

Evolution of the Angiosperms

CHAPTER OUTLINE

Relationships of the Angiosperms
 Origin and Diversification of the Angiosperms
 Evolution of the Flower
 Evolution of Fruits
 Biochemical Coevolution

In a letter to a friend, Charles Darwin once referred to the apparently sudden appearance of the angiosperms in the fossil record as “an abominable mystery.” In the early fossil-bearing strata, about 400 million years old, one finds simple vascular plants, such as rhyniophytes and trimerophytes. Then there is a Devonian and Carboniferous proliferation of ferns, lycophytes, sphenophytes, and progymnosperms, which were dominant until about 300 million years ago. The early seed plants first appeared in the Late Devonian period and led to the gymnosperm-dominated Mesozoic floras. Finally, early in the Cretaceous period, and at least 130 million years ago, angiosperms appear in the fossil record, gradually achieving worldwide dominance in the vegetation by about 90 million years ago. By about 75 million years ago, many modern families and some modern genera of this phylum already existed.

CHECKPOINTS

By the time you finish reading this chapter, you should be able to answer the following questions:

1. What are the current hypotheses on the origin of angiosperms, and what is the presumed relationship among the monocots, the eudicots, and the magnoliids?
2. What are the four principal evolutionary trends among flowers?
3. What feature has evolved in angiosperms that has allowed them directed mobility in seeking a mate?
4. How do beetle-, bee-, moth-, and bat-pollinated flowers differ from one another?
5. What are some of the adaptations of fruits, in relation to their dispersal agents?
6. How, apparently, have secondary metabolites influenced angiosperm evolution?

Despite their relatively late appearance in the fossil record, why did the angiosperms rise to world dominance and then continue to diversify to such a spectacular extent? In this chapter, we shall attempt to answer this question, centering our discussion on the relationships of the angiosperms, their origin and diversification, the evolution of the flower and its pollinators (Figure 20–1), the evolution of fruits, and the role of certain chemical substances in angiosperm evolution. All five topics will illustrate some of the reasons for the evolutionary success of the group.



20–1 Angiosperms and pollinators The evolution of the flowering plants is, to a large extent, the story of increasingly specialized relationships between flowers and their insect pollinators, in which beetles played an important early role. A longhorn beetle (family Cerambycidae), laden with pollen, is shown here visiting the flowers of death camas (*Zigadenus elegans*) in the mountains of northeastern Arizona.

Relationships of the Angiosperms

Since the time of Darwin, scientists have attempted to understand the ancestry of the angiosperms. One approach has been to search for their possible ancestors in the fossil record. In this effort, particular emphasis has been placed on assessing the ease with which the ovule-bearing structures of various gymnosperms could be transformed into a carpel. Recently, phylogenetic analyses (cladistics) based on fossil, morphological, and molecular data have revitalized attempts to define the major natural groups of seed plants and to understand their interrelationships.

Based on morphological and structural analyses, it appears that Bennettitales (page 413) and gnetophytes (page 431) are the seed plants most closely related to angiosperms, although the application of recent molecular data has not yet been fully incorporated into the interpretation of these patterns. The term “anthophytes” (not to be confused with the use of the term Anthophyta here to refer to angiosperms) has been proposed to refer collectively to the Bennettitales, gnetophytes, and angiosperms. It emphasizes the shared possession of flowerlike reproductive structures by these three groups of seed plants. Two contrasting hypotheses have been proposed for the phylogenetic relationships among anthophytes. One hypothesis proposes that the gnetophytes are monophyletic, and the derived similarities that *Gnetum* (Figure 18–36) and *Welwitschia* (Figure 18–38) share with angiosperms are interpreted as examples of convergent evolution (Figure 20–2a). The second hypothesis considers the gnetophytes to be paraphyletic, with *Gnetum* and *Welwitschia* as sister groups to angiosperms (Figure 20–2b). The latter hypothesis interprets the derived similarities of *Gnetum*, *Welwitschia*, and angiosperms to be homologous.

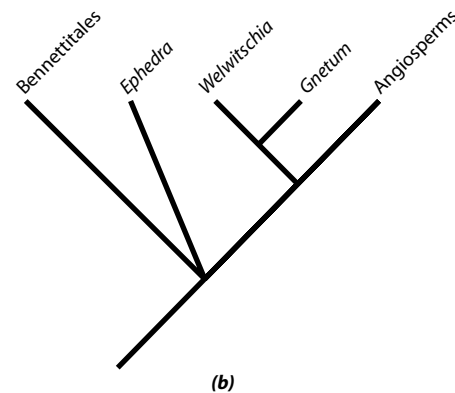
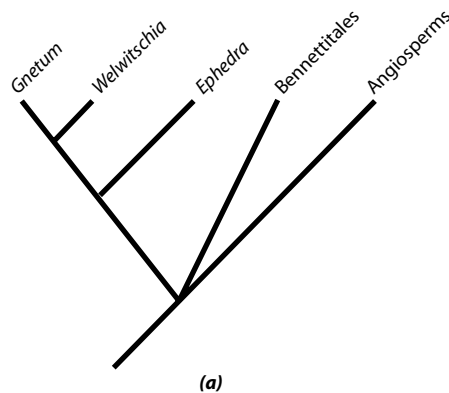
It is significant that the Bennettitales and gnetophytes first appear in the fossil record in the Triassic period, about 225 million years ago. This seems to place some constraints on the possible earliest date of the appearance of the angio-

sperms—that is, on the possibility that they could have arisen any earlier.

Origin and Diversification of the Angiosperms

The unique characteristics of the angiosperms include flowers, closed carpels, double fertilization leading to endosperm formation, a three-nucleate microgametophyte, an eight-nucleate megagametophyte, stamens with two pairs of pollen sacs, and the presence of sieve tubes and companion cells in the phloem (see Chapter 23). These similarities clearly indicate that the members of this phylum were derived from a single common ancestor. This common ancestor of the angiosperms ultimately would have been derived from a seed plant that lacked flowers, closed carpels, and fruits. The earliest known fossils of angiosperms are flowers and pollen grains up to 130 million years old, from the Early Cretaceous period. The earliest angiosperm fossils from which we can gain a good impression of the whole plant are those of *Archaeofructus* (see Figure 20–7). Current evidence does not support the hypothesis that angiosperms originated much earlier than this time, although we have only recently come to understand the features to look for in such early fossils. Certainly all of the characteristic features of angiosperms did not appear together in one ancestral plant, so that the time and nature of the origin of the group will certainly be a matter of definition when we have accumulated enough evidence.

Like the gymnosperms, the earliest angiosperms clearly had pollen with a single aperture, as found in monocots and a few other groups of angiosperms, as well as cycads, *Ginkgo*, and other groups. This feature can therefore be considered an ancestral one that has been retained in the course of evolution. Angiosperms that produce single-aperture pollen, therefore, cannot be shown, on the basis of this character, to have had a common ancestor distinct from other angiosperms.



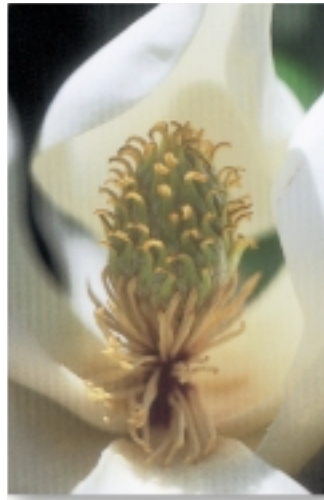
20–2 Two hypotheses for the phylogenetic relationships among anthophytes (a) One hypothesis states that the Gnetales are monophyletic, and the derived similarities of *Gnetum*, *Welwitschia*, and angiosperms are interpreted as convergent evolution. (b) According to another hypothesis, the Gnetales are paraphyletic,

with *Gnetum* and *Welwitschia* as the sister groups to the angiosperms. This hypothesis interprets the derived similarities of *Gnetum*, *Welwitschia*, and angiosperms as being homologous. Both of these hypotheses are in conflict with some analyses of relationships based on molecular data.



(a)

20-3 Magnolia Flowers and fruits of the southern magnolia (*Magnolia grandiflora*), a woody magnoliid. The cone-shaped receptacle bears numerous spirally arranged carpels from which curved styles emerge. Below the styles in (a) and (b) are the cream-white stamens. (a) The anthers have not yet shed their pollen,



(b)



(c)

whereas the stigmas are receptive. Such flowers are said to be protogynous. (b) The floral axis of a second-day flower, showing stigmas that are no longer receptive and stamens that are shedding pollen. (c) Fruit, showing carpels and bright red seeds, each protruding on a slender stalk.

Some Flowering Plants Are Neither Monocots Nor Eudicots

In Chapter 19, we discussed the two largest classes of angiosperms, the monocots and the eudicots, which between them comprise 97 percent of the members of the phylum. The monocots clearly had a common ancestor, as indicated by their single cotyledon and a number of other features. The same is true of the eudicots, which have a characteristic derived feature, their triaperturate pollen (pollen with three slits or pores, and also pollen types derived from the triaperturate group).

The remaining 3 percent of living angiosperms include those with the most archaic features. They consist of a number of evolutionary lines that are quite distinct from one another. Their relationships with the other groups of angiosperms have been specified more precisely in recent years, thanks to macromolecular comparisons and strict analyses of the relationships between evolutionary lines based on their ancestral and derived characteristics.

Several evolutionary lines of angiosperms arose before the split between the monocots and eudicots. All of these plants had been regarded as “dicots” until recently, but they are no more dicots than monocots. All of these plant groups, like the monocots, have pollen with a single aperture or some modification of this type, indicating that the three-aperturate pollen of the eudicots is a derived characteristic that marks that group.

On the evolutionary line leading to eudicots are the magnoliids, including the magnolia family (Magnoliaceae; Figure 20-3), in which the flowers have numerous, spirally arranged flower parts. Also included are their relatives, such as the laurel family (Lauraceae), pepper family (Piperaceae), pipevine family (Aristolochiaceae; Figure 20-4); and spice-



20-4 Dutchman's pipe *Aristolochia gigantea*, the Dutchman's pipe, belongs to the pipevine, or birthwort, family (Aristolochiaceae), a magnoliid. The flowers of *Aristolochia* emit odors ranging from lemony to foul-smelling rotted meat, all of which attract their insect pollinators.



20–5 Waterlilies *Fragrant water lilies (Nymphaea odorata) are native to the eastern United States but have become widespread and even invasive. Pollen-covered insects, attracted by the sweet fragrance, fall into fluid produced in the cuplike center of the flower. Pollen washes off the insect and onto the stigmas of the flower, resulting in pollination.*

bush family (Calycanthaceae). A number of other families of plants with similar features are also included, many of them concentrated in or restricted to the Australasian region and the Southern Hemisphere generally. One of their characteristic features is that the leaves of most magnoliids contain oil cells with ethereal (ether-containing) oils, the basis of the characteristic scents of nutmeg, pepper, and laurel leaves. There are about 20 families of plants in the magnoliids with living representatives.

In addition to the magnoliids, there are a few families of plants that represent evolutionary lines that arose before the divergence between monocots, on the one hand, and magnoliids-eudicots on the other. These include a number of relatively small, isolated families, the best known of which are the waterlilies (Nymphaeaceae; Figure 20–5). The first of these surviving evolutionary lines to have split from the others that make up the rest of the angiosperms is the family Amborellaceae, consisting of a single species restricted to the South Pacific island of New Caledonia (Figure 20–6).



(a)



(b)



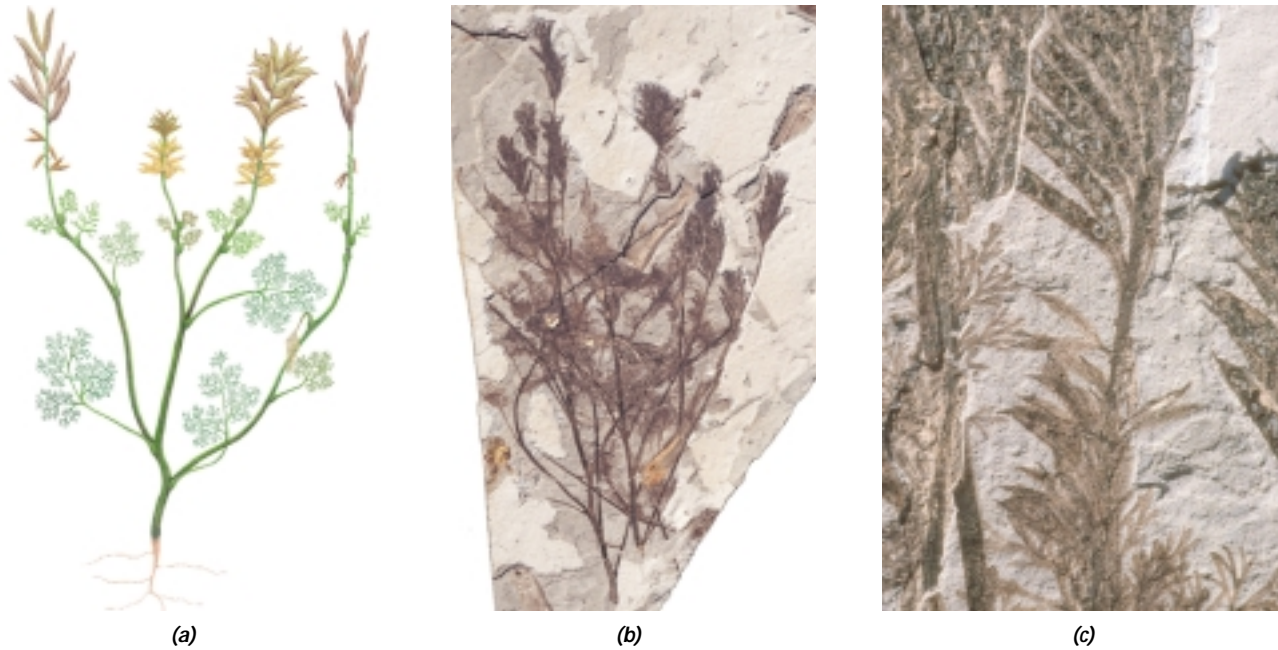
(c)



(d)

20–6 Amborella trichopoda (a) The woody, evergreen plant *Amborella trichopoda* is the only species in the family Amborellaceae. It is a sprawling shrub with small flowers in which the segments of the perianth (petals and sepals in many groups of plants) are undifferentiated. *Amborella* is dioecious, meaning that the (b) staminate and (c) carpellate flowers are found on different

plants. The stamens are rather undifferentiated, with no stalks, and the few carpels in the carpellate flowers develop into (d) small fruits (drupes) containing pockmarked stones mixed with resinous deposits. New Caledonia, which split from Australia/Antarctica some 80 million years ago, is home to more groups of angiosperms with archaic features than any other place on Earth.



20-7 Archaeofructus sinensis The fossils of *Archaeofructus sinensis*, the earliest well-known flowering plant, are approximately 125 million years old. They were recovered from semi-aquatic beds preserved in northern China. **(a)** Reconstruction of a whole plant,

showing the slender roots, dissected leaves, and floral axes with closed carpels above, closed stamens below. **(b)** Whole specimen minus the roots. **(c)** Full view of a fertile fruiting axis showing the closed carpels and stamens and some leaf material.

The earliest representative of an angiosperm well documented in the fossil record is *Archaeofructus*, recently discovered in China (Figure 20-7). It can be recognized as an angiosperm because it has seeds enclosed in carpels or fruits. The simple roots, herbaceous stems, dissected leaves, stamens, and carpels are known from sediments dated by argon-argon radiometric methods at 125 million years old (Lower Cretaceous Period). The highly dissected leaves, herbaceous stems, and numerous associated fish fossils suggest that the plant stood in shallow water with the branches bearing stamens and carpels extending above the water's surface. No petals or sepals were present, suggesting that this fossil may represent a very early stage in the evolution of flowering plants, before showy flowers existed. The numerous stamens may have attracted pollinators. The aquatic nature of this early angiosperm may indicate that the early evolution of the angiosperms took place in open wet or aquatic environments subject to frequent disturbances. Such conditions would have favored small, fast-growing plants with a short generation time, a set of features that is still characteristic of many angiosperms today.

Prior to the last decade or so, most botanists considered the earliest angiosperms to have had large flowers with numerous, spirally arranged (rather than whorled) flower parts, thus resembling the flowers of a magnolia (Figure 20-3). With the discovery of *Archaeofructus*, however, and the elucidation of its characteristics by David Dilcher of the University of Florida and his colleagues, it became clear that plants with characteristics similar to those of *Amborella* predate the appearance of plants with magnolia-like flowers by perhaps 10 to 20 million years. Thus it now seems much more likely that the flowers of the original angiosperms were

probably smaller, simpler, and not showy, with simple pollination systems, and that magnolia flowers and all of the floral diversity that marks modern angiosperms arose long after the appearance of the group. Angiosperms spread rapidly around the world and differentiated as the boundaries between the major climatic zones have become more pronounced, especially during the last 70 million years or so.

Evolution of the Flower

What were the flowers of the earliest angiosperms like? Of course, we do not know this from direct observation, but we can deduce their nature from what we know of certain living plants and from the fossil record. In general, the flowers of these plants were diverse, both in the numbers of floral parts and in the arrangement of these parts. Most modern families of angiosperms tend to have more fixed floral patterns that do not vary much in their basic structural features within a particular family. We shall discuss the derivation of these patterns over the course of evolution in the following sections, which deal with the different whorls of the flower from the outside in, moving from the perianth inward to the androecium and the carpel.

The Parts of the Flower Provide Clues to Angiosperm Evolution

The Perianth of Early Angiosperms Did Not Have Distinct Sepals and Petals In the earliest angiosperms, the perianth, if present, was never sharply divided into calyx and corolla. Either the sepals and petals were identical, or there was a gradual transition in appearance between these

whorls, as in modern magnolias and water lilies. In some angiosperms, including the water lilies, petals appear to have been derived from sepals. In other words, the petals can be viewed as modified leaves that have become specialized for attracting pollinators. In most angiosperms, however, petals were probably derived originally from stamens that lost their sporangia—becoming “sterilized”—and then were specially modified for their new role. Most petals, like stamens, are supplied by just one vascular strand. In contrast, sepals are

normally supplied by the same number of vascular strands as are the leaves of the same plant (often three or more). Within sepals and petals alike, the vascular strands usually branch so that the number of strands that enter them cannot be determined from the number of veins in the main body of the structures.

Petal fusion has occurred a number of times during the evolution of the angiosperms, resulting in the familiar tubular corolla that is characteristic of many families (Figure 20–8c).



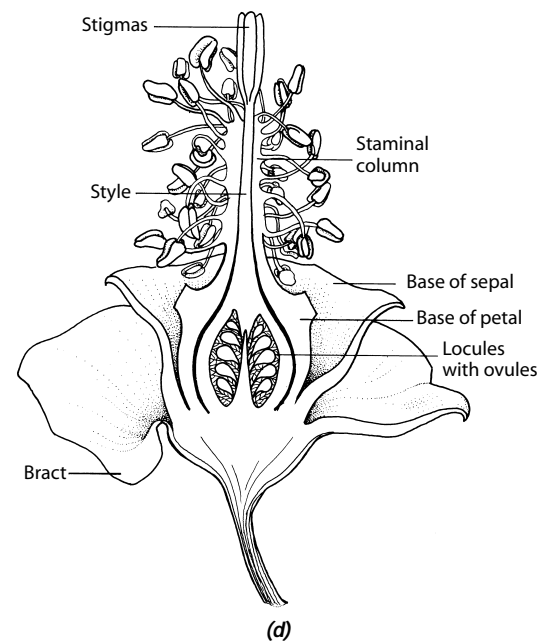
(a)



(b)



(c)



(d)

20–8 Examples of specialized flowers (a) Wintergreen, *Chimaphila umbellata*. The sepals (not visible) and petals are reduced to five each, the stamens to ten, and the five carpels are fused into a compound gynoecium with a single stigma. (b) Lotus, *Nelumbo lutea*. The undifferentiated sepals and the numerous petals and stamens are spirally arranged; the carpels are embedded in a flat-topped receptacle. (c) Chaparral honeysuckle, *Lonicera hispidula*. The ovary is inferior and has two or three locules; the sepals are reduced to small teeth at its apex. The petals are fused into a corolla tube in the zygomorphic (bilaterally

symmetrical) flower, and the five stamens, which protrude from the tube, are attached to its inner wall. The style is longer than the stamens, and the stigma is elevated above them. A pollinator visiting this flower would contact the stigma first, so that if it were carrying pollen from another flower, it would deposit that pollen on the stigma before reaching the anthers. Fruits of this species are shown in Figure 20–27b. (d) A diagram of a longitudinal section of a cotton (*Gossypium*) flower, of the mallow family, with the sepals and petals removed and showing the column of stamens fused around the style.

When a tubular corolla is present, the stamens often fuse with it and appear to arise from it. In a number of evolutionarily advanced families, the sepals are also fused into a tube.

The Stamens of Early Angiosperms Were Diverse in Structure and Function The stamens of some families of woody magnoliids are broad, colored, and often scented, playing an obvious role in attracting floral visitors. In other archaic angiosperms, the stamens, although relatively small and often greenish, may also be fleshy. Many living angiosperms, in contrast, have stamens with generally thin filaments and thick, terminal anthers (for example, see Figure 19–6). In general, the stamens of monocots and eudicots seem to be much less diverse in structure and function than the stamens of magnoliid angiosperms.

In some specialized flowers the stamens are fused together. Their fused filaments may then form columnar structures, as in the members of the pea, melon, mallow (Figure 20–8d), and sunflower (Figure 20–9d) families, or they may be fused with the corolla, as in the phlox, snapdragon, and mint families. In certain plant families, some of the stamens have become secondarily sterile: they have lost their sporangia and become transformed into specialized structures, such as nectaries. Nectaries are glands that secrete **nectar**, a sugary fluid that attracts pollinators and provides food for them. Most nectaries are not modified stamens but arose instead in other ways. During the course of evolution of the angiosperm flower, the sterilization of stamens, as noted above, also played an important role in the evolution of petals.

The Carpels of Many Early Angiosperms Were Unspecialized A number of woody magnoliids have generalized and sometimes leaflike carpels, with no specialized areas for the entrapment of pollen grains comparable to the specialized stigmas of most living angiosperms. The carpels of many woody magnoliids and other plants that retain archaic features are free from one another, instead of being fused together as in most contemporary angiosperms. In a few living woody magnoliids, the carpels are incompletely closed, although pollination is always indirect, that is, the pollen does not contact the ovules directly. In the vast majority of living angiosperms, the carpels are closed (a condition that gave rise to the name of the phylum) and sharply differentiated into stigmas, styles, and ovaries. There is much variation in the arrangement of the ovules among contemporary groups of angiosperms, which often have fewer ovules than do some of the more generalized and archaic families of the phylum.

Four Evolutionary Trends among Flowers Are Evident

Insect pollination quite probably triggered the early evolution of angiosperms, both through the possibilities it provided for isolating small populations and with indirect pollination fostering competition between many pollen grains as they grew through the stigmatic tissue. The flowers of the earliest members of the phylum probably were bisexual, but

unisexual flowers appeared very early in many different families. The undifferentiated perianth of early angiosperms soon gave rise to distinct petals and sepals. As the angiosperms continued to evolve, and relationships with specialized pollinators became more tightly linked, the number and arrangement of floral patterns became more stereotyped. The following four trends are evident (Figure 20–8):

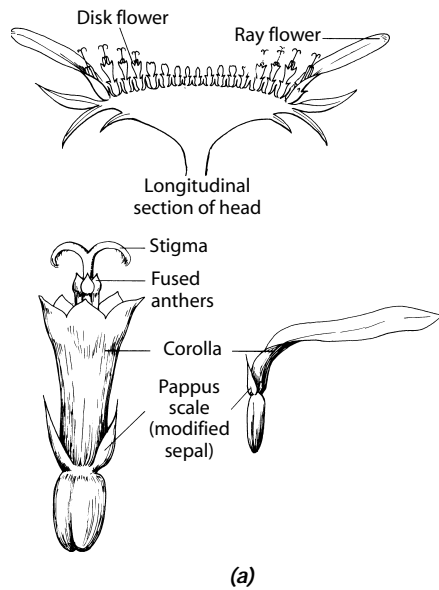
1. From flowers with few to many parts that are indefinite in number, flowers have evolved toward having few parts that are definite in number.
2. The number of floral whorls has been reduced from four in early flowers to three, two, or sometimes one in more advanced ones. The floral axis has become shortened so that the original spiral arrangement of parts is no longer evident. The floral parts often have become fused.
3. The ovary has become inferior rather than superior in position, and the perianth has become differentiated into a distinct calyx and corolla.
4. The radial symmetry (regularity), or actinomorphy, of early flowers has given way to bilateral symmetry (irregularity), or zygomorphy, in more advanced ones.

The Asteraceae and Orchidaceae Are Examples of Specialized Families

Among the most evolutionarily specialized of flowers are those of the family Asteraceae (Compositae), which are eudicots, and those of the family Orchidaceae, which are monocots. In number of species, these are the two largest families of angiosperms.

The Flowers of the Asteraceae Are Closely Bunched Together into a Head In the Asteraceae (the composites), the epigynous flowers are relatively small and closely bunched together into a head. Each of the tiny flowers has an inferior ovary composed of two fused carpels with a single ovule in one locule (Figure 20–9).

In composite flowers, the stamens are reduced to five in number and are usually fused to one another (connate) and to the corolla (adnate). The petals, also five in number, are fused to one another and to the ovary, and the sepals are absent or reduced to a series of bristles or scales known as the **pappus**. The pappus often serves as an aid to dispersal by wind, as it does in the familiar dandelion, a member of the Asteraceae (Figure 20–9c; see also Figures 20–24 and 20–25b). In other members of this family, such as beggarticks (*Bidens*), the pappus may be barbed, serving to attach the fruit to a passing animal and thus to enhance its chances of being dispersed from place to place. In many members of the family Asteraceae, each head includes two types of flower: (1) disk flowers, which make up the central portion of the aggregate, and (2) ray flowers, which are arranged on the outer periphery. The ray flowers are often carpellate, but sometimes they are completely sterile. In some members of the Asteraceae, such as sunflowers, daisies, and black-eyed



20–9 Composites (family Asteraceae) (a) A diagram showing the organization of the head of a member of this family. The disk and ray flowers are subordinated to the overall display of the head, which functions as a single large flower in attracting pollinators. (b) Thistle, *Cirsium pastoris*. Members of the thistle tribe have only disk flowers. This particular species of thistle has bright red flowers and is regularly

visited by hummingbirds, which are its primary agents of pollination. (c) *Agoseris*, a wild relative of the dandelion *Taraxacum*. In the inflorescences of the chicory tribe (the group of composites to which dandelions and their relatives belong), there are no disk flowers. The marginal ray flowers, however, are often enlarged. (d) Sunflower, *Helianthus annuus*.

Susans, the fused bilaterally symmetrical (zygomorphic) corolla of each ray flower forms a long strap-shaped “petal.”

In general, the composite head has the appearance of a single large flower. Unlike many single flowers, however, the head matures over a period of days, with the individual flowers opening serially in an inward-moving spiral pattern. As a consequence, the ovules in a given head may be fertilized by several different pollen donors. The success of this plan as an evolutionary strategy is attested by the great

abundance of the members of the Asteraceae and also their great diversity, which, with about 22,000 species, makes them the second largest family of flowering plants.

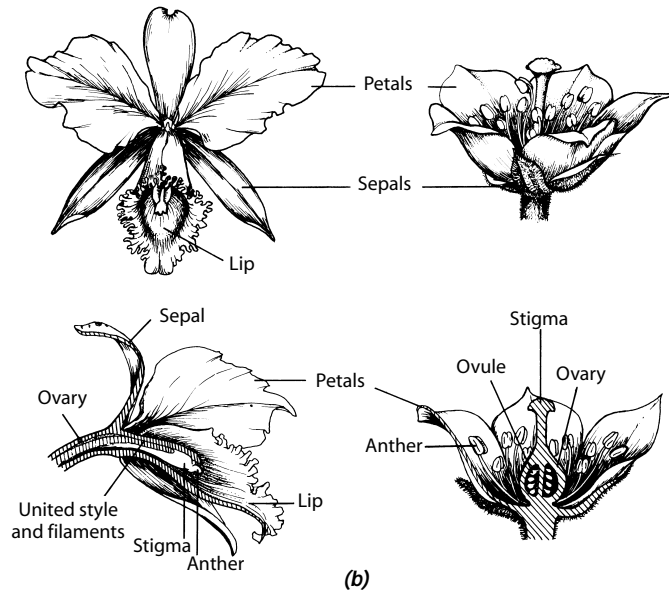
Orchidaceae Is the Largest Angiosperm Family Another successful flower plan is that of the orchids (Orchidaceae), which, unlike the composites, are monocots. There are probably at least 24,000 species of orchids, making them the largest family of flowering plants. In contrast to the composites,



(a)

however, individual species of orchids are rarely very abundant. Most species of orchids are tropical, and only about 140 are native to the United States and Canada, for example. In the orchids, the three carpels are fused and, as in the composites, the ovary is inferior (Figure 20–10). Unlike the composites, however, each orchid ovary contains many thousands of minute ovules. Consequently, each pollination event may result in the production of a huge number of seeds. Usually only one stamen is present (in one subfamily, the lady-slipper orchids, there are two), and this stamen is characteristically fused with the style and stigma into a single complex structure—the **column**. The entire contents of an anther are held together and dispersed as a unit—the **pollinium**. The three petals of orchids are modified so that the two lateral ones form wings and the third forms a cup-like lip that is often very large and showy. The sepals, also three in number, are often colored and similar to petals in appearance. The flower is always bilaterally symmetrical and often bizarre in appearance.

Among the orchids are some species with flowers the size of a pinhead and others with flowers more than 20 centimeters in diameter. Several genera contain saprophytic species. Two Australian species grow entirely underground, their flowers appearing in cracks in the ground, where they are pollinated by flies. In the commercial production of orchids, the plants are cloned by making divisions of meri-



20–10 Orchids (family Orchidaceae) (a) An orchid of the genus *Cattleya*. Orchids have extremely specialized flowers. (b) A comparison of the parts of an orchid flower, shown on the left, with those of a radially symmetrical flower, shown on the right. The “lip” is a modified petal that serves as a landing platform for insects.

stematic tissue, and thousands of identical plants can be produced rapidly and efficiently (Chapter 10). There are more than 60,000 registered hybrids of orchids, many of them involving two or more genera. The seed pods of orchids of the genus *Vanilla* are the natural source of the popular flavoring of the same name.

Animals Serve As the Primary Agents of Floral Evolution

Plants, unlike most animals, cannot move from place to place to find food or shelter or to seek a mate. In general, plants must satisfy those needs by growth responses and by the structures that they produce. Many angiosperms, however, have evolved a set of features that, in effect, allows them directed mobility in seeking a mate. This set of features is embodied in the flower. By attracting insects and other animals with their flowers, and by directing the behavior of these animals so that cross-pollination (and therefore cross-fertilization) will occur at a high frequency, the angiosperms have transcended their rooted condition. In this one respect, they have become just as mobile as animals. How was this achieved?

Flowers and Insects Have Coevolved The earliest seed-bearing plants were pollinated passively. Large amounts of

pollen were blown about by the wind, reaching the vicinity of the ovules only by chance. The ovules, which were borne on the leaves or within cones, exuded sticky drops of sap from their micropyles. These drops served to catch the pollen grains and to draw them to the micropyle. As in most modern cycads (page 431) and gnetophytes, insects feeding on the pollen and other flower parts began returning to these new-found sources of food and thus transferred pollen from plant to plant. Such a system is more efficient than passive pollination by the wind. It allowed much more accurate pollination with many fewer pollen grains involved.

Attraction of insects to the naked ovules of these plants sometimes resulted in the loss of some of the ovules to the insects. The evolution of a closed carpel, therefore, gave certain seed plants—the ancestors of the angiosperms—a reproductive, and thus a selective, advantage. Further changes in the shape of the flower, such as the evolution of the inferior ovary, may have been additional means of protecting the ovules from being eaten by insects and other animals, thus providing a further reproductive advantage.

Another important evolutionary development was the appearance of the bisexual flower. The presence of both carpels and stamens in a single flower (in contrast, for instance, to the separate microsporangiate and megasporangiate cones of living conifers) offers a selective advantage by making each visit by a pollinator more effective. The pollinator can both pick up and deliver pollen at each stop.

If a given plant species is pollinated by only one or a few kinds of visitors, selection favors specializations related

to the characteristics of these visitors. Many of the modifications that have evolved in flowers promoted consistency in the specific type of visitor to that particular kind of flower. For example, many modern angiosperms are pollinated solely or chiefly by beetles, others by flies (Figure 20–11). Both depend on floral odors that are fruity or resemble dung or carrion, and in beetle-pollinated flowers, essential floral parts are often covered and thus protected from their gnawing visitors.

Bees, however, are the most important group of flower-visiting insects, responsible for the pollination of more groups of plants than any other group. In fact, bees and flowering plants have become diverse together over the course of the past 80 million years.

Both male and female bees live on nectar, and the females also collect pollen to feed the larvae. Bees have mouthparts, body hairs, and other appendages with special adaptations that make them suitable for collecting and carrying nectar and pollen (Figure 20–12). As Karl von Frisch and other investigators of insect behavior have shown, bees can learn quickly to recognize colors, odors, and outlines. The portion of the light spectrum that is visible to most insects, including bees, is somewhat different from the portion visible to humans. Unlike human beings, bees perceive ultraviolet as a distinct color; however, they don't perceive red, which therefore tends to merge with the background.

Bee flowers have showy, brightly colored petals that are usually blue or yellow. They often have distinctive patterns by which bees can efficiently recognize them. Such patterns



(a)

20–11 Beetle- and fly-pollinated flowers (a) A pollen-eating beetle, *Asclera ruficornis*, at the open, bowl-shaped flowers of round-leaved hepatica (*Anemone americana*). The species of the family (Oedemeridae) to which this beetle belongs feed only on pollen as



(b)

adults. (b) The foul-scented and often dark-colored flowers of many species of milkweeds (family Apocynaceae), such as those of this African succulent plant, *Stapelia schinzii*, are pollinated by carrion flies.



20–12 Bee pollination Bees have become as highly specialized as the flowers they have been associated with during the course of their evolution. Their mouthparts have become fused into a sucking tube containing a tongue. The first segment of each of the three pairs of legs has a patch of bristles on its inner surface. Those of the first and second pairs are pollen brushes that gather the pollen that sticks to the bee's hairy body. On the third pair of legs, the bristles form a pollen comb that collects pollen from these brushes and from the abdomen. From the comb, the pollen is forced up into pollen baskets, concave surfaces fringed with hairs on the upper segment of the third pair of legs. Shown here is a honeybee (*Apis mellifera*) foraging in a flower of rosemary (*Rosmarinus officinalis*). In the rosemary flower, the stamens and stigma arch upward out of the flower, and both come into contact with the hairy back of any visiting bee of the proper size. Here the anthers can be seen depositing white pollen grains on the bee.

include “honey guides,” which are special markings that indicate the position of the nectar (Figure 20–13).

Flowers that are regularly pollinated with butterflies and diurnal moths (those that are active in the day rather than at night) are similar, in general, to bee-pollinated flowers, but they often have “landing platforms” built into the structure of the flower (Figure 20–14). Those that are pollinated by nocturnal (night-flying) moths are generally white or pale in color, and often have a sweet, penetrating scent that is emitted only after sunset. The nectary in a moth or butterfly flower is often located at the base of a long, slender corolla tube or a spur and is usually accessible only to the long, sucking mouthparts of these insects.

Bird- and Bat-Pollinated Flowers Produce Copious Nectar Bird-pollinated flowers produce large amounts of nectar and are often red and odorless (Figure 20–15). They generally have a copious, thin nectar but usually have little odor because the sense of smell is poorly developed in birds. Birds, however, have a keen sense of color, and the flowers they visit regularly are colorful, with red and yellow ones being the most common. Such flowers include red columbine, scarlet passion flower, hibiscus, and poinsettia.

Some plant groups, especially in the tropics, have flowers that are regularly pollinated by bats. The bats that do obtain most of their food at flowers have slender, elongated muzzles and long, extensible tongues, sometimes with a brushlike tip (Figure 20–16). Most of the flowers that are pollinated by bats produce copious nectar and are dull colored, and many of them open only at night. Such flowers often hang down on long stalks below the foliage, or are borne on the trunks of trees, where the bats can get to them easily. Bat flowers characteristically have either very strong



20–13 Honey guides So-called honey guides on the flowers of the foxglove (*Digitalis purpurea*) serve as distinctive signals to insect visitors. The lower lip of the fused corolla serves as a landing platform of the kind that is commonly found in bee flowers.



20–14 Butterfly pollination

Copper butterfly (*Lycaena gorgon*) sucking nectar from the flowers of a daisy. The long sucking mouthparts of moths and butterflies are coiled up at rest and extended when feeding. They vary in length from species to species. Only a few millimeters long in some of the smaller moths, they are 1 to 2 centimeters long in many butterflies, 2 to 8 centimeters long in some hawkmoths of the North Temperate zone, and as long as 25 centimeters in a few kinds of tropical hawkmoths.

fermenting or fruitlike odors, or musty scents resembling those produced by bats to attract one another.

Wind-Pollinated Flowers Produce No Nectar Wind-pollinated flowers, which do not rely on animal pollinators, produce no nectar, have dull colors, and are relatively odorless. The petals of these flowers are either small or absent, and the sexes are often separated on the same plant. They are best represented in temperate regions, with many plants of the same species often growing together and pollen dispersal often occurring in early spring, before the plants have formed their leaves. Oaks, birches (Figure 20–17a), and grasses (Fig-

ure 20–17b, c) are familiar examples of wind-pollinated plants. Wind-pollinated flowers usually have well-exposed anthers that readily lose their pollen to the wind. The large stigmas are characteristically exposed, and they often have branches



20–15 Bird pollination A male Anna's hummingbird (*Calypte anna*) at a flower of the scarlet monkey-flower (*Mimulus cardinalis*) in southern California. Note the pollen on the bird's forehead, which is in contact with the stigma of the flower.



20–16 Bat pollination By thrusting its face into the tubular corolla of a flower of an organ-pipe cactus (*Stenocereus thurberi*), the bat *Leptonycteris curasoae* is able to lap up nectar with its long, bristly tongue. Some of the pollen clinging to the bat's face and neck is transferred to the next flower it visits. This species of bat, which is one of the more specialized nectar-feeding bats, migrates from central and southern Mexico to the deserts of the southwestern United States during late spring and early summer. There it feeds on the nectar and pollen of organ-pipe and saguaro cacti and on the flowers of agaves.



(a)



(b)



(c)

20–17 Wind pollination Shown here are flowers of two kinds of wind-pollinated plants. **(a)** The staminate flowers of paper birch (*Betula papyrifera*) hang down in flexible, thin tassels several centimeters long. These tassels are whipped by passing breezes, and the pollen, when mature, is scattered about by the wind. **(b)** Grasses, such as maize (*Zea*

mays), characteristically have enlarged, often feathery stigmas that efficiently catch the wind-blown pollen shed by the hanging anthers. The “silk” on the ears of corn, or maize, consists of many stigmas, each leading to a grain on the young cob below. **(c)** Stamen-bearing (staminate) inflorescences, the “tassels,” at the top of the maize stem.

or feathery outgrowths adapted for intercepting wind-borne pollen grains.

The Most Important Pigments in Floral Coloration Are the Flavonoids

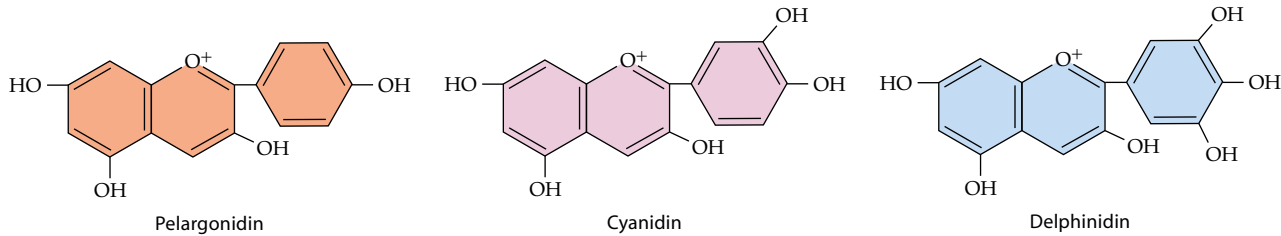
Color is one of the most conspicuous features of angiosperm flowers—a characteristic by which members of the phylum are easily recognized. The varied colors of different kinds of flowers evolved in relation to their pollination systems and, in general, are advertisements for particular kinds of animals, as we have just seen.

The pigments that are responsible for the colors of angiosperm flowers are generally common in all vascular plants. However, it is the way in which they are concentrated in angiosperm flowers, and particularly in their corollas, that is a special characteristic of the flowering plants. Surprisingly, all flower colors are produced by a small number of pigments. Many red, orange, or yellow flowers owe their color to the presence of carotenoid pigments similar to those that occur in leaves (and in all plants, in green algae, and in some other organisms as well). The most important pigments in floral coloration, however, are **flavonoids**, which are com-

pounds with two six-carbon rings linked by a three-carbon unit. Flavonoids probably occur in all angiosperms, and they are sporadically distributed among the members of other groups of plants. In leaves, flavonoids block far-ultraviolet radiation, which is destructive to nucleic acids and proteins. They usually selectively admit light of blue-green and red wavelengths, which are important for photosynthesis.

Pigments belonging to one major class of flavonoids, the **anthocyanins**, are major determinants of flower color (Figure 20–18). Most red and blue plant pigments are anthocyanins, which are water-soluble and are found in vacuoles. By contrast, the carotenoids are oil-soluble and are found in plastids. The color of an anthocyanin pigment depends on the acidity of the cell sap of the vacuole. Cyanidin, for example, is red in acid solution, violet in neutral solution, and blue in alkaline solution. In some plants, the flowers change color after pollination, usually because of the production of large amounts of anthocyanins, and then they become less conspicuous to insects.

The **flavonols**, another group of flavonoids, are very commonly found in leaves and also in many flowers. A number of these compounds are colorless or nearly so, but they may contribute to the ivory or white hues of certain flowers.



20–18 Anthocyanins These three anthocyanin pigments are the basic pigments on which flower colors in many angiosperms depend: pelargonidin (red), cyanidin (violet), and delphinidin (blue). Related compounds known as flavonols are yellow or ivory, and the carotenoids are red, orange, or yellow. Betacyanins (betalains) are red

pigments that occur in one group of eudicots. Mixtures of these different pigments, together with changes in cellular pH, produce the entire range of flower color in the angiosperms. Changes in flower color provide “signals” to pollinators, telling them which flowers have opened recently and are more likely to provide food.

For all flowering plants, different mixtures of flavonoids and carotenoids (as well as changes in cellular pH) and differences in the structural, and thus the reflective, properties of the flower parts produce the characteristic colors. The bright fall colors of leaves come about when large quantities of colorless flavonols are converted into anthocyanins as the chlorophyll breaks down. In the all-yellow flowers of the marsh marigold (*Caltha palustris*), the ultraviolet-reflective outer portion is colored by carotenoids, whereas the ultraviolet-absorbing inner portion is yellow to our eyes because of the presence of a yellow chalcone, one of the flavonoids. To a bee or other insect, the outer portion of the flower appears to be a mixture of yellow and ultraviolet, a color called “bee’s purple,” whereas the inner portion appears pure yellow (Figure 20–19). Most, but not all, ultraviolet reflectivity in flowers is related to the presence of carotenoids, and thus ultraviolet patterns are more common in yellow flowers than in others.

In the goosefoot, cactus, and portulaca families and in other members of the order Chenopodiales (Centrospermae), the reddish pigments are not anthocyanins or even flavonoids but a group of more complex aromatic compounds known as **betacyanins** (or betalains). The red flowers of *Bougainvillea* and the red color of beets are due to the presence of betacyanins. No anthocyanins occur in these plants, and the families characterized by betacyanins are closely related to one another.

Evolution of Fruits

Just as flowers have evolved in relation to their pollination by many different kinds of animals and other agents, so have fruits evolved for dispersal in many different ways. Fruit dispersal, like pollination, is a fundamental aspect of the evolutionary radiation of the angiosperms. Before we



(a)

20–19 Bee’s purple The color perception of most insects is somewhat different from that of human beings. To a bee, for example, ultraviolet light (which is invisible to humans) is seen as a distinct color. These photographs show a flower of marsh marigold (*Caltha palustris*) (a) in natural light, showing the solid yellow color as the



(b)

flower appears to humans, and (b) in ultraviolet light. The portions of the flower that appear light in (b) reflect both yellow and ultraviolet light, which combine to form a color known as “bee’s purple,” whereas the dark portions of the flower absorb ultraviolet and therefore appear pure yellow when viewed by a bee.

consider this subject in more detail, however, we must present some basic information about fruit structure.

A Fruit Is a Mature Ovary

A fruit may or may not include some additional flower parts, in addition to the mature ovary. A fruit in which such additional parts are retained is known as an **accessory fruit** (for example, the strawberry; see Figure 20–27a). Although fruits usually have seeds within them, some—**parthenocarpic fruits**—may develop without seed formation. The cultivated strains of bananas are familiar examples of this exceptional condition.

Fruits are generally classified as simple, multiple, or aggregate, depending on the arrangement of the carpels from which the fruit develops. **Simple fruits** develop from one carpel or from several united carpels. **Aggregate fruits**, such as those of magnolias, raspberries, and strawberries, consist of a number of separate carpels of one gynoecium. The individual parts of aggregate fruits are known as **fruitlets**; they can be seen, for example, in the magnolia fruit shown in Figure 20–3c. **Multiple fruits** consist of the gynoecia of more than one flower. The pineapple, for example, is a multiple fruit consisting of an inflorescence with many previously separate ovaries fused on the axis on which the flowers were borne. (The other flower parts are squeezed between the expanding ovaries; hence, the pineapple is also an accessory fruit.)

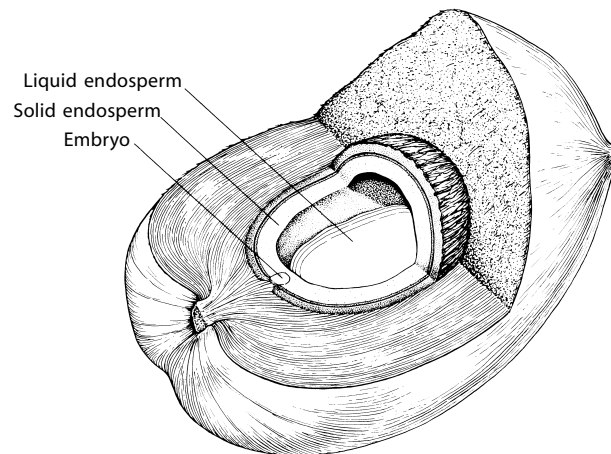
Simple fruits are by far the most diverse of the three groups. When ripe, they may be soft and fleshy, dry and woody, or papery. There are three main types of fleshy fruits—berries, drupes, and pomes. In **berries**—examples of which are tomatoes, dates, and grapes—there may be one to several carpels, each of which is typically many-seeded. The inner layer of the fruit wall is fleshy. In **drupe**s, there may also be one to several carpels, but each carpel usually contains only a single seed. The inner layer of the fruit is stony and usually tightly adherent to the seed (Figure 20–6d). Peaches, cherries, olives, and plums are familiar drupes. Coconuts are drupes whose outer layer is fibrous rather than fleshy, but in temperate regions we usually see only the coconut seed with the adherent stony inner layer of the fruit (Figure 20–20). **Pomes** are highly specialized fleshy fruits that are characteristic of one subfamily of the rose family. The pome is derived from a compound inferior ovary in which the fleshy portion comes largely from the enlarged base of the perianth; hence, a pome is also an example of an accessory fruit. The inner portion, or endocarp, of a pome resembles a tough membrane, as you know from eating apples and pears, the two most familiar examples of this kind of fruit.

Dry simple fruits are classified as either dehiscent (Figures 20–21 and 20–22) or indehiscent (Figure 20–23). In **dehiscent fruits**, the tissues of the mature ovary wall (the pericarp) break open, freeing the seeds. In **indehiscent fruits**, on the other hand, the seeds remain in the fruit after the fruit has been shed from the parent plant.

There are several kinds of dehiscent simple dry fruits. The **follicle** is derived from a single carpel that splits down



(a)



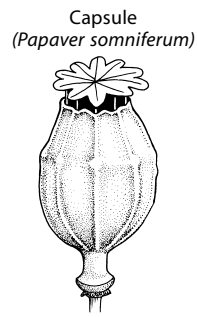
(b)

20–20 Coconut, a drupe The coconut palm (*Cocos nucifera*) has a very wide range on ocean shores throughout the world because its fruits are able to float for long periods and then germinate when they reach land. (a) A coconut germinating on the beach in Florida. (b) Diagram of a coconut fruit. The coconut milk is liquid endosperm. Cell walls form around the nuclei in the liquid endosperm, which becomes solid by the time of germination. When coconuts are transported commercially, their husks are usually removed first, so that in temperate countries people usually see only the stony inner shell of the fruit surrounding the seed.

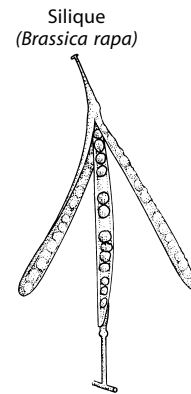
one side at maturity, as in the columbines, milkweeds (Figure 20–21a), and magnolias (Figure 20–3c). In the pea family (Fabaceae), the characteristic fruit is a **legume**. Legumes resemble follicles, but they split along both sides (Figure 20–22). In the mustard family (Brassicaceae), the fruit is called a **siliqua** and is formed of two fused carpels. At maturity, the two sides of the fruit split off, leaving the seeds attached to a persistent central portion (Figure 20–21c). The most common sort of dehiscent simple dry fruit is the **capsule**, which is formed from a compound ovary in plants with either a superior or an inferior ovary. Capsules shed their seeds in a variety of ways. In the poppy family (Papaveraceae), the seeds are often shed when the capsule splits lon-



(a)



(b)



(c)

20–21 Dehiscent fruits (a) Bursting follicles of a milkweed (*Asclepias*). (b) In some members of the poppy family (*Papaveraceae*), such as poppies (genus *Papaver*), the capsule sheds its seeds through pores near the top of the fruit. (c) Plants of the mustard family (*Brassicaceae*) have a characteristic fruit known as a silique, in which the seeds arise from a central partition, and the two enclosing valves fall away at maturity.

gitudinally, but in some members of this family they are shed through holes near the top of the capsule (Figure 20–21b).

Indehiscent simple dry fruits are found in many different plant families. Most common is the **achene**, a small, single-seeded fruit in which the seed lies free in the cavity except for its attachment by the funiculus. Achenes are characteristic of the buttercup family (*Ranunculaceae*) and the buck-

wheat family (*Polygonaceae*). Winged achenes, such as those found in elms and ashes, are commonly known as **samaras** (Figure 20–23). The achenelike fruit that occurs in grasses (*Poaceae*) is known as a **caryopsis**, or grain; in it, the seed coat is firmly united to the fruit wall. In the *Asteraceae*, the complex, achenelike fruit is derived from an inferior ovary; technically, it is called a **cypsela** (Figure 20–24). Acorns and



(a)



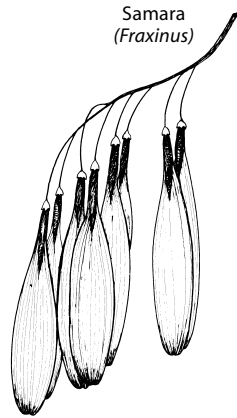
(b)



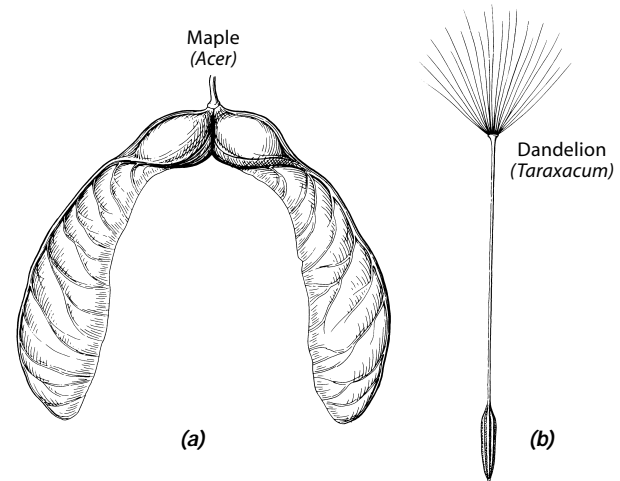
(c)

20–22 Legumes, dehiscent fruits The legume, a kind of fruit that is usually dehiscent, is the characteristic fruit of the pea family, *Fabaceae* (also called *Leguminosae*). With about 18,000 species, *Fabaceae* is one of the largest families of flowering plants. Many members of the family are capable of nitrogen fixation because of the presence of nodule-forming bacteria of the genera *Bradyrhizobium* and *Rhizobium* on their roots (see Chapter 29). For this reason, these plants are often the first colonists

on relatively infertile soils, as in the tropics, and they may grow rapidly there. The seeds of a number of plants of this family, such as peas, beans, and lentils, are important foods. (a) Legumes of the garden pea, *Pisum sativum*. (b) Legumes of *Albizzia polyphylla*, growing in Madagascar. Each seed is in a separate compartment of the fruit. (c) Legume of *Griffonia simplicifolia*, a West African tree. The two valves of the legume are split apart, revealing the two seeds inside.



20–23 Indehiscent fruit The samara, a winged indehiscent fruit characteristic of ashes (*Fraxinus*) and elms (*Ulmus*), retains its single seed at maturity. Samaras are dispersed by wind.



20–25 Wind-dispersed fruits (a) In maples (*Acer*), each half of the schizocarp has a long wing. (b) The fruits of the dandelion (*Taraxacum*) and many other composites have a modified calyx, called the pappus, which is adherent to the mature cypsel and may form a plumelike structure that aids in wind dispersal.

hazelnuts are examples of nuts, which resemble achenes but have a stony fruit wall and are derived from a compound ovary. Finally, in the parsley family (*Apiaceae*) and the maples (*Aceraceae*), as well as a number of other, unrelated groups, the fruit is a **schizocarp**, which splits at maturity into two or more one-seeded portions (Figure 20–25a).



20–24 Cypselas The familiar small, indehiscent fruits of dandelions, which are technically known as cypselas (but often loosely called achenes), have a plumelike, modified calyx (the pappus) and are spread by the wind. This photograph shows the fruiting heads of a plant of the genus *Agoseris*, which is closely related to the dandelions.

Fruits and Seeds Have Evolved in Relation to Their Dispersal Agents

Just as flowers have evolved according to the characteristics of the pollinators that visit them regularly, so have fruits evolved in relation to their dispersal agents. In both coevolutionary systems, there have, in general, been many changes in relation to different dispersal agents within individual families and a great deal of convergent evolution toward similar-appearing structures with similar functions. We shall review some of the adaptations of fruits here, in relation to their dispersal agents.

Many Plants Have Wind-Borne Fruits and Seeds

Some plants have light fruits or seeds that are dispersed by the wind (Figures 20–21a, 20–23 through 20–25). The dust-like seeds of all members of the orchid family, for example, are wind-borne. Other fruits have wings, which are sometimes formed from perianth parts, that allow them to be blown from place to place. In the schizocarps of maples, for example, each carpel develops a long wing (Figure 20–25a). The two carpels separate and fall when mature. Many members of the *Asteraceae*—dandelions, for example—develop a plumelike pappus, which aids in keeping the light fruits aloft (Figures 20–24 and 20–25b). In some plants, the seed itself, rather than the fruit, bears the wing or plume. The familiar butter-and-eggs (*Linaria vulgaris*) has a winged seed, and both fireweed (*Chamaerion*) and milkweed (*Asclepias*; Figure 20–21a) have plumed seeds. In willows and poplars (family *Salicaceae*), the seed coat is covered with woolly hairs. In tumbleweeds (*Salsola*), the whole plant (or a portion of it) is blown along by the wind, scattering seeds as it moves.

Other plants shoot their seeds aloft. In touch-me-not (*Impatiens*), the valves of the capsules separate suddenly, throwing seeds for some distance. In the witch hazel (*Hama-*

melis), the endocarp contracts as the fruit dries, discharging the seeds so forcefully that they sometimes travel as far as 15 meters from the plant. Another example of self-dispersal is shown in Figure 20–26. In contrast to these active methods of dispersal, the seeds or fruits of many plants simply drop to the ground and are dispersed more or less passively (or sporadically, such as by rainwater or floods).

Fruits and Seeds Adapted for Floating Are Dispersed by Water The fruits and seeds of many plants, especially those growing in or near water sources, are adapted for floating, either because air is trapped in some part of the fruit or because the fruit contains tissue that includes large air spaces. Some fruits are especially adapted for dispersal by ocean currents. Notable among these is the coconut (Figure 20–20), which is why almost every newly formed Pacific atoll quickly acquires its own coconut tree. Rain, also a common means of fruit and seed dispersal, is particularly important for plants that live on hillsides or mountain slopes.

Fruits and Seeds That Are Fleshy or Have Adaptations for Attachment Are Dispersed by Animals The evolution of sweet and often highly colored, fleshy fruits was clearly involved in the coevolution of animals and flowering plants. The majority of fruits in which much of the pericarp is fleshy—bananas, cherries, raspberries, dogwoods, grapes—are eaten by vertebrates. When such fruits are eaten by birds or mammals, the seeds the fruits contain are spread by being passed unharmed through the digestive tract or, in birds, by being regurgitated at a distance from the place where they were ingested (Figure 20–27). Sometimes, partial digestion aids the germination of seeds by weakening their seed coats.

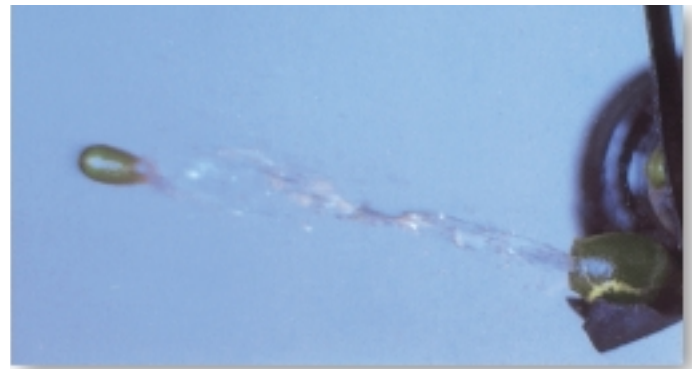
When fleshy fruits ripen, they undergo a series of characteristic changes, mediated by the hormone ethylene, which will be discussed in Chapter 27. Among these changes are a rise in sugar content, a softening of the fruit caused by the breakdown of pectic substances, and often a change in color from inconspicuous, leaflike green to bright red (Figure 20–27a), yellow, blue, or black. The seeds of some plants, especially tropical ones, often have fleshy appendages, or arils, with the bright colors characteristic of fleshy fruits and, like these fruits, are aided in their dispersal by vertebrates.

A number of angiosperms have fruits or seeds that are dispersed by adhering to fur or feathers (Figure 20–28). These fruits and seeds have hooks, barbs, spines, hairs, or sticky coverings that allow them to be transported, often for great distances, attached to the bodies of animals.

Other important agents of seed dispersal in some plants are ants. Such plants have evolved a special adaptation on the exterior of their seeds, called an elaiosome, a fleshy pigmented appendage that contains lipids, protein, starch, sugars, and vitamins. The ants usually carry such seeds back to their nests, where the elaiosomes are consumed by other workers or larvae and the seeds are left intact. The seeds readily germinate in this location, and seedlings often become established, protected from their predators and perhaps benefiting from nutrient enrichment as well. Up to a third of the species in some plant communities, such as the herb understory communities in the deciduous forests of the central and eastern United States, are dispersed by ants in this way. These plants include such familiar species as spring beauty (*Claytonia virginiana*), Dutchman's-breeches (*Dicentra cucullaria*), bloodroot (*Sanguinaria canadensis*), many species of violets (*Viola*; see Figure 12–2), and *Trillium* (see Figure 1–5).



(a)



(b)

20–26 Self-dispersal of seeds Dwarf mistletoe (*Arceuthobium*), a parasitic eudicot that is the most serious cause of loss of forest productivity in the western United States. (a) A plant growing on a pine branch in California. (b) Seed discharge. Very high hydrostatic pressure builds up in the fruit and shoots the seeds as much as 15 meters

laterally. The seeds have an initial velocity of about 100 kilometers per hour. This is one of the ways in which the seeds are spread from tree to tree, although they are also sticky and can be carried from one tree to another over much longer distances by adhering to the feet or feathers of birds.



(a)



(b)

20–27 Fleshy fruits The seeds of fleshy fruits are usually dispersed by vertebrates that eat the fruits and either regurgitate the seeds or pass them as part of their feces. Examples of vertebrate-dispersed fruits are shown here. **(a)** Strawberries (*Fragaria*), an example of both an aggregate fruit and an accessory fruit. The achenes are borne on the surface of a fleshy receptacle, which constitutes most of the fruit. Immature strawberries, like the immature stages of many bird- or mammal-dispersed fruits, are green, but they become red when the seeds are mature and thus ready for dispersal. **(b)** Berries of chaparral honeysuckle, *Lonicera hispidula*. These berries develop from inferior ovaries, and they therefore have fused portions of the outer floral whorls—accessory tissues—incorporated in them. A flower of this species is shown in Figure 20–8c.



(a)



(b)

20–28 Hooks and spines **(a)** The fruits of the African plant *Harpagophytum*, a member of the sesame family (*Pedaliaceae*), are equipped with “grappling hooks,” which catch in the fur on the legs of large mammals. In this way, the fruits are spread from place to place.

(b) Mature inflorescences of cocklebur (*Xanthium*), which attach themselves to passing animals and are dispersed. In this case, the entire inflorescence is the dispersal unit, rather than the fruits alone, as in *Harpagophytum*. Cocklebur is a member of the family *Asteraceae*.

Biochemical Coevolution

Also important in the evolution of angiosperms are the so-called **secondary metabolites**, or **secondary plant products** (pages 27 to 33). Once thought of as waste products, these include an array of chemically unrelated compounds, such as **alkaloids** (including morphine, cocaine, caffeine, and nicotine; Figure 2–22); **terpenoids** (including essential oils, taxol, rubber, cardiac glycosides, and isoprene; Figure 2–23); **phenolics** (including flavonoids, tannins, lignins, catechols, and salicylic acid; Figure 2–28); **quinones** (including coenzyme Q; Figure 6–9); and even **raphides** (needlelike crystals of calcium oxalate; Figure 3–18). The presence of certain of these compounds can characterize whole families, or groups of families, of flowering plants.

In nature, these chemicals appear to play a major role either in restricting the palatability of the plants in which they occur or in causing animals to avoid the plants altogether (Figure 20–29). When a given family of plants is characterized by a distinctive group of secondary plant products, those plants are apt to be eaten only by insects belonging to certain families. The mustard family (Brassicaceae), for example, is characterized by the presence of mustard-oil glycosides, as well as the associated enzymes that break down these glycosides to release the pungent odors associated with cabbage, horseradish, and mustard. Plant-eating insects of most groups ignore plants of the mustard family and will not feed on them even if they are starving. However, certain groups of true bugs and beetles, and the larvae of some groups of moths, feed only on the leaves of plants of the mustard family. The larvae of most of the members of the butterfly subfamily Pierinae (which includes the cabbage butterflies and orange-tips) also feed only on these plants. The same chemicals that act as deterrents to most groups of insect herbivores often act as feeding stimuli for these narrowly restricted feeders. For example, certain moth larvae that feed on cabbage will extrude their mouthparts and go through their characteristic feeding behavior when presented with agar or filter paper containing juices pressed from these plants.

Clearly the ability to manufacture these mustard-oil glycosides and to retain them in their tissues is an important evolutionary step that protects the plants of the mustard family from most herbivores. From the standpoint of herbivores in general, such protected plants represent an unexploited food source for any group of insects that can tolerate or break down the poisons manufactured by the plant. The main evolutionary development of the butterfly group Pierinae probably occurred after its ancestors had acquired the ability to feed on plants of the mustard family by breaking down these toxic molecules.

Herbivorous insects that are narrowly restricted in their feeding habits to groups of plants with certain secondary plant products are often brightly colored. This coloration serves as a signal to their predators that they carry the noxious chemicals in their bodies and hence are unpalatable. For example, the assemblage of insects found feeding on a milkweed plant on a summer day might include bright green chrysomelid beetles, bright red cerambycid beetles and true



20–29 Poison ivy A secondary plant product, 3-pentadecanedieryl catechol, produced by poison ivy (*Toxicodendron radicans*), causes an irritating rash on the skin of many people. The ability to produce this phenolic presumably evolved under the selective pressure exerted by herbivores. Fortunately, the plant is easily identifiable by its characteristic compound leaves with their three leaflets.

bugs, and orange and black monarch butterflies, among others (see Figure 2–25). Milkweeds (Apocynaceae) are richly endowed with alkaloids and cardiac glycosides, heart poisons that have potent effects on vertebrates, the main potential predators of these insects. If a bird ingests a monarch butterfly, severe gastric distress and vomiting will follow, and orange-and-black patterns like that of the monarch will be avoided by the predator in the future. Other insects, such as the viceroy butterfly (which also has an orange-and-black pattern), have evolved similar coloration and markings. Thus, they escape predation by capitalizing on their resemblance to the poisonous monarch. This phenomenon, known as **mimicry**, is ultimately dependent upon the plant's chemical defenses. Various drugs and psychedelic chemicals, such as the active ingredients in marijuana (*Cannabis sativa*) and the opium poppy (*Papaver somniferum*), among others, are also secondary plant products that in nature presumably play a role in discouraging the attacks of herbivores (Figure 20–30).

Still more complex systems are known. When the leaves of potato or tomato plants are wounded, as by the Colorado potato beetle, the concentration of proteinase inhibitors, which interfere with the digestive enzymes in the guts of the beetle, rapidly increases in the wounded tissues. Other plants manufacture molecules that resemble the hormones of insects or other predators and thus interfere with the predators' normal growth and development. One of these natural products that resembles a human hormone is a complex molecule called diosgenin, which is obtained from wild yams. Diosgenin is only two simple chemical steps away from 16-dehydropregnenolone, or 16D, the main active



(a)



(b)



(c)



(d)

20–30 Hallucinogenic and medicinal compounds (a) Mescaline, from the peyote cactus (*Lophophora williamsii*), is used ceremonially by many Native American groups of northern Mexico and the southwestern United States. (b) Tetrahydrocannabinol (THC) is the most important active molecule in marijuana (*Cannabis sativa*). (c) Quinine, a valuable drug formerly used in the treatment and prevention of malaria, is derived from tropical trees and shrubs of the genus *Cinchona*. (d) Cocaine (see

page 28), a drug that has recently been abused to an unparalleled extent, is derived from coca (*Erythroxylum coca*), a cultivated plant of northwestern South America. A Peruvian woman is shown here harvesting the leaves of cultivated coca. The secondary plant products identified in these plants presumably protect them from the depredations of insects, but they are also physiologically active in their vertebrate predators, including humans.

ingredient in many oral contraceptives, and wild yams were once a major source for the manufacture of 16D. Unfortunately, these plants grow slowly, and the supply of wild yams was soon largely exhausted. Species of *Solanum* are being cultivated as alternative sources of molecules suitable for simple conversion to 16D.

As mentioned previously, pollination and fruit-dispersal systems have developed particular coevolutionary patterns in which many of the possible variants have evolved not once but several times within a particular plant family or even

genus. The resulting array of forms gives many groups of angiosperms a wide variety of pollination and fruit-dispersal mechanisms. In the case of biochemical relationships, however, the evolutionary steps appear to have been large and definitive, and whole families of plants can be characterized biochemically and associated with major groups of plant-eating insects. These biochemical relationships appear to have played a key role in the success of the angiosperms, which have a vastly more diverse array of secondary plant products than any other group of organisms.

SUMMARY

The Angiosperms' Closest Relatives Are Thought to Be the Bennettitales and Gnetophytes

The ancestry of the angiosperms, long a subject of debate, has been investigated by phylogenetic analyses. Currently such methods have defined seed plants as one evolutionary line, or clade, and the Bennettitales and gnetophytes as the seed plants most closely related to angiosperms. All three groups possess flowerlike reproductive structures and collectively are referred to as “anthophytes.” Only the angiosperms, however, belong to the phylum Anthophyta.

Several Factors Help Explain the Worldwide Success of Angiosperms

The earliest definite angiosperm remains are from the Early Cretaceous period, about 130 million years ago; they include both flowers and pollen. The flowering plants became dominant worldwide between 90 and 80 million years ago. Possible reasons for their success include various adaptations for drought resistance, including the evolution of the deciduous habit, as well as the evolution of efficient and often specialized mechanisms for pollination and seed dispersal.

A Few Relatively Small Groups of Angiosperms Retain Archaic Features

Some angiosperms have features retained from the early history of the group. These include evolutionary lines such as the New Caledonian shrub *Amborella* and the water lilies. Another such evolutionary line consists of the magnoliids, with about 20 families, including the magnolia and laurel families. All of these plant groups have pollen with a single pore (or furrow), as do the monocots, which constitute about 22 percent of living angiosperms. The eudicots, with pollen that has three apertures (pores or furrows), comprise about three-quarters of the species of angiosperms.

The Four Whorls of Flower Parts Have Evolved in Different Ways

Most angiosperm flowers consist of four whorls. The outermost whorl consists of sepals, which are specialized leaves that protect the flower in bud. In contrast, the petals of most angiosperms have evolved from stamens that have lost their sporangia during the course of evolution. Stamens with anthers that comprise two pairs of pollen sacs are one of the diagnostic features of angiosperms. In the course of evolution, differentiation between the anther and the slender filament seems to have increased. Carpels are somewhat leaflike structures that have been transformed during the course of evolution to enclose the ovules. In most plants, the carpels have become specialized and differentiated into a swollen, basal ovary, a slender style, and a receptive terminal stigma. The loss of individual floral whorls and fusion within and between adjacent whorls have led to the evolution of many specialized floral types, which are often characteristic of particular families.

Angiosperms Are Pollinated by a Variety of Agents

Pollination by insects is basic in the angiosperms, and the first pollinating agents were probably beetles. The closing of the carpel, in an evolutionary sense, may have contributed to protection of the ovules from visiting insects. Pollination interactions with more specialized groups of insects seem to have evolved later in the history of the angiosperms, and wasps, flies, butterflies, and moths have each left their mark on the morphology of certain angiosperm flowers. The bees, however, are the most specialized and constant of flower-visiting insects and have probably had the greatest effect on the evolution of angiosperm flowers. Each group of flower-visiting animals is associated with a particular group of floral characteristics related to the animals' visual and olfactory senses. Some angiosperms have become wind-pollinated, shedding copious quantities of small, nonsticky pollen and having well-developed, often feathery stigmas that are efficient in collecting pollen from the air. Water-pollinated plants have either filamentous pollen grains that float to submerged flowers or various ways of transmitting pollen through or across the surface of the water.

Various Factors Affect the Relationship between Plant and Pollinator

Flowers that are regularly visited and pollinated by animals with high energy requirements, such as hummingbirds, hawkmoths, and bats, must produce large amounts of nectar. These sources of nectar must then be protected and concealed from other potential visitors with lower energy requirements. Such visitors might satiate themselves with nectar from a single flower (or from the flowers of a single plant) and therefore fail to move on to another plant of the same species to effect cross-pollination. Wind pollination is most effective when individual plants grow together in large groups, whereas insects, birds, or bats can carry pollen great distances from plant to plant.

Flower Colors Are Determined Mainly by Carotenoids and Flavonoids

Carotenoids are yellow, oil-soluble pigments that occur in plastids (chloroplasts and chromoplasts) and act as accessory pigments in photosynthesis. Flavonoids are water-soluble ring compounds present in the vacuole. Anthocyanins, which are blue or red pigments that constitute one major class of flavonoids, are especially important in determining the colors of flowers and other plant parts.

Fruits Are Basically Mature Ovaries

Fruits are just as diverse as the flowers from which they are derived, and they can be classified either morphologically, in terms of their structure and development, or functionally, in terms of their methods of dispersal. Fruits are basically mature ovaries, but if additional flower parts are retained in their mature structure, they are said to be accessory fruits. Simple fruits are derived from one carpel or from a group of united carpels, aggregate fruits from the free carpels of one flower, and multiple fruits from the fused carpels of several

or many flowers. Dehiscent fruits split open to release the seeds, and indehiscent fruits do not.

Fruits and Seeds Are Dispersed by Wind, Water, or Animals

Wind-borne fruits or seeds are light and often have wings or tufts of hairs that aid in their dispersal. The fruits of some plants expel their seeds explosively. Some seeds or fruits are borne away by water, in which case they must be buoyant and have water-resistant coats. Others are disseminated by birds or mammals and frequently have fleshy coverings that are tasty or hooks, spines, or other devices that adhere to the coats of mammals or to feathers. Ants disperse the seeds and fruits of many plants; such dispersal units typically have an oily appendage, an elaiosome, which the ants consume.

Secondary Metabolites Are Important in the Evolution of Angiosperms

Biochemical coevolution has been an important aspect of the evolutionary success and diversification of the angiosperms. Certain groups of angiosperms have evolved various secondary products, or secondary metabolites, such as alkaloids, which protect them from most foraging herbivores. However, certain herbivores (normally those with narrow feeding habits) are able to feed on those plants and are regularly

found associated with them. Potential competitors are excluded from the same plants because of their inability to handle the toxins. This pattern indicates that a stepwise pattern of coevolutionary interaction has occurred, and it appears likely that the early angiosperms also may have been protected by their ability to produce some chemicals that functioned as poisons for herbivores.

QUESTIONS

1. What concept is embodied in the term “anthophyte” (not to be confused with Anthophyta)?
2. What unique characteristics of Anthophyta (angiosperms) indicate that the members of this phylum were derived from a single common ancestor?
3. Evolutionarily, petals apparently have been derived from two different sources. What are they?
4. Explain what is meant by coevolution, and provide two examples involving different insects and flowers.
5. Why are wind-pollinated angiosperms best represented in temperate regions and relatively rare in the tropics?
6. Distinguish among simple, aggregate, and multiple fruits, and give an example of each.