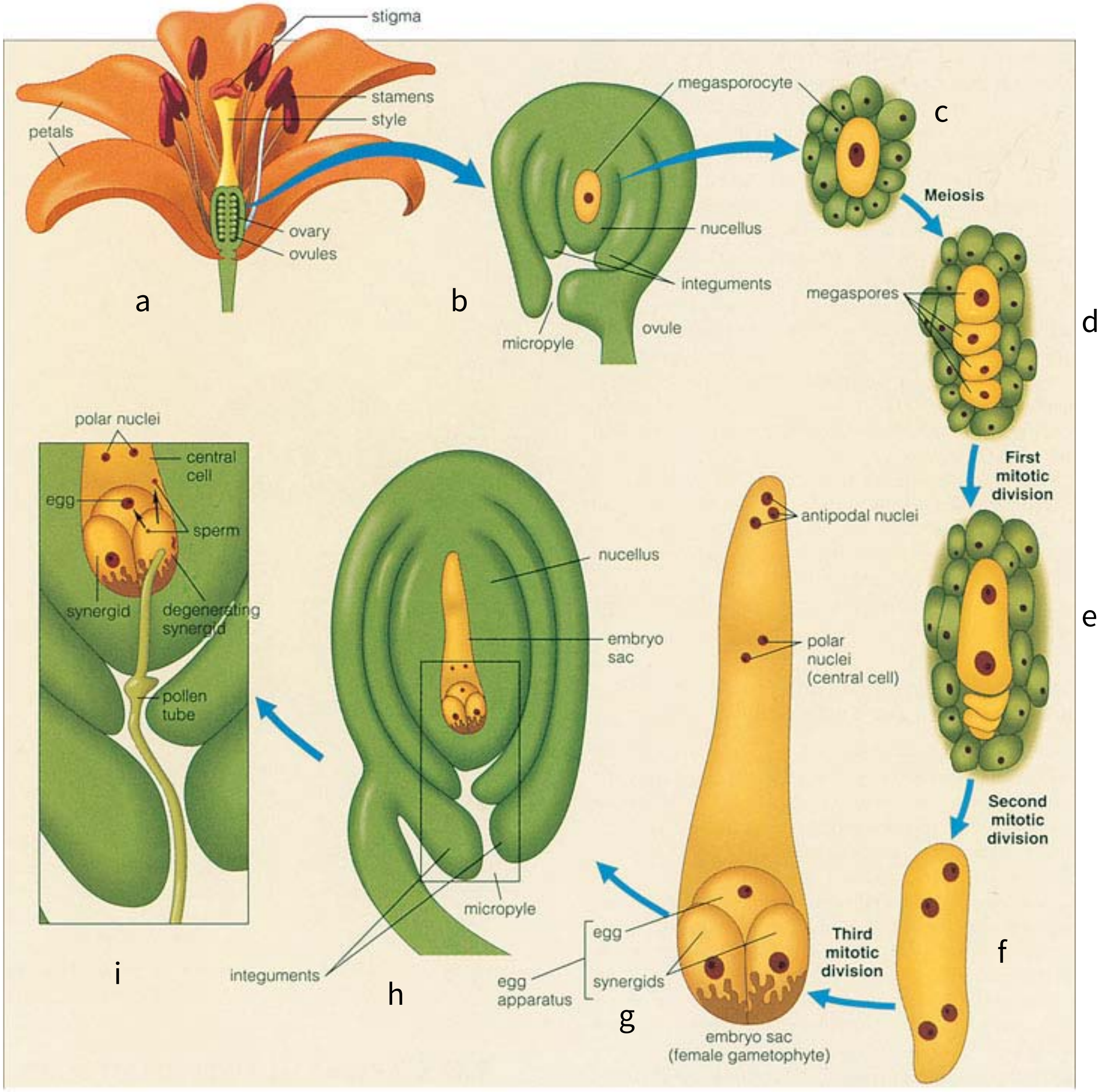


Figure 13.7. Embryo sac development in cotton (*Gossypium hirsutum*). (a) Mature flower. (b) Magnified longitudinal section of an ovule. (c) Megasporocyte before meiosis. (d) Four *n* megaspores after meiotic division of the megasporocyte; the three megaspores closest to the micropyle disintegrate. (e) First mitotic division of the megaspore. (f) Second mitotic division. (g) Third mitotic division and the resulting three antipodal nuclei, the egg, two synergids, and the two polar nuclei. All have a *n* chromosome number. (h) Mature embryo sac; the antipodals disintegrate at this stage in cotton. (i) Pollen tube penetration through the nucellus into a partially degenerated synergid.

Double Fertilization Produces an Embryo and the Endosperm

As we have seen, germination of a pollen grain produces a pollen tube, which grows down through the stigma and style and enters the ovary (Fig. 13.7i). While the pollen tube is growing, the generative cell within it divides by mitosis to form two sperm cells. In some plants, such as sunflower *(Helianthus annuus),* the sperm cells form even before the pollen are shed from the anther. Many pollen grains may germinate, and their pollen tubes may grow through the pistil, but only one usually enters an ovule and its embryo sac.

How is the pollen tube directed into the embryo sac? The answer has been partially worked out for cotton. In the embryo sac, one or both of the synergid cells begins to shrivel and die before the pollen tube enters. It is conjectured that, in the process, the synergids release chemicals that may influence the direction in which the pollen tube grows. Two observations favor this idea. First, the cell wall at the base of the synergids is highly convoluted (see Fig. 13.7g); in other parts of the plant, cell walls like these (transfer cells; see Chapter 4) are associated with active transport or absorption. The second bit of circumstantial evidence is that sometimes the pollen tube actually penetrates one of the synergids and, upon rupturing, empties its contents into the synergid. The two sperm then pass through an incomplete upper cell wall of the synergid, one moving to fuse with the egg and the other with the central cell.

The sperm and egg nuclei fuse to form a diploid (2n) **zygote**, which will grow into the embryo. The other sperm nucleus fuses with the polar nuclei of the central cell (Fig. 13.7i) to form a triploid (3n) **primary endosperm nucleus**, which will divide to become a food reserve tissue called the **endosperm**. This double fusion of egg with sperm and polar nuclei with sperm is called **double fertilization**. The antipodals and synergids usually degenerate. Now the conditions are set for development of the seed and fruit (discussed in Chapter 14).

13.3 APICAL MERISTEMS: SITES OF FLOWER DEVELOPMENT

During vegetative growth, the shoot apex produces stems and leaves. At some time during the growing season, a signal (for example, day length or temperature) will trigger a change in the metabolism of the shoot apex, thereby starting its transformation into a floral apex. The first step in the transition of the apex is a broadening of the apical dome (Fig. 13.8), accompanied by a general increase in RNA and protein synthesis and in the rate of cell division in the apical dome. The first organs to form from the floral apex are bracts. These modified leaves develop at the lower periphery of the floral apex. Floral organs usually form in whorls or in spirals, and the internodes between

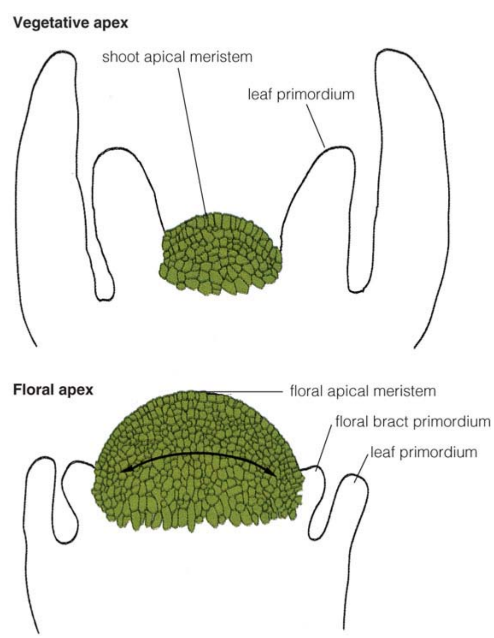


Figure 13.8. Comparison of vegetative and floral apices.

successive sets of floral organs are usually very short. The floral organs are modified leaves, so the flower itself is really a much shortened and very modified branch.

In pheasant-eye (*Adonis aestivalis*), the sepals and petals form after the bracts, followed by several spirals of stamens and carpels (Fig. 13.9b-d). Each new floral organ forms closer to the floral apex. Eventually, carpels develop at the tip, terminating any further growth of the floral apex (Fig. 13.9d, e).

The development of an inflorescence, a group of flowers from the same apex, follows a spatial sequence: bracts form first, followed by flowers, starting at the periphery of the inflorescence apex and progressing toward the center and the tip. The parts of the flowers (sepals, petals, stamens, and carpels) on the inflorescence develop in the same sequence as they do in individual flowers.

Flowers Vary in Their Architecture

Botanists have been studying flowers and plant reproduction for a long time, and consequently there are many terms to describe flower types. Flowers may be complete or incomplete, perfect or imperfect. A flower that develops all four sets of floral leaves--sepals, petals, stamens, and carpels--is said to be a **complete flower**. An **incomplete flower** lacks one or more of these four sets.

Unisexual flowers are either **staminate** (stamen bearing) or **pistillate** (pistil bearing) and are said to be **imperfect**. Bisexual flowers are **perfect**. When staminate and pistillate flowers occur on the same individual plant, as they do in corn (*Zea mays*), English walnut (*Juglans regia*), and many other species, the plant is called **monoecious** (Fig. 13.10). When staminate and pistillate flowers are borne on separate individual plants, as in *Asparagus* or willow (*Salix*), the plant is said to be **dioecious**.

Flowers may also be classified according to their symmetry, which may be regular or irregular. In many flowers, such as stonecrop (*Sedum*) (Fig. 13.11a), the corolla is made up of petals of similar shape that radiate from the center of the flower and are equidistant from each other. Such flowers are said to have **regular symmetry**. In these cases, even though there may be an uneven number of parts in the perianth, any line drawn through the center of the flower will divide the flower into two similar halves. The halves are either exact duplicates or mirror images of each other.

Flowers with **irregular symmetry**, such as garden pea (*Pisum sativum*) (Fig. 13.11b), have parts arranged in such a way that only one line can divide the flower into equal halves; the halves are usually mirror images of each other.

The parts of the flower may be free or united. In the flower of stonecrop (*Sedum,* Fig. 13.11a), the parts of the flower are separate and distinct. Each sepal, petal, stamen, and carpel is attached at its base to the receptacle. In many flowers, however, members of one or more whorls are to some degree united with one another. The union of parts of the same whorl is termed **connation**. Union of flower parts from two different whorls is known as **adnation**.

The position of the ovary differs among flowers. In tulip (*Tulipa*) flowers (Fig. 13.12a), the receptacle is convex or conical, and the different flower parts are arranged one on top of another. The gynoecium (whorl of pistils) is thus situated on the receptacle above the points of origin of the perianth (whorls of sepals and petals) and androecium (whorl of stamens). An ovary in this position is said to be a **superior ovary**. In the daffodil (*Narcissus*

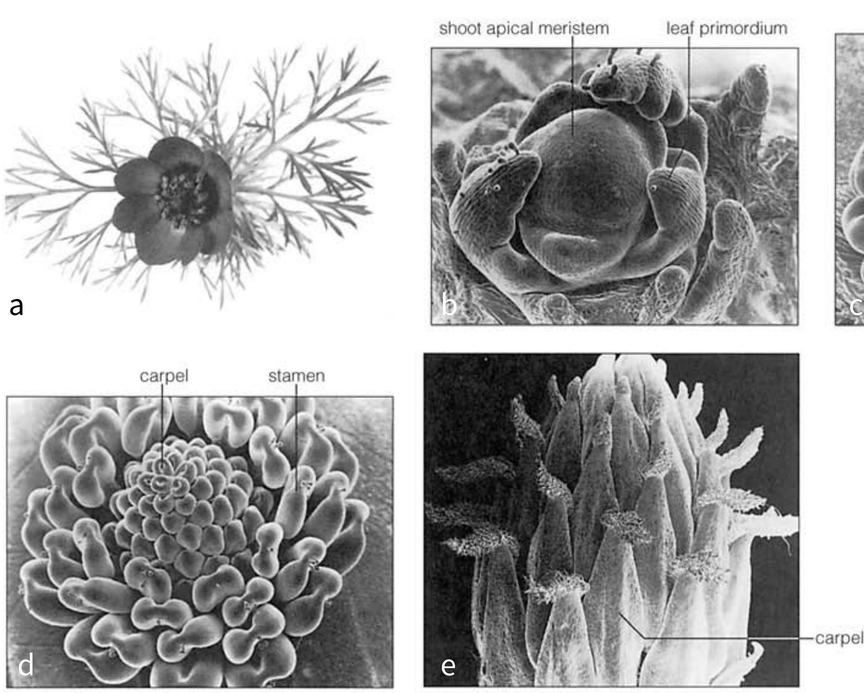


Figure 13.9. Development of a flower from the floral apex. (a) Flower of pheasant-eye (*Adonis aestivalis*). (b) Early phase floral apex. X35. (c) Late floral apex showing stamens and then carpels near the apex tip. X52. (d) Nearly formed flower. The meristem has now completely formed all the flower parts. The carpels are in the middle surrounded by the stamens. X54. (e) Mature carpels with feathery stigmas. X17.

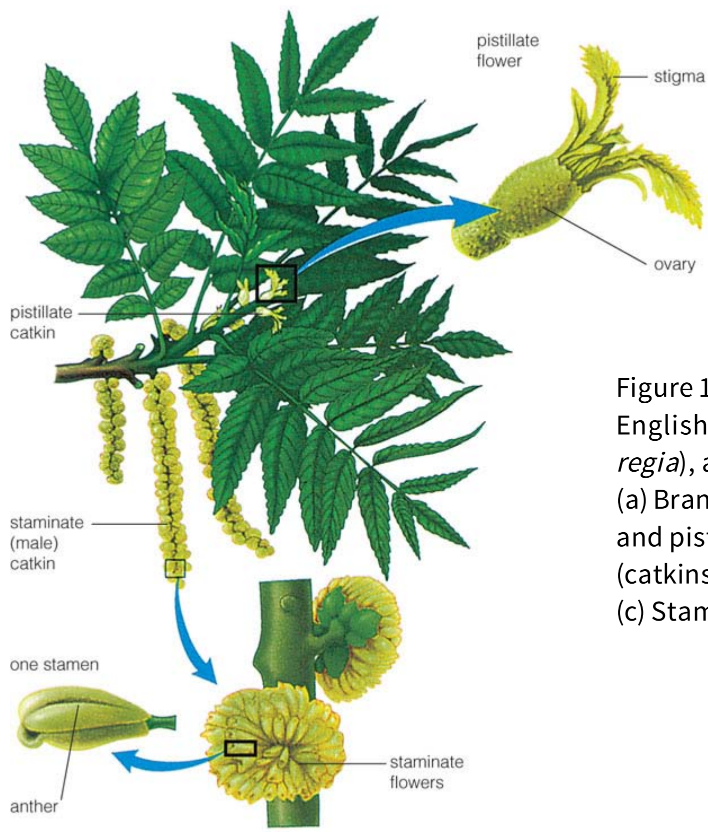
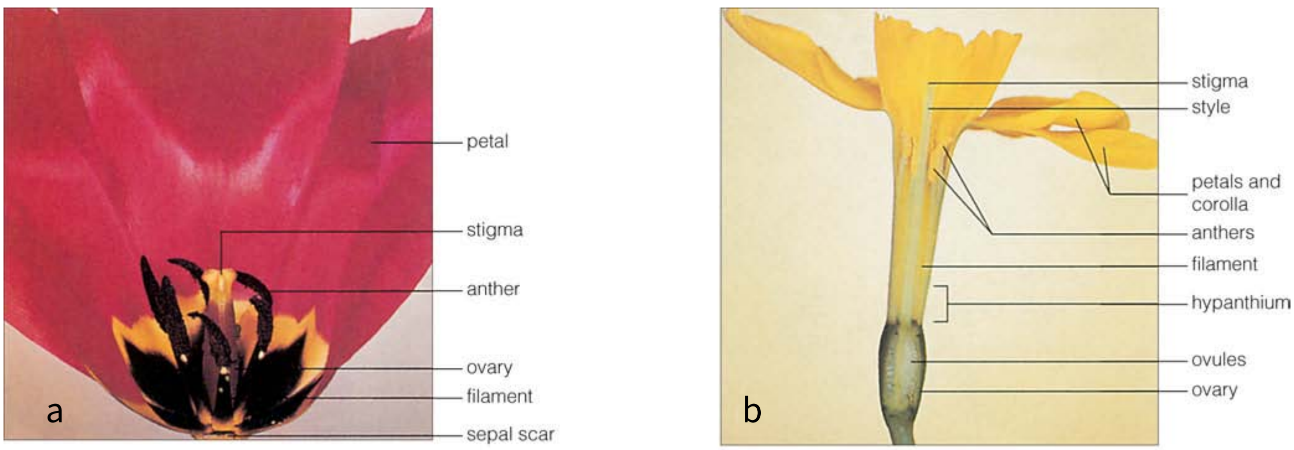


Figure 13.10. Flowers of English walnut (*Juglans regia*), a monoecious plant. (a) Branch with staminate and pistillate inflorescences (catkins). (b) Pistillate flower. (c) Staminate flowers.

Figure 13.11. Floral symmetry. (a) Regular flower of stonecrop (*Sedum* sp.). (b) Irregular flower of garden pea (*Pisum sativum*).



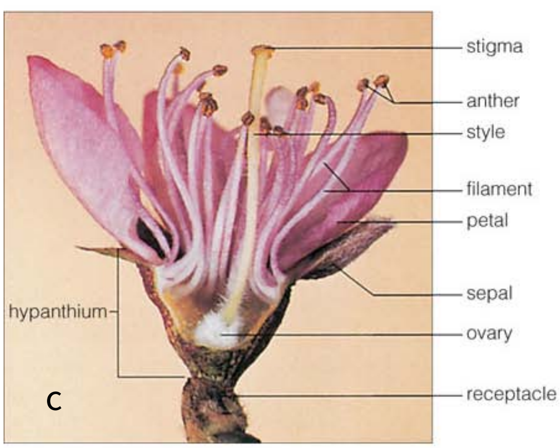


Figure 13.12. Variations in the elevation of floral parts relative to the ovary. (a) Superior ovary in the tulip flower (*Tulipa*). (b) Inferior ovary in daffodil flower (*Narcissus pseudonarcissus*). (c) In almond flower (*Prunus* sp.) the hypanthium is not fused to the ovary.

pseudonarcissus) (Fig. 13.12b), the ovary appears to be below the apparent points of attachment of the perianth parts and the stamens. This is an **inferior ovary**. In a flower with an inferior ovary, the lower portions of the three outer whorls--calyx, corolla, and androecium–have fused to form a tube, the **hypanthium**, which is also fused to the ovary. In some flowers, such as those of cherry, peach, and almond (all in the genus *Prunus),* the hypanthium does not become fused to the ovary (Fig. 13.12c).

Often Flowers Occur in Clusters, or Inflorescences

In many flowering plants, flowers are borne in clusters or groups known as inflorescences. An **inflorescence** is a flowering branch; some of the most common ones are illustrated in Figure 13.13.

A very simple type of inflorescence, called a **raceme**, is found in such plants as currant *(Ribes)* and radish *(Raphanus).* The main axis has short branches, each of which terminates in a flower; the short branches are **pedicels**. The oldest flowers are at the base of the inflorescence and the youngest at the apex. A branched raceme is called a **panicle** (Fig. 13.13).

In a **spike**, the main axis of the inflorescence is elongated, as in a raceme or panicle, but the flowers have no pedicels. A **catkin** is a spike that usually bears only pistillate or staminate flowers. Examples are walnut (see Fig. 13.10) and willow (see Fig. 13.20).

An **umbel** inflorescence has a short floral axis, and the flowers arise umbrella-like from approximately the same level (Fig. 13.13). Onion (*Allium cepa*) and carrot (*Daucus carrota*) are examples.

A **head** is an inflorescence in which the flowers lack pedicels and are crowded together on a very short axis. Members of the sunflower family (Astareaceae) have this type of inflorescence (Fig. 13.13).

In a **cyme**, the apex of the main axis produces a flower that involves the entire apical meristem, so that the axis itself does not elongate (Fig. 13.13). Other flowers arise on lateral branches farther down the axis. The youngest flowers in any cluster occur farthest from the tip of the main stalk. Chickweed *(Cerastium)* is an example.

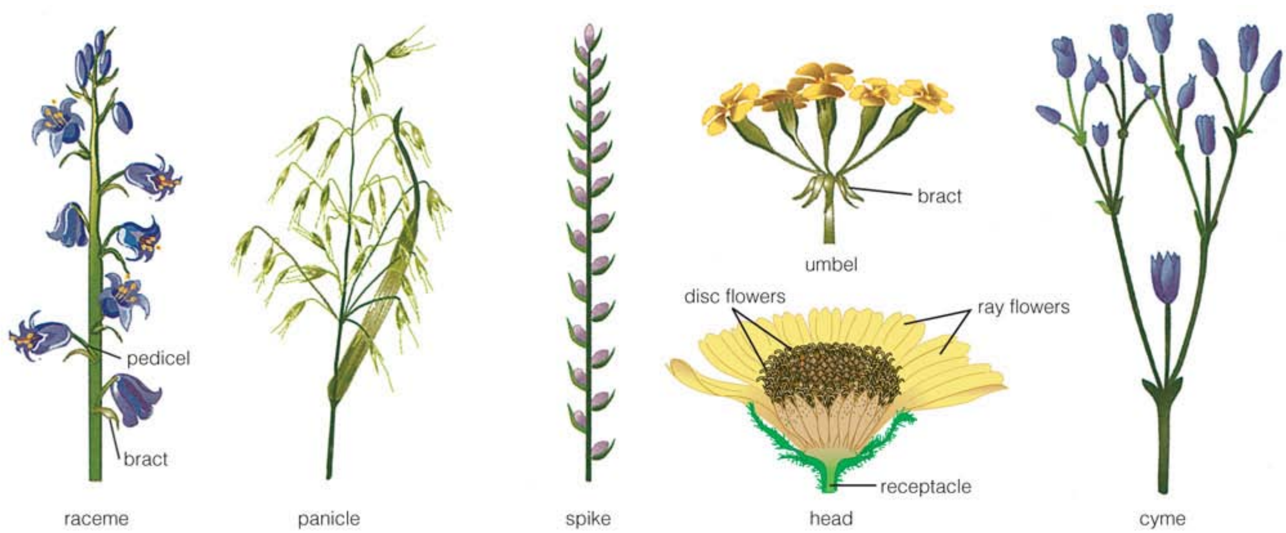


Figure 13.13. Types of inflorescences.

13.4 REPRODUCTIVE STRATEGIES: SELF-POLLINATION AND CROSS-POLLINATION

The importance of pollen to plant reproduction was first demonstrated in the 1760s by Joseph Koelreuter, who created hybrid plants by dusting the stigma on one species with the pollen of another. Three decades later, Christian Sprengel correctly distinguished between self-pollinating and cross-pollinating species and described the role of wind and insects as pollen vectors. Koelreuter and Sprengel are the founders of a field of study called *pollination ecology.*

There are essentially two different kinds of pollination. Transfer of pollen from the anther to the stigma in the same flower and transfer of pollen from one flower to another on the same plant are types of **self-pollination** or **selfing**. Genetic recombination (see Chapter 16) does not result from such crosses, because only one plant is involved. The other kind of pollination, **cross-pollination** or **outcrossing**, involves transfer of pollen from one genetically distinct plant to the stigma of another. Cross-pollination results in genetic recombination, leading to genetically diverse offspring.

Various plant traits encourage the success of either selfing or outcrossing. Separation of sexes onto different individual plants ensures outcrossing. Plants that have both sexes on the same individual can prevent selfing by inhibiting pollen tube growth through the style or by inhibiting the formation of a zygote. Selfing is also prevented when the anthers mature or release their pollen some time before (or after) the stigmas on the same plant mature and are receptive to pollen.

Selfing does have advantages, even though genetic diversity is sacrificed. Selfing is a necessary means of reproduction for scattered populations in extreme habitats such as arctic tundra, where pollinating insects are few and the odds of pollen from one plant reaching another are low. Selfing is also common among plants of disturbed habitats, and it permits weedy species (for example, many grasses) to multiply and spread even if only one parent reaches a site. Selfing also saves pollen (and the metabolic energy required to produce it) because selfers generally produce fewer pollen grains per flower or per ovule than outcrossers. Selfing also increases the probability that pollen will reach a stigma because the distance traveled and the time needed for travel are so short. The time element is important because pollen is quite sensitive to low humidity and to ultraviolet rays of sunlight; consequently pollen ordinarily has a short life span, measured in hours or days for most species.

Extreme examples of self-pollinating species have flowers that never open. They remain small and budlike, and the pollen falls from the anther sacs onto the stigma while the flower parts are still close together.

Production of Some Seeds Does Not Require Fertilization

Apomixis refers to a form of asexual reproduction in which no fusion of sperm and egg occurs. Normally, egg nuclei will not embark on the series of changes that leads to an embryo unless fertilization has occurred. Occasionally, however, an embryo does develop from an unfertilized egg. This type of apomixis is called **parthenogenesis**. Another type occurs when the embryo plant arises from diploid tissue surrounding the embryo sac. These *adventitious* embryos occur in *Citrus* and other plants.

Apomixis also has other variations, but all forms of this phenomenon involve the origin of new individuals without nuclear or cellular fusion of sperm and egg. In some plants, deposition of pollen on the stigma is a prerequisite to apomictic embryo development, even though a pollen tube does not grow down the style and nuclear fusion does not take place. In such instances, there is evidence that hormones formed in the stigma, or furnished by the pollen, move to the unfertilized, but diploid, egg cell (in this case meiosis is omitted during embryo sac formation), initiating embryo development.

Pollination Is Effected by Vectors

Pollen may be moved by either biotic (animal) or abiotic (wind and water) vectors. The set of unique flower and pollen traits that adapt a plant for pollination by a particular vector is its **pollination syndrome** (Table 13.1).

Table 13.1 Pollination Syndromes: Traits of Flowers Pollinated by Different Vectors

	Vector							
Trait	Beetle	Fly	Bee	Butterfly	Moth	Bird	Bat	Wind
Color	Dull white or green	Pale and dull to dark brown or purple; sometimes flecked with translucent patches	Bright white, red yellow, blue, or ultraviolet	Bright, including red and purple	Pale and dull red, purple, pink, or white	Scarlet, orange, red, or white	Dull white, green, or purple	Dull green, brown, or colorless; petals may be absent or reduced
Nectar guides	Absent	Absent	Present	Present	Absent	Absent	Absent	Absent
Odor	None to strongly fruity or fetid	Putrid	Fresh, mild, pleasant	Faint but fresh	Strong and sweet; emitted at night	None	Strong and musty; emitted at night	None
Nectar	Sometimes present; not hidden	Usually absent	Usually present; somewhat hidden	Ample; deeply hidden	Abundant; deeply hidden	Abundant; deeply hidden	Abundant; somewhat hidden	None
Pollen	Ample	Modest in amount	Limited; often sticky and scented	Limited	Limited	Modest	Ample	Abundant; small, smooth, and not sticky
Flower shape	Large, regular dishlike; erect	Funnel-like or a complex trap	Regular or irregular; often tubular with a lip; erect	Regular; tubular with a lip; erect	Regular; tubular without a lip; closed by day; pendant or horizontal	Regular or irregular; tubular without a lip; pendant or horizontal	Regular; trumpet-like; closed by day; pendant or borne on truck	Regular; small; anthers and stigmas exserted
Examples	Tulip tree, magnolia, dogwood	Skunk cabbage, philodendron	Larkspur, snapdragon, violet	Phlox	Tobacco, Easter lily, some cacti	Fuchsia, hibiscus	Banana, sausage tree, agave	Walnut, grasses

Animal pollinators are not altruistic. They visit flowers for some reward, and only incidentally do they transfer pollen. The most common rewards are pollen and nectar, but sometimes they are waxes or oils.

Because of the great cost and consequences of wasting rewards, plants have evolved various strategies to prevent rewards from being stolen by non-pollinating animals. For example, the rewards are offered in such a precise way that only pollinators are attracted or able to reach them. In more than a few cases, instead of offering any real reward, plants mimic insects or food which tricks the pollinator into visiting its flower. In effect, such plants are parasitizing animals for their energy as carriers of pollen. When a reward is actually offered, the interaction is mutualistic--of benefit to both partners.

Pollen is an excellent food for animals. Its tough outer wall resists digestion, but once it is pierced or chewed, the cytoplasm within typically provides protein (15 to 30% by weight), sugar (around 15%), fat (3 to 13%), starch (1 to 7%), plus trace amounts of vitamins, essential elements, and secondary substances. Most pollen is yellow to orange, and highly noticeable. Many pollen grains have a distinctive odor. The timing of pollen maturation can be very precise, coinciding with the seasonal or daily activity of pollinators. The anthers of corn (*Zea mays*), for example, split open in the morning; those of crocus *(Crocus)* split in midday, and those of apple in the afternoon. Certain bat-pollinated flowers release pollen only at night.

Nectar is sugary water transported by the phloem into specialized secretory structures called **nectaries**. The sugar solution from nectaries may run down into elongated petal spurs, or it may form pools at the base of the floral tube. Like pollen, it may have a very limited, precise time of availability. Nectar usually contains 15 to 75% sugar (glucose, fructose, and sucrose). Amino acids are present only in minor amounts, but these are significant to pollinators such as butterflies that are completely dependent on nectar for all their nutrition for a period of several months. All 13 essential amino acids for insects are present. Lipid is also often a minor component.

BIOTIC POLLEN VECTORS Beetles, flies, bees, butterflies, moths, birds, and bats are all pollinators. Beetles are among the oldest insect groups, already in existence when flowering plants first evolved. The flowers pollinated by beetles today have many primitive traits: regular symmetry, large single flowers, bowl-shaped architecture, and many floral parts that are not fused. Beetles are clumsy fliers. The bowl-shaped flowers attract beetles by odor (Table 13.1), and they provide a large target. Beetles chew a path through the sexual organs. By possessing many stamens and pistils, flowers are sure to have some that not only survive the attack but are pollinated. Many beetle-pollinated species are tropical. The temperate-zone tulip tree *(Liriodendron tulipifera)* flower (Fig. 13.14) is a good example of this syndrome.

Flies are very diverse, and some have evolved to mimic bees, bumblebees, wasps, and hawk moths. For this reason, there is no single syndrome of floral traits for fly pollination. However, the skunk cabbage (*Lysichtum americanum*), in the fly-pollinated arum family (Fig. 13.15), is unique. Their trumpet-shaped petals or bracts often have a checkered mosaic of opaque patches. In a breeze, this moving pattern, along with the epidermal hairs flicking in the wind, attracts flies. The effect may be a mimicry of many moving flies, which will attract other flies. These flowers emit the odor of decaying protein in carrion or dung. Some fly-pollinated flowers trap the insects for several hours.

Bees and butterflies are active by day, and they must have a landing platform, usually the flower petals. Moths can hover, so they don't require a corolla lip; and they are active by night or at dawn and dusk. Bees, butterflies, and moths harvest nectar as their reward, but the flowers they pollinate are strikingly different (see Table 13.1). Butterfly flowers are vividly colored, emit faint odors, have a broad blossom rim, are erect, and exhibit prominent **nectar guides** (Fig. 13.16). These are various markings that direct the pollinator to the flower's sexual organs and source of nectar. Moth flowers are white or faintly colored, emit heavy odors that penetrate the night air, have a fringed blossom rim, are pendant or horizontal, and have no nectar guides.

Figure 13.14. A beetle pollinated plant. Tulip tree (*Liriodendron tulipifera*) has the characteristic syndrome of beetle-pollinated flowers, though it may be visited by other insects as well. Some of the numerous stamens and carpels will be destroyed by the chewing behavior of pollinating beetles.

Figure 13.15. A fly-pollinated plant, skunk cabbage (*Lysichitum americanum*), a member of the arum family. Many small flowers give off a putrid odor. The funnel-shaped "corolla" is actually a modified leaf called a spathe.

Figure 13.16. *Phlox diffusa*, a butterfly-pollinated flower.

Moth flowers are often closed during the day. Both butterfly and moth flowers have long, narrow tubes (impossible for bees and beetles to enter) with pools of nectar at their base. Bee pollination is discussed in the sidebar, "Bee-Pollinated Flowers."

Birds were not recognized by botanists as pollinators until relatively recently. Now we know that thousands of plant species are pollinated by birds in many parts of the world--by hummingbirds in North and South America, sunbirds and sugar birds in Africa and Asia, honeyeaters and honey creepers on Pacific islands, and honey parrots or lorikeets in Australia. Flowers that birds visit for nectar have strikingly similar syndromes. The flowers range from scarlet to red to orange and generally lack nectar guides. They have very deep tubes usually without a landing platform, are pendant or horizontal, and have abundant nectar but emit no odor (see Table 13.1). Columbine (*Aquilegia formosa*) flowers have this syndrome (Fig. 13.17a). Other bird-pollinated flowers have brush-type flowers, with elongate stamens that stick out in all directions (Fig. 13.17b).

Most bats eat insects, but some are vegetarian; these have longer snouts and tongues, smaller teeth, larger eyes, and a better sense of smell. Bat flowers open at night, just as moth flowers do. They are positioned below the foliage of the parent tree--hanging pendant on a long pedicel or attached to the trunk or low limbs. Bats are color-blind, so bat flowers are drab white, green, or purple. The flowers exude a strong musty odor at night, reminiscent of fermenting fluid, cabbage, or bats themselves. Bat flowers are large and tough, with lots of pollen (some have more than 1300 anthers) and nectar (7 to 15 ml). Bat flowers include *Musa* (banana; Fig. 13.18), *Adansonia* (baobab), *Kigelia* (sausage tree), *Ceiba* (kapok), and *Agave*.

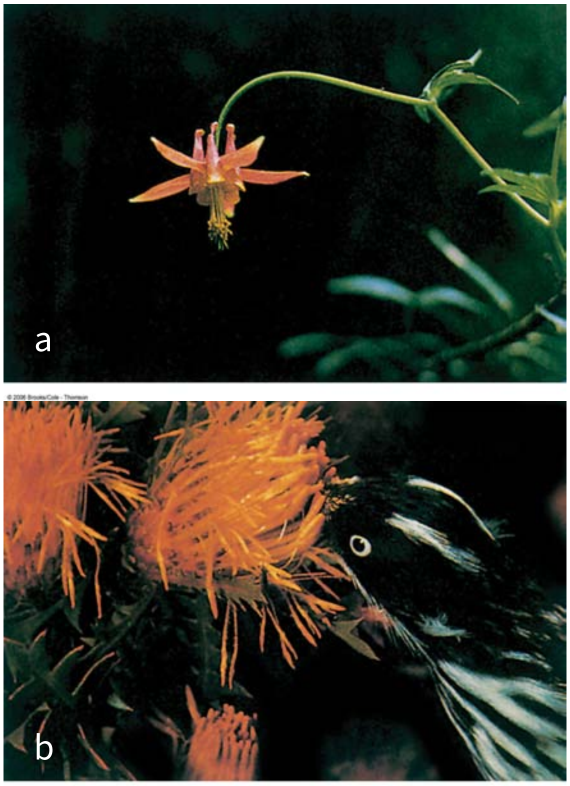


Figure 13.17. Bird-pollinated flowers. (a) Columbine (*Aquilegia formosa*), pollinated by humming birds, is a tubular type. (b) *Dryandra hewardiana* pollinated by honey eaters, is a brush type.

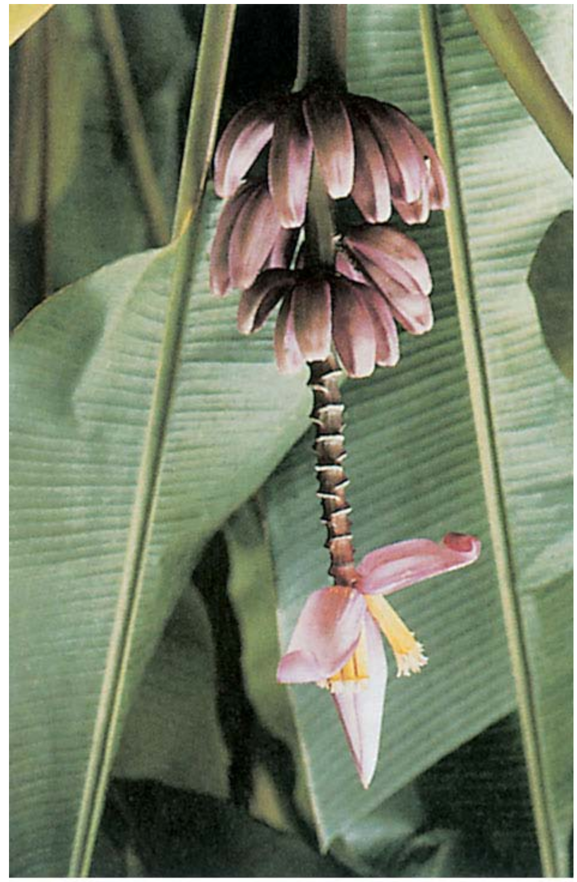


Figure 13.18. Banana (*Musa velutina*), a bat-pollinated flower.

ABIOTIC POLLEN VECTORS Wind and water both carry pollen. Typical wind-pollinated flowers are small, colorless, odorless, and lacking in nectar. Petals are often lacking or are reduced to small scales. The flowers or inflorescences are positioned to dangle or wave in the open. Trees such as walnut (*Juglans*), hazelnut (*Corylus*), and oak (*Quercus*) produce flowers before new leaves emerge in the spring. Grasses and sedges (for example, *Cyperus*) position their flowers well above the leaves so they are exposed to wind currents.

The pollen grains of such plants are generally smaller, smoother, and drier than those of animal-pollinated species. Wind-carried pollen grains are 20 to 60 μm in diameter, while insect-carried pollen grains are 13 to 300 μm. The pollen often changes shape from spherical to frisbee-like upon release to dry air, improving its aerodynamic form. Wind-pollinated flowers also produce more pollen grains per ovule (500 to 2.5 million) than animal-pollinated flowers (5 to 500). The volume of pollen released is tremendous: a single rye *(Secale cereale)* or corn *(Zea mays)* plant releases 20 million grains, and one plant of dock *(Rumex acetosa)* can release 400 million.

Stigmatic surfaces are enlarged and elaborate, often extending outside the flower. Architecture of the flower and the inflorescence creates vortices that trap pollen and permit the grains to settle onto stigmas at a rate greater than predicted by chance (Fig. 13.19).

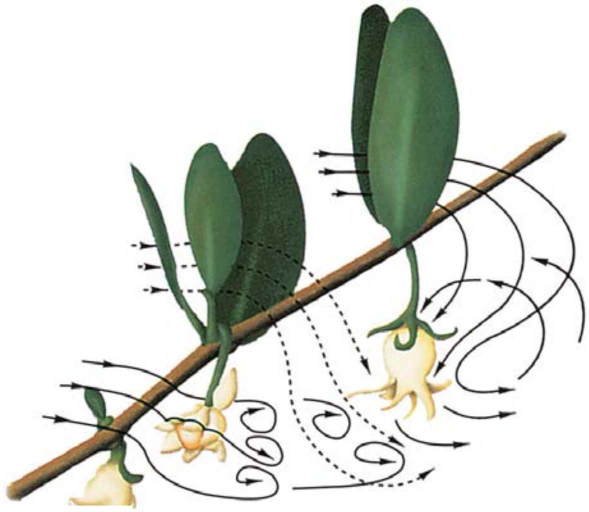


Figure 13.19 (above). Wind-pollinated flower. The architecture of jojoba flowers (*Simondsia chinensis*) creates vortices of air currents which bring pollen grains to the stigmatic surfaces.

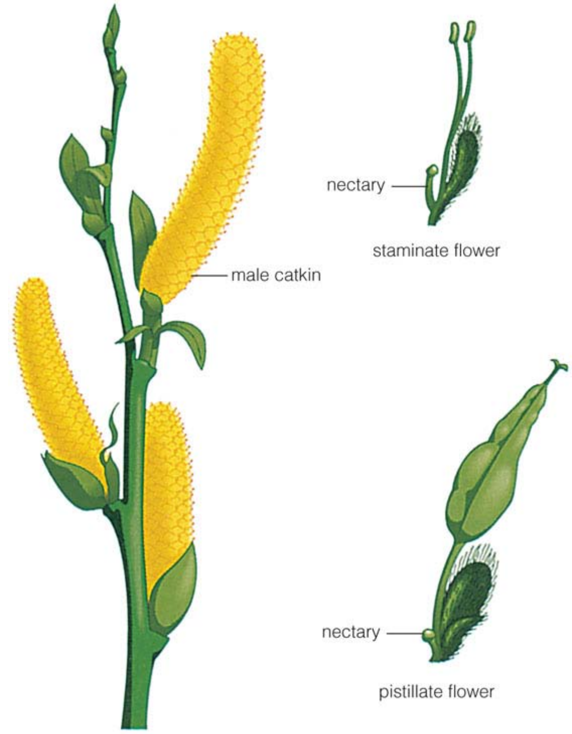


Figure 13.20 (right). Wind- and insect-pollinated flowers. The staminate and pistillate flowers of willow (*Salix*), a dioecious plant, have typical features of a wind-pollinted plant; they lack a corolla and are grouped into catkins that appear before the leaves emerge in spring. Yet, the flowers have nectaries and the pollen grains are rather large and intensely yellow colored. Some species of willow rely predominantly on bees as pollen vectors, wind being relatively unimportant.

To their advantage, many wind-pollinated species are also visited by insects. For example, arroyo willow *(Salix lasiolepis;* Fig. 13.20) flowers have nectaries, and bees are responsible for more than 90% of seed set. Pollen of corn and of some sedge *(Carex)* species is scented and attractive to insects. Bees are known to collect pollen from grass flowers, even though they lack nectar, color, and odor. So wind pollination and insect pollination syndromes are not mutually exclusive.

Most aquatic plants produce flowers that project above the water surface. Some of these--such as pondweed (*Potamogeton*)--are pollinated by wind; others--including water lily (*Nymphaea*)--by insects. Other plants produce flowers just at the water surface, and the pollen floats from anther to stigma; ditch-grass (*Ruppia*) is an example. Only a few plants actually transfer pollen in the water, below the surface, and these employ a variety of syndromes. The pollen grains of water-nymph (*Najas*) are heavy and spherical and sink from the anthers into trumpet-shaped stigmas below them. In eelgrass (*Zostera),* the pollen grains are elongate and threadlike. They actively coil around any narrow object, such as a stigma, that they encounter.

KEY TERMS

adnation
androecium
angiosperms
anther
antipodal cells
apomixis
axile placentation
calyx
carpels
catkin
central cell
central placentation
complete flower
compound pistil
connation
corolla
cross-pollination (outcrossing)
cyme
dioecious
double fertilization
egg apparatus
egg cell
embryo sac
endosperm
female gametophyte
filament
generative cell
gynoecium
head (inflorescence)
hypanthium
imperfect flower
incomplete flower
inferior ovary
inflorescence
integuments
irregular symmetry
locules
male gametophyte
megaspores
megasporocyte
micropyle
microsporocytes
monoecious
nectar guides
nectarines
nucellus
ovary
ovules
panicle
parietal placentation
parthenogenesis
pedicels
perfect flower
perianth
petals
pistil
pistillate flower
placenta
placentation
polar nuclei
pollen grain
pollen sacs
pollen tube
pollination
pollination syndrome
primary endosperm nucleus
raceme
regular symmetry
self-pollination (selfing)
sepals
simple pistil
sperm cells
spike
stamens
staminate flower
stigma
style
superior ovary
synergid cells
tube cell
umbel
zygote

SUMMARY

1. The flower, the distinguishing structure of the flowering plants (angiosperms), is formed of four whorls of parts specialized to carry out sexual reproduction, including pollination, fertilization, and seed production.

2. The four whorls are (a) the calyx, composed of sepals; (b) the corolla, composed of petals; (c) the androecium, composed of stamens; and (d) the gynoecium, composed of carpels.

3. The stamen has two parts: the pollen-producing anther and the filament.

4. The gynoecium consists of one or more pistils. A simple pistil is made of only one carpel; if it consists of two or more fused carpels, it is a compound pistil.

5. A pistil consists of three parts: the stigma, the style, and the ovary. The stigma is receptive to pollen, and the ovary encloses the ovules. At the time of fertilization, the ovules consist of integuments, the nucellus, and the embryo sac.

6. Meiosis takes place in both the anthers and the ovule.

7. Pollen is a two-celled haploid plant or male gametophyte, protected by a cell wall, that is frequently elaborately sculptured. Two sperm cells are produced by the generative cell.

8. The embryo sac is a seven-celled haploid plant, or female gametophyte. There are two synergids, one egg, three antipodals, and a central cell with the two polar nuclei (seven cells and eight nuclei).

9. Pollination is the transfer of pollen from anthers to stigmas. A cellular recognition system regulates the germination of compatible pollen. A pollen tube that grows down the style to the ovule carries the two sperm to the embryo sac.

10. Double fertilization involves the union of one sperm with the egg (to form the zygote) and the union of a second sperm with the polar nuclei (to form the primary endosperm nucleus). This double process is unique to the flowering plants.

11. The embryo plant develops from the zygote. The endosperm develops from the primary endosperm nucleus, and it becomes the nutrient source for the developing embryo.

12. A floral apex has lost its ability to elongate and its potential for vegetative growth.

13. Species that have male and female sexes on different plants are dioecious. Species with staminate and pistillate flowers on the same plant are monoecious.

14. Variation in floral architecture arises from (a) variation in number of parts in a given whorl; (b) symmetry in floral parts; (c) connation of floral parts; (d) adnation of floral parts; (e) superior or inferior ovary; and (f) the presence or absence of certain whorls.

15. Flowers are either solitary on flower stalks or grouped in various inflorescences such as heads, spikes, catkins, umbels, panicles, racemes, and cymes.

16. There are essentially two types of pollination: cross-pollination, which involves more than one plant and results in much variation in progeny, and self-pollination, which involves a single plant and results in progeny having great similarities.

17. Apomixis is a type of asexual reproduction in which an unfertilized egg develops into an embryo.

18. Pollination occurs by means of biotic and abiotic vectors. Biotic vectors are animals that transfer pollen accidentally and secondarily; t heir primary objective is to obtain rewards for visiting flowers. The rewards commonly include pollen, nectar, oil, wax, and odors. The

rewards cost the plant metabolic energy to produce, but this cost is balanced against the surety of cross-pollination. The plant-animal interaction is mutualistic because there are benefits to both partners. Some flowers attract pollinators without providing any rewards; in such cases the relationship is parasitic rather than mutualistic.

19. Animal vectors include beetles, flies, bees, butterflies, moths, birds, and bats. Each animal visits flowers with a particular syndrome of traits. The traits--shape, color, odor, timing of opening, nature of rewards offered--attract the animal and permit it to function as a pollinator.

20. Abiotic vectors include wind and water. Wind-dispersed pollen is distinctly different from animal-dispersed pollen; it is smaller, the outer wall is smoother, and the grains are not sticky. The amount of pollen produced is also much greater, and the ratio of pollen grains to ovules is orders of magnitude larger.

Questions

1. Define each of the following terms:
   sepal, petal
   pistil, carpel, stigma, style, ovary
   stamen, filament, anther
   calyx, corolla, gynoecium, androecium

2. Make a detailed diagram showing the steps that occur in the anther leading to the formation of the pollen grains (the male gametophyte).

3. Make a detailed diagram showing the steps that occur in the ovule leading to the formation of the embryo sac (the female gametophyte).

4. Make labeled diagrams of a mature pollen grain and a mature embryo sac. Show all of the cells and nuclei found in each of them.

5. Describe the process of double fertilization. What are the products of each sperm fusion?

6. Explain why a flower is actually a shortened shoot and the flower parts are modified leaves.

7. Explain the following terms: regular versus irregular flowers; complete versus incomplete flowers; free versu united flower parts.

8. Distinguish between a simple flower and an inflorescence.

9. Explain the difference between self-pollination and cross-pollination. Is one of these strategies better than the other? Why?

10. Pollination syndromes involve pollination strategies that have evolved between particular flowers and particular vectors--for example, bees. Describe an example of a pollination syndrome involving a biotic vector and another involving an abiotic vector.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Bee-Pollinated Flowers*

Bees are among the most "intelligent" insects. Their sense of color is well developed, in contrast to beetles and flies. They are receptive to blue, yellow, white, and ultraviolet wave-lengths. They cannot see red, but they will visit red flowers that also reflect ultraviolet light (Fig. 1). These colors are produced by carotenoid and flavonoid pigments in the chromoplasts or vacuoles of petal cells. Splotches, dots, or lines of contrasting color, called nectar guides, often lead toward the sexual organs (Fig. 2).

Bees are sensitive to sweet odors and to sugary nectar, and both are often present in bee-pollinated flowers, especially during the day (Fig. 2). Odors come from organic molecules in the pollen or petals. Bees can discern the intensity of sweetness, and they favor the sweetest nectars. Unless the sugar concentration is greater than 18%, honeybees operate at a loss; that is, their expenditure of metabolic energy exceeds that of the reward.

Pollen is a major reward, and bees carry the pollen in their crop, on abdominal hairs, or in hairy "baskets" on their hind legs (Fig. 3). One insect can carry as many as a million pollen grains. A bee's proboscis (tubelike snout) is very sensitive, and petal hairs often force the insect to enter the flower by a certain

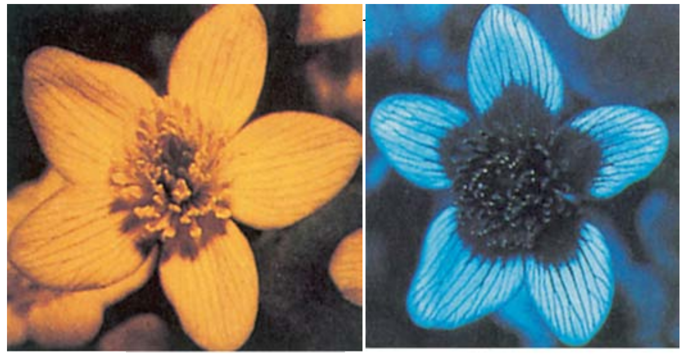


Figure 1. A flower that reflects ultraviolet (UV) light. Evening primrose (*Oenothera fruticosa*) is photographed with normal light-sensitive film on the left and with UV-sensitive film on the right. Unlike humans, bees are able to see the reflected UV light.

Figure 2. Nectar guides. (left) In *Viola*, splashes of color and lines lead to the throat of the corolla. (right) *Nasturtium* flower sectioned to show guide lines and hairs leading to the entrance of the tubular spur where the nectar accumulates.

Figure 3. The scotch broom (*Cytisus scoparius*) landing platform corresponds to bee size and shape. A bee's weight forces its petals apart, releasing the stamens. These dust the bee with pollen. A bee grooms itself and packs pollen (the orange mass) inside "baskets" of leg hairs.

Only recently has the importance of oil as a reward for pollinating bees been recognized. More than 2000 species in 13 plant families produce oil instead of nectar. Their flowers are visited by specialized bees with long, densely hairy forelegs; these forelegs slice open *elaiophores* (the oil-containing equivalent of nectaries) and soak up oil like a wick. The bees also wag their abdomens over the petals to mop up oil onto body hairs. The energy content of oil--twice that of sugar--makes it a suitable food for bee larvae.

A few genera of orchids (including Calypso and *Ophrys)* mimic the odor, color, and shape of female bees (Fig. 4). Males are attracted, land on the flower, and try to copulate with it. In the process, wads of sticky pollen become attached to their bodies, and these are transferred to another orchid when copulation is again attempted. Some South American species of the orchid *Oncidium* vibrate in the wind and mimic male bees; these are attacked by territorial bees. The diving attack often results in pollen becoming attached to the bee and then transferred to another flower. Other orchids mimic insect prey of female wasps, which land on and sting the petals. They pick up sticky pollen in the process and take it to the next mimic. In these cases, there is no reward for the insect.

Figure 4. Some orchids imitate the odor, shape, and color of insects, and they attract pollinators without offering any rewards. Species of *Ophrys* attract male bees who attempt to copulate with the flower.

Photo Credits

Figure 13.1 – from 1st ed.
Figure 13.2a-f – originally from Weier 6th
Figure 13.3a&b – originally from Weier 6th
Figure 13.4 – from Drs. Robert Preston and Maureen Stanton (UC Davis)
Figure 13.5 – from 1st ed
Figure 13.6 – from 1st ed
Figure 13.7a-i – from 1st ed, redrawn from Weier 6th (b-h redrawn from U. R. Gore, Amer. J. Bot. 19:795-802 [1932]; (i) modified and redrawn from W. A. Jensen. Amer. J. Bot 52: (1965) 781-797.)
Figure 13.8 – from 1st ed
Figure 13.9a-e – from Dr. Joe Lin, Davis, CA
Figure 13.10 – from 1st ed
Figure 13.11a – from 1st ed., 13.11b - from Thomas L. Rost
Figure 13.12 a-c – from 1st ed
Figure 13.13 – 1st ed
Figure 13.14 –1st ed
Figure 13.15- 1st ed
Figure 13.16 – 1st ed
Figure 13.17 – 1st ed
Figure 13.18 – from Prof. Grady Webster, U.C. Davis
Figure 13.19 – redrawn from an article in the American Journal of Botany 1985: 530-539 by K. J. Niklas and S.L. Buchmann, Cornell University.
Figure 13.20 – 1st ed

SIDEBAR – Figure 1 – from Thomas Eisner, Cornell University
Figure 2 – Weier 6th
Figure 3 – Edward S. Ross
Figure 4 – Dr. Robert Norris, UC Davis