cells), biseriate (with two rows of cells), or multiseriate (with several rows of cells)? Some taxa have two or more kinds of hairs mixed together on their leaves or stems; for example, many species have nonglandular, unicellular hairs intermixed with gland-headed, multicellular hairs. The types of hairs, along with their density and distribution on the plant, are often of taxonomic value.

**Domatia and glands** Domatia are "tiny homes" for organisms, usually mites or ants, that occur on the leaves of many angiosperms (Brouwer and Clifford 1990). Arthropod inhabitants of domatia assist the plant by deterring herbivory; in return, the plant provides not only a home but sometimes food as well. Ant domatia usually are pouchlike and are typically found at the base of the leaf blade. Mite domatia are smaller, are usually at vein junctions, and may be bowl-shaped, volcano-like, pocket-shaped, formed by axillary hair tufts, or formed by a revolute margin. Various glandular structures may also occur on leaves. These usually secrete nectar and attract ants, which protect against herbivory.

**FLORAL MORPHOLOGY**

The reproductive structures of angiosperms are called flowers. We will focus on angiosperms here; the specialized reproductive structures of the free-sporing plants, conifers, and cycads are described in Chapter 7. A flower is a highly modified shoot bearing specialized appendages (modified leaves) (Figure 4.16). The modified shoot (or floral axis) is called the **receptacle**, while the floral stalk is referred to as the **pedicel**. Flowers are usually borne in the axil of a more or less modified leaf, or **bract**; smaller, leaflike structures, the **bracteoles**, are often borne along the pedicel.

Flowers have up to three major parts: **perianth** (outer protective and/or colorful structures), **androecium** (pollen-producing structures), and **gynoecium** (ovule-producing structures). Flowers that have all three of these parts are said to be **complete**. If any of the three is lacking, the flower is **incomplete**. If at least the androecium and gynoecium are present, the flower is termed **bisexual** (or **perfect**). If either is lacking, the flower is **unisexual** (or **imperfect**); it may be either **staminate**, if only the androecium is present, or **carpellate**, if only the gynoecium is present. In **monoecious** species both staminate and carpellate flowers are borne on a single individual, while in **dioecious** species the staminate and carpellate flowers are borne on separate individual plants. Various intermediate conditions, of course, exist. **Polygamous** species have both bisexual and unisexual flowers (staminate and/or carpellate) on the same plant. The perianth is always outermost in the flower, followed in nearly all flowers by the androecium, with the gynoecium in the center of the flower.

The perianth parts may be undifferentiated, and the perianth composed merely of **tepals**. Alternatively, the perianth may be differentiated into a **calyx** and **corolla**, in which case it is composed of an outer whorl (or whorls or spirals) of **sepals** (collectively called the calyx) and an inner whorl (or whorls or spirals) of **petals** (collectively called the corolla). The sepals typically protect the inner flower parts in bud, while the petals are usually colorful and assist in attracting pollinators (see also the section on pollination biology below). Corollas have evolved independently in various groups of angiosperms; in some families it is clear that the petals are showy, sterile stamens, while in others the petals are modified sepals. It is

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**Figure 4.16** Parts of a generalized flower. Collective terms are boldfaced.
important to remember that although these perianth terms are useful in practical identification, they need to be used with caution in phylogenetic studies. Homology should not be assumed merely on the basis of a general similarity of form and function.

The androecium comprises all the stamens of the flower. Stamens are usually differentiated into an anther and a filament, although some are petal-like and are not differentiated into these two parts. Anthers usually contain four pollen sacs (or microsporangia), and these are often confluent in two pairs. The pollen sacs are joined to each other and to the filament by a connective, which is occasionally expanded, forming various appendages or a conspicuous sterile tissue separating the pollen sacs. Meiosis occurs within the pollen sacs, leading to the production of pollen grains (male gametophytes, or microgametophytes). The androecium is therefore often referred to as the “male part” of the flower. Of course, flowers, as part of the diploid plant (or sporophyte), cannot properly be said to be male (or female) because the sporophyte is involved only in spore production (associated with meiosis). Only the haploid plant (or gametophyte) is involved in gamete production (see Figure 4.17). Anthers open by various mechanisms, and pollen usually is released through longitudinal slits, although transverse slits, pores, and valves also occur. Anthers that open toward the center of the flower are said to be introrse, while those that shed pollen toward the periphery are extrorse.

Figure 4.17  Angiosperm life cycle. See also Figure 4.40. (Modified from Singer 1997.)
The gynoecium comprises all the carpels of the flower. The carpel is the site of pollination and fertilization. Carpels are typically composed of a stigma (which serves to collect and facilitate the germination of the pollen carried to it by wind, water, or various animals), a style (a usually slender region specialized for pollen tube growth), and an ovary (an enlarged basal portion that surrounds and protects the ovules). The stigmatic surface may be variably papillate, and may be wet or dry. Each ovule contains the megagametophyte (female gametophyte, or embryo sac), which produces an egg and is usually provided with two protective layers called integuments. The ovule is attached to the ovary wall by a stalk called the funiculus. The gynoecium is often called the “female part” of the flower, although, as noted above, this is technically incorrect. As the ovule develops into a seed, the surrounding ovary develops into a fruit.

Various floral parts may be modified for the production of nectar (or other pollinator attractants, such as oils or fragrances). Nectaries (nectar-producing glands) often form projections, lobes, or disklike structures. Nectaries are often produced near the base of the androecium and gynoecium, or in nectar spurs formed by floral parts such as petals. Some flowers have an “extra” series of floral parts, often showy, called a corona. Coronal structures may be outgrowths of the perianth parts, stamens, or receptacle, and are extremely diverse in form and function. (For a detailed discussion of the diversity of these as well as other floral structures, see Weberling 1989.)

The variation in floral features can be efficiently summarized by the use of floral formulas and diagrams (see Box 4A).

**Floral symmetry** The parts of some flowers are arranged so that two or more planes bisecting the flower through the center will produce symmetrical halves. Such flowers have radial symmetry, and are also called actinomorphic or regular (Figure 4.18). The parts of other flowers are arranged so that they can be divided into symmetrical halves on only one plane. These flowers have bilateral symmetry, and are also called zygomorphic or irregular. A few flowers have no plane of symmetry (and are asymmetrical). In determining the symmetry of a flower, the position of the more conspicuous structures, that is, the perianth and/or androecium, is considered.

**Fusion of floral parts** Floral parts may be fused together in various ways. Fusion of like parts (e.g., petals united to petals) is called connation. When like parts are not fused, they are said to be distinct. Fusion of unlike parts (e.g., stamens united to petals) is called adnation; the contrasting condition is called free (e.g., stamens free from petals). Fused structures may be united from the moment of origin onward, or they may grow together later in development. Various other specialized terms are used for various types of connation and adnation; some of these terms are listed below:

- apocarpous: carpels distinct
- apopetalous: petals distinct
- aposepalous: sepals distinct
- apotepalous: tepals distinct
- diadelphous: stamens connate by their filaments in two groups
- epipetalous: stamens adnate to corolla
- monadelphous: stamens connate by their filaments in a single group
- sympetalous: petals connate
- synandrous: stamens connate
- syncarpous: carpels connate
- synneseous: stamens connate by their anthers
- synsepalous: sepals connate
- syntepalous: tepals connate

**Carpel versus pistil** The term pistil is sometimes used for the structure(s) in the center of the flower that contain(s) the ovules. Does this term differ from carpel, the term introduced above (and used throughout this book)? Carpels are the basic units of the gynoecium; they may, of course, be distinct or connate. If they are distinct, then the term pistil is equivalent in meaning to the term carpel. If, however, the carpels are connate, then the terms are not equivalent because each carpel constitutes only one unit within a pistil, which is then considered to be compound (Figure 4.19).

**Number of parts** Flowers differ in numbers of sepals, petals, stamens, and carpels. The number of parts is usually easily determined by counting, but extreme connation, especially of the carpels, may cause difficulties. Fused carpels often can be counted by using the number of styles, stigmas, or stigmatic lobes (Figure 4.20). Placenta (see below) may also be useful in determining carpel numbers.
Most flowers are based on a particular numerical plan; that is, on patterns of three, four, five, or various multiples of those numbers. For example, a flower may have four sepals, four petals, eight stamens, and four carpels. Such a flower would be described as 4-merous; the ending -merous, along with a numerical prefix, is used to indicate a flower’s numerical plan.

**Insertion** Attachment of floral parts is called insertion. Floral parts may be attached to the receptacle (or floral axis) in various ways. Three major insertion types are recognized: hypogynous, perigynous, and epigynous. The position of the ovary in relation to the attachment of floral parts also varies from superior to inferior (Figure 4.21). Flowers in which the perianth and androecium are inserted below the gynoecium are called hypogynous; the ovary of such flowers is said to be superior. Flowers in which a cuplike or tubular structure surrounds the gynoecium are called perigynous. In such flowers the perianth and androecium are attached to the rim of this structure, which is called the hypanthium (or floral cup or floral tube). The ovary of such flowers is superior. Hypanths have evolved from various structures, such as, from the fused basal portion of the perianth parts and stamens or from the receptacle. Flowers in which the perianth and stamens appear to be attached to the upper part of the ovary due to fusion of the hypanthium (or bases of floral and androecial parts) to the ovary are called epigynous. The ovary of such flowers is said to be inferior. In some epigynous flowers the hypanthium may extend beyond the top of the ovary, forming a cup or tube around the style. If the hypanthium is fused only to the lower portion of the ovary, the latter is considered half-inferior. Insertion type and ovary position are best determined by making a longitudinal section of the flower.

Floral parts making up adjacent whorls normally alternate with each other, so that one would expect to find a petal, for example, inserted at the point between two adjacent sepals. An understanding of this common pattern can assist in interpreting the number of floral parts, especially when they are obscured by connation or adnation.

The gynoecium, or androecium and gynoecium, occasionally are borne on a stalk (the gynophore or androgynophore, respectively).

**Placentation** Ovules are arranged in various patterns within an ovary, allowing the recognition of various placentation types. Ovaries may contain from one to several chambers, or locules. The wall separating adjacent locules is called a septum (plural septa). The placentae (plural placentae) is the part of the ovary
to which the ovules are attached. Major placentation types are illustrated in Figure 4.22. The number of ovules has no necessary correlation to the number of carpels, number of placenta, or placentation type.

Placentation type can be quite useful in determining the number of fused carpels in a flower. If the placentation is axile, the number of locules usually is indicative of the number of carpels. In parietal placentation, the number of placenta usually equals the carpel number.

*Miscellaneous floral terms* A few other floral terms commonly encountered in plant descriptions are listed below.

- **basified**: a structure, such as an anther, that is attached at its base
- **carpellode**: a sterile carpel
- **centrifugal**: developing first at the center and then gradually toward the outside
- **centripetal**: developing first at the outside and then gradually toward the center
- **didynamous**: having two long and two short stamens
- **exserted**: sticking out, as in stamens extending beyond the corolla
- **included**: hidden within, as in stamens not protruding from the corolla
- **pistillode**: a sterile pistil
- **staminode**: a sterile stamen
- **tetradynamous**: having four long and two short stamens
- **versatile**: a structure, such as an anther, that is attached at its midpoint

**Pollination Biology**

Plants are stationary, and thus depend upon external forces to bring their gametes together. The sperm of ferns swim through water to reach the egg, whereas the sperm of seed plants are packaged in pollen grains for transport, a process referred to as pollination. Conifer pollination occurs largely via wind. Most flowering plants are animal-pollinated, although wind pollination predominates in some large and ecologically dominant families and occurs sporadically in many others. Water pollination is rare.

Pollination has interested people since at least 1500 B.C., when Babylonians discovered that date palm (*Phoenix dactylifera*, Arecaceae) flowers produce a yellow powder (pollen). By careful observation, they found that this powder must be applied to the flowers of fruit-bearing trees in order for the trees to produce fruit. This important discovery made it possible for them to increase the production of dates simply by spreading the yellow powder on date flowers by hand. Pollination remains essential to human welfare today. The great majority of human nutrition comes from cereal grains (Poaceae) and beans (Fabaceae), all of which are the result of pollination. Other edible fruits, such as apples, coconuts, figs, strawberries, and tomatoes, also would not exist without pollination.

Flowers are adaptations for pollination. One can often infer the pollen vector from the morphology of a flower, as Darwin did when he predicted that there had to be a moth in Madagascar with a tongue long enough to reach the nectary in the 30-cm long spur of the orchid *Angraecum sesquipedale* (see Chapter 6). The linkage between floral color, scent, time of flowering, structure, and rewards on the one hand and animal pollinator sensory capacity, behavior, and diet on the other is the basis of floral pollination syndromes. This linkage may be strong enough that a plant and a pollinator adapt to each other. We will examine an example of such coevolution involving the plant genus *Yucca* and its pollinator, the yucca moth.

**POLLINATION SYNDROMES**

**Wind and water pollination** Wind-pollinated flowers are characterized by the production of a large amount of pollen that is readily transported by wind currents and by efficient means of trapping airborne pollen. They are small and lack much of a corolla (see, for example, illustrations of Betulaceae, Cynareae, Fagaceae, Juglandaceae, and Poaceae in Chapter 8). If you walk in a pine forest during pollen shed and pass by a pond, its surface may be covered by a yellow film of pine pollen. The pollen grains of wind-pollinated plants are often small, light, and have a smooth surface, but some species have larger grains with air spaces, which lower...