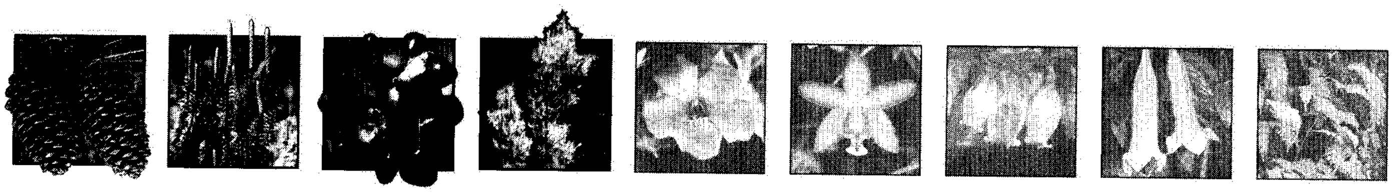
Judd et al. *Plant Systematics: a Phylogenetic Approach (2nd ed.)*
Pp. 55-69; 75-81

4 Taxonomic Evidence: Structural and Biochemical Characters



Taxonomic evidence consists of the characters used in the phylogenetic analyses upon which plant classifications are based, and it includes characters used in describing patterns of variation at or below the species level (see Chapter 6). Taxonomic evidence can be gathered from a wide variety of sources, from all parts of a plant during all stages of its development. In this chapter we summarize the use of characters from morphology, anatomy, embryology, chromosomes, palynology, secondary plant compounds, and proteins. Nucleic acids (DNA and RNA) provide an increasingly important source of taxonomic characters; their use in plant taxonomy and the rapidly developing field of molecular systematics is discussed in detail in Chapter 5.

The practical discussion of plant characters in this chapter and the next provides a useful counterpart to the more theoretical discussion of characters in Chapter 2.

Morphology

Morphological characters are features of external form or appearance. They currently provide the characters used for practical plant identification and some of those used for hypothesizing phylogenetic relationships. These features have been used for a longer time than anatomical or molecular evidence, and they were the only source of taxonomic evidence in the beginnings of plant systematics. Morphological characters are easily observed and find practical use in keys and descriptions; the characters used in phylogeny reconstruction may not be so easily observed. Characters of both sorts are found in all parts of the plant, both vegetative and reproductive.

The vegetative parts of angiosperms are **roots**, **stems**, and **leaves**, and the reproductive parts are **flowers**, **fruits**, and **seeds**. The terms used in tracheophytes (vascular plants) to describe variation in these parts are outlined in the discussion that follows, although the reproductive terms strongly emphasize the angiosperms because they are the dominant group of vascular plants. (Specialized vegetative and especially reproductive terms relating to other groups of vascular plants are covered in Chapter 8.)

Many, if not all, of the terms outlined here should be considered merely convenient points along a continuum of variation in form. Although they are useful in communication, intermediate conditions will be encountered.

DURATION AND HABIT

Duration is the life span of an individual plant. An **annual** plant lives for a single growing season. A **biennial** plant lives for two seasons, growing vegetatively during the first and flowering in the second. A **perennial** plant lives for three or more years and usually flowers and fruits repeatedly. Perennials may be herbaceous (lacking woody tissue), with only the underground portions living for several years, or woody, with a persistent aerial stem.

The general appearance, or **habit**, of plants varies greatly. Woody tissue is present in **trees** and **shrubs** but is lacking in **herbs**. Trees produce one main **trunk** (or **bole**); shrubs are usually shorter and produce several trunks. Climbing plants may be woody (**lianas**), or herbaceous (**vines**). **Suffrutescent** plants are intermediate between woody and herbaceous.

The characteristic shape of a tree or shrub often relates to its pattern of growth or architecture, which is often of systematic value. Stems form the major plant axes and may be erect (**orthotropic**) or horizontal (**plagiotropic**). **Monopodial shoots** grow through the action of a single **apical meristem**—a single region of dividing, elongating, and differentiating cells at the tip of the shoot. In other plants, axillary branches take over the role of the main axis and provide for continuing growth, while the main axis slows growth or dies; a series of such axillary branches constitutes a **sympodial shoot**.

Stems are provided with **buds**, which are small embryonic shoots, often protected by modified leaves (bud scales) or hairs. Buds may show a period of dormancy and, when they eventually grow out, may leave scars at the base of the new shoot. Such shoots are called **proleptic**. On the other hand, buds may develop and elongate at the same time as the shoot on which they are borne, in which case the new shoot usually lacks basal scars and has an elongated first internode. These shoots are called **sylleptic**.

Proleptic shoots are characteristic of temperate species, while sylleptic shoots are common in tropical plants. Some taxa, such as many Lauraceae, have both sylleptic and proleptic shoots. All shoots on a plant may be the same, or there may be two or more kinds of shoots. Thus *Ginkgo* and *Cercidiphyllum* both have some shoots with elongated internodes (**long shoots**), and others that produce only a few leaves and scales each year, all with only very short internodes (**short shoots**). These and other criteria are combined in various ways to produce an array of distinctive architectural growth patterns in trees and shrubs (see Hallé et al. 1978). Three examples are shown in Figure 4.1.

Axillary branches are initiated externally, in tissues immediately under the epidermis. Xylem and phloem are often arranged in a ring surrounding the **pith**, a central region with more or less isodiametric cells.

ROOTS

Roots usually branch irregularly. Lateral roots are initiated internally, in the endodermis and pericycle (the cell layers surrounding the conducting tissues) and erupt

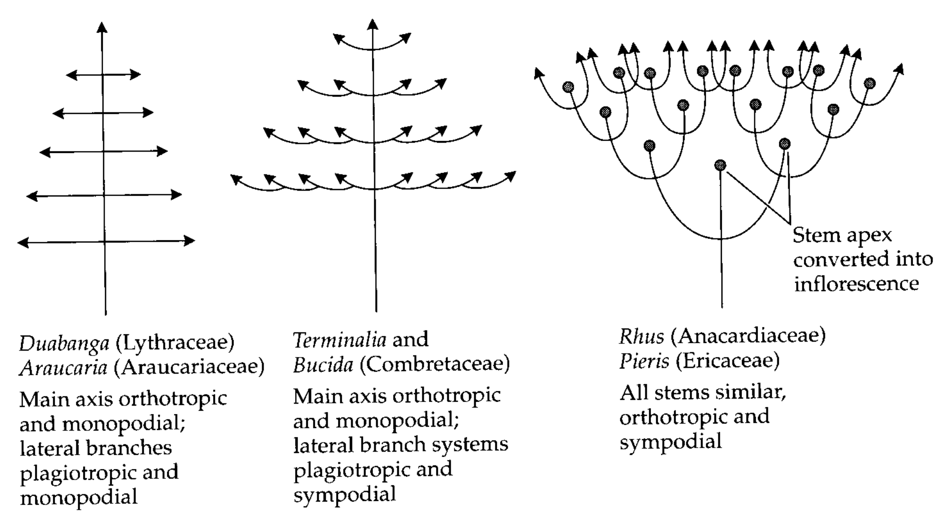


Figure 4.1 Three architectural patterns of plant growth; branching is rythmic in all three.

through the cortex, although lycophyte roots branch by a forking of the apical meristem. The xylem and phloem are situated in the central portion of the root, usually resulting in a lack of pith. Roots also lack the nodes and internodes that characterize stems (see the next section), and they are usually found underground.

The primary functions of roots are to hold the plant in place, to absorb water and minerals, and to store water and carbohydrates. Some roots are specialized for other functions, such as photosynthesis (as in some reduced epiphytic Orchidaceae), penetration of the tissues of a host species (as in parasitic species such as mistletoes, Viscaceae), constriction of the trunks of supporting trees (as in strangler figs, Moraceae), or aboveground support for the trunk or branches (as in banyan figs, Moraceae, and some mangroves, Rhizophoraceae).

Some plants, such as epiphytic aroids (Araceae), have dimorphic roots, with some functioning in water and mineral uptake and others providing attachment. Most roots grow downward, but exceptions occur, as in **pneumatophores**, which are specialized roots involved in gas exchange in some mangrove or swamp species.

Roots are quite uniform in appearance, and a plant usually cannot be identified without its aboveground parts. Roots are useful, however, in determining whether a plant is an annual or a perennial, and variation in the root system is sometimes taxonomically significant. Here are a few important terms relating to roots:

adventitious developing from any plant part other than the embryonic root (radicle) or another root
aerial growing above ground or water
fibrous with all portions of the root system being of more or less equal thickness, often well branched, the primary root (taproot) absent or not obvious
fleshy thick with water or carbohydrate storage tissue
haustorial specialized for penetrating other plants and absorbing water and nutrients from them (as in parasites)
taproot the major root, usually enlarged and growing downward

STEMS

Stems—the axes of plants—consist of **nodes** (where leaves and axillary buds are produced) separated by **internodes** (Figure 4.2). They are frequently useful in identification and provide numerous systematically important characters.

Stems are usually elongated and function in exposing leaves to sunlight, flowers to pollinating agents, and fruits to dispersal agents. Some, however, are the primary photosynthetic organ of the plant (as in asparagus, Asparagaceae, and many cacti, Cactaceae), store water or carbohydrates (as in many cacti and other succulents), climb (as in hooked or twining stems of vines and lianas), or protect the plant (as in plants with thorns).

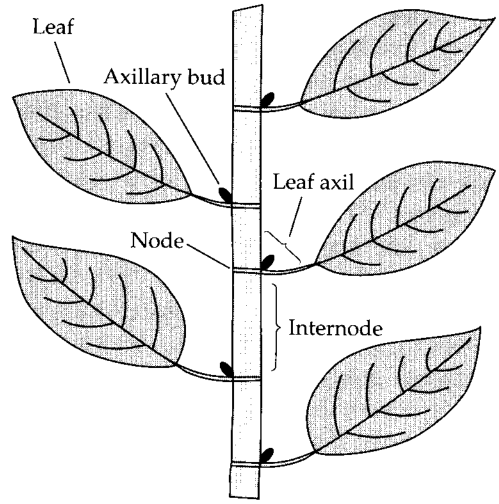


Figure 4.2 Generalized angiosperm stem showing nodes and internodes, leaves, leaf axils, and axillary buds.

Some important stem-related vocabulary is listed here.

acaulescent having an inconspicuous stem
bulb a short, erect, underground stem surrounded by thick, fleshy leaves or leaf bases
caulescent having a distinct stem
corm a short, erect, underground, more or less fleshy stem covered with thin, dry leaves or leaf bases
herbaceous not woody; dying down at the end of the growing season
internode the part of the stem between two adjacent nodes
lenticel a wartlike protuberance on the stem surface involved in gas exchange
long shoot a stem with long internodes; this term is applied only in plants in which internode length is clearly bimodal and both long and short shoots are present
node region of the stem where the leaf and bud are borne
pith soft tissue in the center of the stem, usually consisting of more or less isodiametric cells
rhizome a horizontal stem, more or less underground, bearing scale-like leaves; often called a stolon (or runner) if above ground and having an elongated internode
scape an erect, leafless stem bearing an inflorescence or flower at its apex; usually composed of a single elongated internode
scar the remains of a point of attachment, as in leaf scar, stipule scar, bud-scale scar
short shoot a stem with short internodes, other shoots having distinctly longer internodes; see long shoot
thorn a reduced, sharp-pointed stem [In contrast, a reduced, sharp-pointed leaf or stipule, or sharp-pointed marginal tooth is called a spine, and a sharp-pointed

hair (involving epidermal tissue) or emergence (involving both epidermal and subepidermal tissues) is called a prickle.]

tuber a swollen, fleshy portion of a rhizome involved in water or carbohydrate storage

twining spiraling around a support in order to climb

woody hard in texture, containing secondary xylem, and persisting for more than one growing season

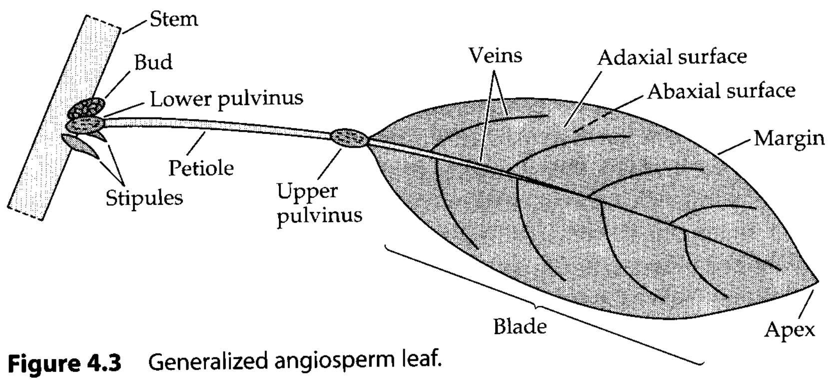


Figure 4.3 Generalized angiosperm leaf.

BUDS

Buds are short embryonic stems. They may be protected by **bud scales** (modified leaves that are sometimes represented only by stipules), a dense covering of hairs, and/or a sticky secretion. In angiosperms buds are found at the nodes, in the **leaf axil** (the angle formed by the stem and the petiole of the leaf; see Figure 4.2), or at the end of the stem. They are especially useful for identifying twigs in winter condition. Some common terms pertaining to buds are listed here.

accessory bud an extra bud (or buds) produced on either side of, or above or below, the main axillary bud

axillary bud a bud located in the leaf axil

flower bud a bud containing embryonic flowers

leaf bud a bud containing embryonic leaves

mixed bud a bud containing both embryonic flowers and leaves

naked not covered by bud scales

pseudoterminal bud an axillary bud that takes over the function of a terminal bud in sympodial shoots

superposed bud a bud located above or below the axillary bud

terminal bud a bud at the apex of a stem (monopodial shoot)

LEAVES

Leaves are the major photosynthetic parts of most plants. They are borne at the nodes of a stem, usually below a bud (see Figures 4.2 and 4.3). In contrast to stems, leaves usually do not continue to grow year after year. They are usually flat, and have one surface facing toward the stem axis (the **adaxial**, or upper, surface) and another surface facing away from the stem axis (the **abaxial**, or lower, surface). Most leaves are **bifacial**, having definite adaxial and abaxial surfaces, but sometimes they are **unifacial**, lacking such differentiation.

Leaves are homologous structures among the angiosperms, but not among vascular plants as a whole (see Chapters 7, 8 and 9). In addition to their obvious function in photosynthesis, leaves may be modified for protection, forming sharp-pointed **spines**; for water storage, as in many succulents; for climbing, as in vines or lianas with tendril leaves; for capturing insects, as in carnivorous plants; or for providing homes for ants or mites (domatia, described later).

The major parts of a leaf are shown in Figure 4.3. The base of the **petiole** may have a narrow to broad point of attachment and may obscure the axillary bud. In monocots the leaf is almost always broadly sheathing at the base, with the edges either fused or overlapping. In taxa such as grasses (Poaceae) and gingers (Zingiberaceae) there is an adaxial flap or **ligule** at the junction of the sheath and blade. A leaf that lacks a petiole is said to be **sessile**.

Pulvini (singular **pulvinus**), somewhat swollen and morphologically distinct parts of the petiole, are often present and involved in leaf movement. These may be at the leaf base; at the apex of the petiole, as in prayer plants (Marantaceae); in the middle of the petiole, as in a few Araceae; or on the petioles of leaflets (of compound leaves, as described in the section on "Leaf Structure").

Stipules are usually paired appendages located on either side of (or on) the petiole base. Stipules are some-

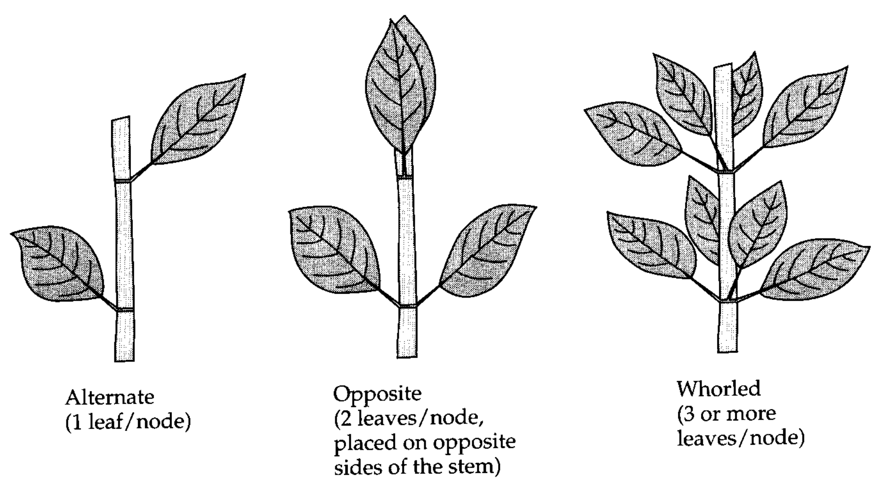


Figure 4.4 Three major patterns of leaf arrangement.

times single, in which case they are borne between the petiole and stem. They may be leaflike, scale-like, tendril-like, spinelike, glandular, very reduced, or completely lacking. They have various functions, but most often they help in protecting young leaves. Stipules are not always homologous.

Leaf arrangement Leaves may be arranged in one of three major patterns (Figure 4.4). **Alternate** leaves are borne singly and are usually arranged in a spiral pattern along the stem. Various kinds of spirals occur; they can be evaluated by determining the angle around the stem between the points of insertion of any two successive leaves or by following the spiral around the stem from any older, lower leaf to the first younger leaf directly in line above it. Alternate leaves are sometimes placed along just two sides of the stem (2-ranked, or distichous), or only three sides of the stem (3-ranked, or tristichous). (Two-ranked leaves that are flattened in the same plane with both surfaces identical, as in irises (Iridaceae), are called **equitant**.)

In contrast, **opposite** leaves are borne in pairs, the members of which are positioned on opposing sides of the stem. Opposite leaves may be spiraled, as in red mangroves (*Rhizophora*, Rhizoporaceae); 2-ranked, as in many Zygophyllaceae; or **decussate** (the leaves of adjacent nodes rotated 90°). The decussate arrangement is the most common condition among vascular plant species.

Finally, when three or more leaves are positioned at a node, they are considered to be **whorled**.

Leaf structure A leaf with a single blade is termed **simple**; a leaf with two or more blades, or **leaflets**, is said to be **compound**. The distinction between simple and compound leaves can be made by locating an axillary bud: An axillary bud is subtended by the entire leaf and never by individual leaflets. Leaflets may be arranged in various ways, as shown in Figure 4.5.

Leaf duration Leaves may function from a few days to many years, but most leaves function for only one or two growing seasons. **Deciduous** leaves fall (are abscised) at the end of the growing season; **evergreen** plants are leafy throughout the year. Some leaves, such as those of many members of Fagaceae, are **marcescent**; that is, they wither but do not fall off during the winter or dry season.

Venation types If there is one most prominent vein in a leaf, it is called the midvein or primary vein; branches from this vein are called secondary veins. Tertiary veins usually link the secondaries, forming a ladderlike (**percurrent** or **scalariform**) or netlike (**reticulate**) pattern (Figure 4.6).

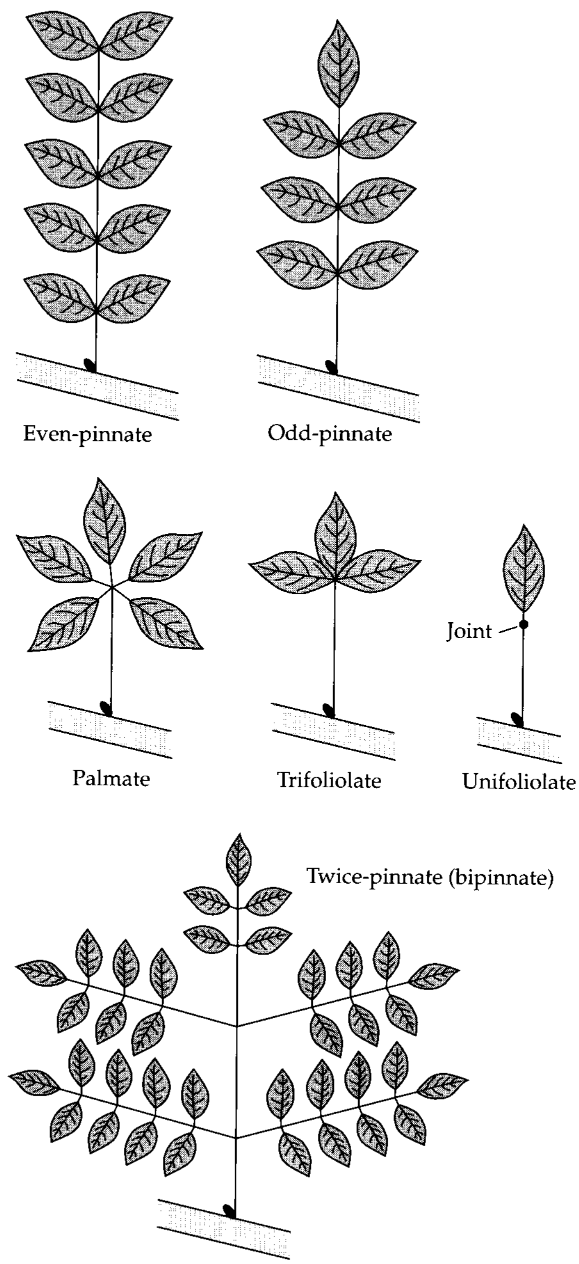


Figure 4.5 Arrangements of leaflets in compound leaves.

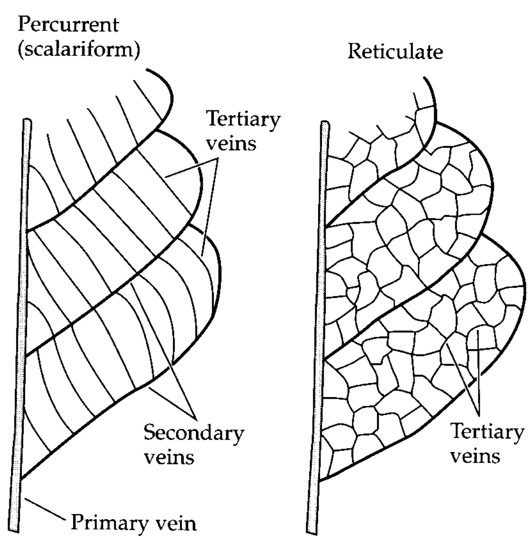


Figure 4.6 Two patterns of tertiary veins.

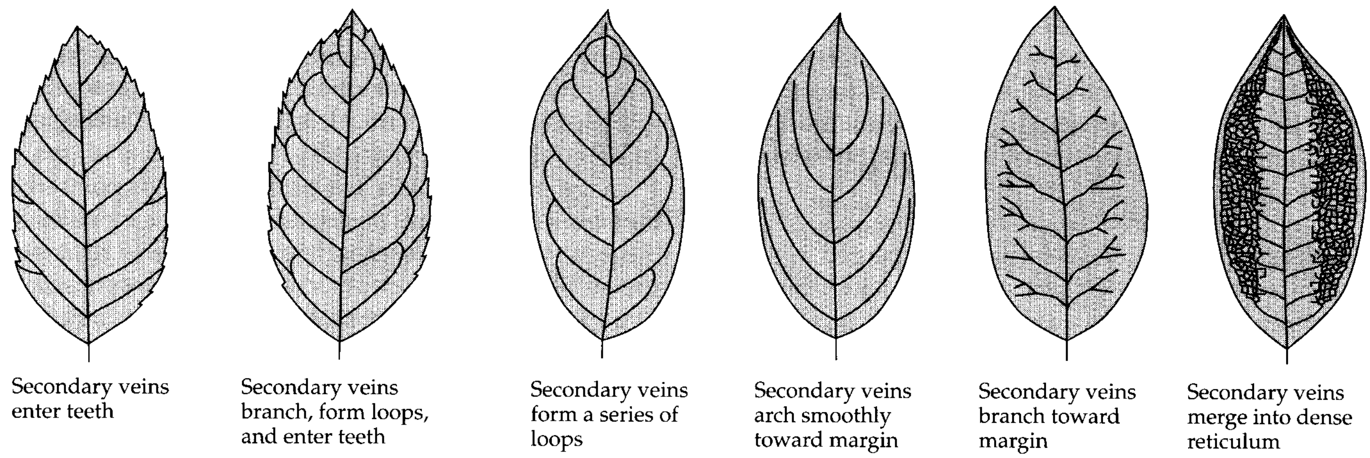


Figure 4.7 Some kinds of pinnate venation. (After Hickey 1973.)

There are three major patterns of organization of the major veins. The leaf may have a single primary vein with the secondary veins arising along its length like the teeth of a comb; this pattern is termed **pinnate**. Or the leaf may have several major veins radiating from the base (or near the base) of the blade, like fingers from a palm; this pattern is called **palmate**. Many different kinds of pinnate (Figure 4.7) and palmate (Figure 4.8A) venation have been characterized (they are discussed in more detail in Hickey 1973 and Dilcher 1974). Finally, the leaf may have many parallel veins, a pattern termed **parallel** venation (Figure 4.8B).

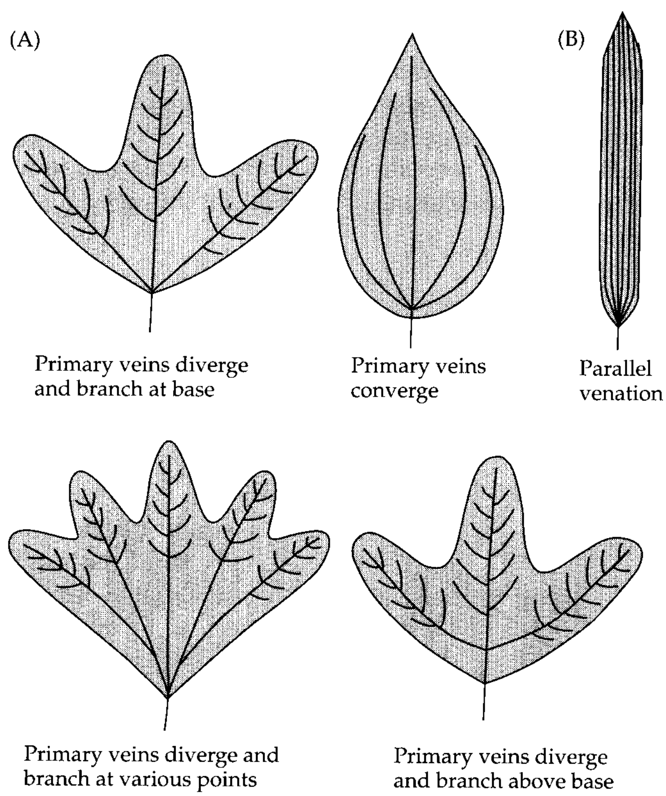


Figure 4.8 (A) Four kinds of palmate venation. (B) Parallel venation. (After Hickey 1973.)

Leaf shapes A leaf may be considered to have one of four major shapes (**ovate**, **obovate**, **elliptic**, **oblong**) depending on where the blade is the widest (Figure 4.9) (Hickey 1973). The meanings of these shape terms may be adjusted by the use of modifiers such as *broadly* or *narrowly*. If the petiole is attached away from the leaf margin, such that the leaf and its stalk form an "umbrella," the leaf is termed **peltate**, and such leaves may be any of a number of different shapes. A **linear** leaf, on the other hand, is very long and narrow. Various other specialized shape terms are sometimes employed, but their use is avoided as much as possible here. The blade of a leaf may be symmetrical or asymmetrical when viewed from above.

Very different leaf shapes may occur on the same plant, a condition known as **heterophylly**. Juvenile leaves may be quite different from adult leaves, but sometimes even an adult plant will bear several different kinds of leaves (as in *Sassafras*, Lauraceae).

Leaf apex and base Various terms relating to the shape of the leaf apex are illustrated in Figure 4.10. Terms relating to the shape of the leaf base are illustrated in Figure 4.11.

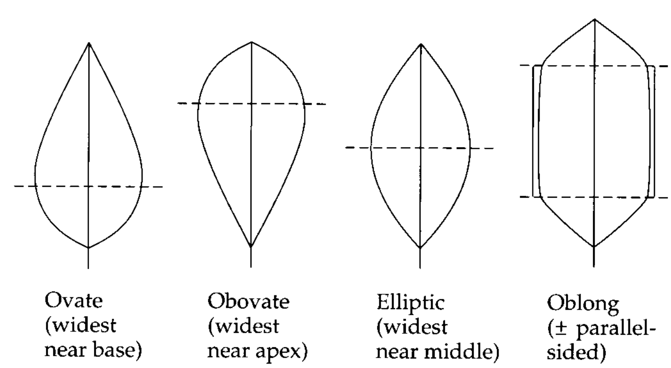


Figure 4.9 Leaf shapes.

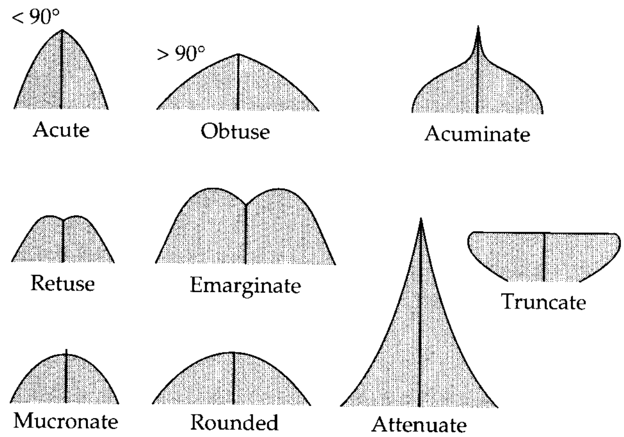


Figure 4.10 Leaf apex shapes.

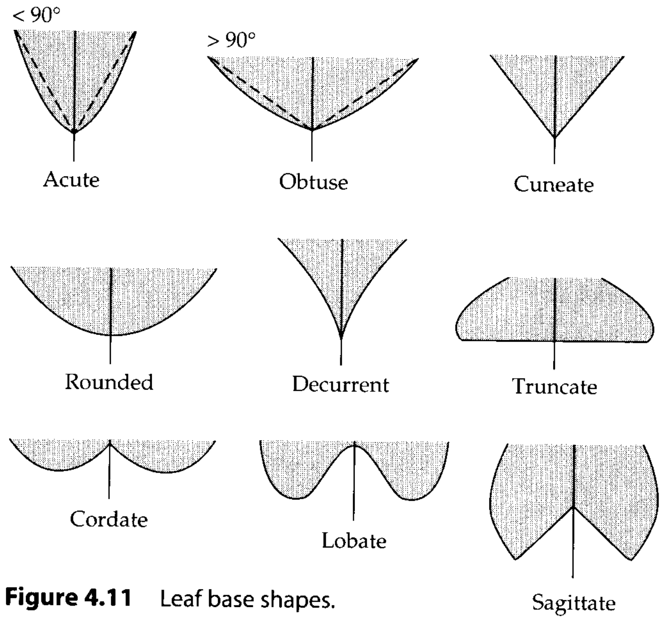


Figure 4.11 Leaf base shapes.

Leaf margin The leaf blade may have **lobed** or **unlobed** margins. These and other margin types are illustrated in Figure 4.12.

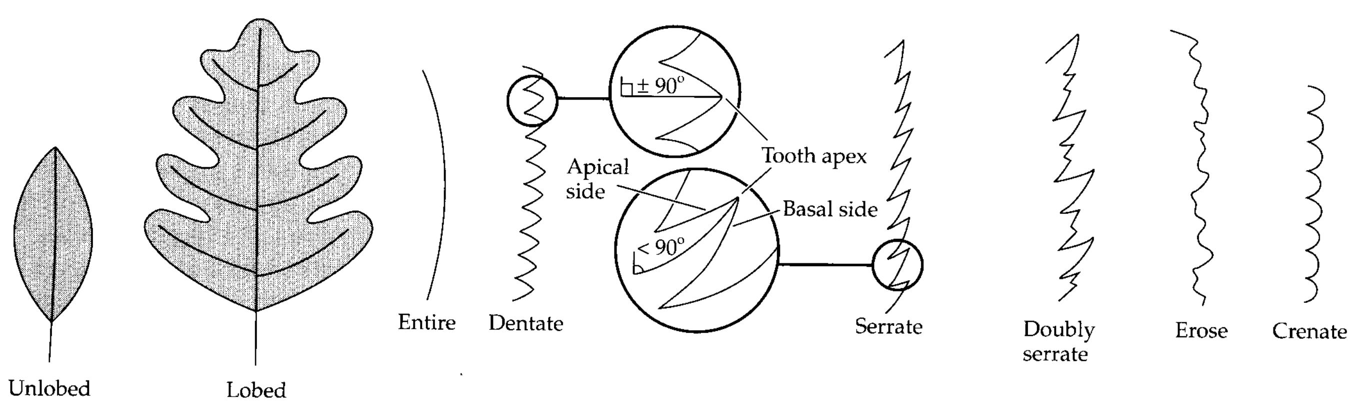
Various kinds of teeth may be defined according to anatomical features such as the pattern of the vein or veins entering the tooth, the shape of the tooth, and characters of the tooth apex such as glandularity. The more common tooth types are illustrated in Figure 4.13; others are defined where first encountered in Chapter 9 (see also Hickey and Wolfe 1975).

Leaf texture The leaf blade may be very thin (**membranous**), papery in texture (**chartaceous**), or very thick (**coriaceous**).

Ptyxis and vernation **Ptyxis** is the way in which an individual leaf is folded in the bud. **Vernation** is the way in which leaves are folded in the bud in relation to one another. Leaves that overlap in the bud are termed **imbricate**, while those with margins merely touching are called **valvate**. These are vernation terms; a few others are defined in Chapter 9 (in the discussion of particular families). A few ptyxis terms are illustrated in Figure 4.14 (see also Cullen 1978).

Indumentum An **indumentum** (plural **indumenta**), or covering of hairs (trichomes), on the surface of an angiosperm gives that surface a particular texture. Most indumentum terms are ambiguous, and we will use only three here: **glabrous** (lacking hairs), **pubescent** (with various hairs), and **glaucous** (with a waxy covering, and thus often blue or white in appearance). A few terms describing the indumentum are listed here; we will not use them in this text, but you may encounter them, as well as many others, in botanical keys and descriptions:

arachnoid having a cobwebby appearance
canescent gray, with dense short hairs
hirsute having long, often stiff, hairs



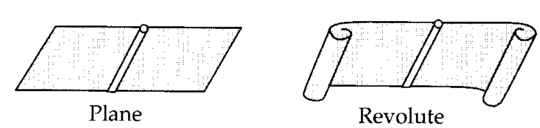


Figure 4.12 Leaf margins.

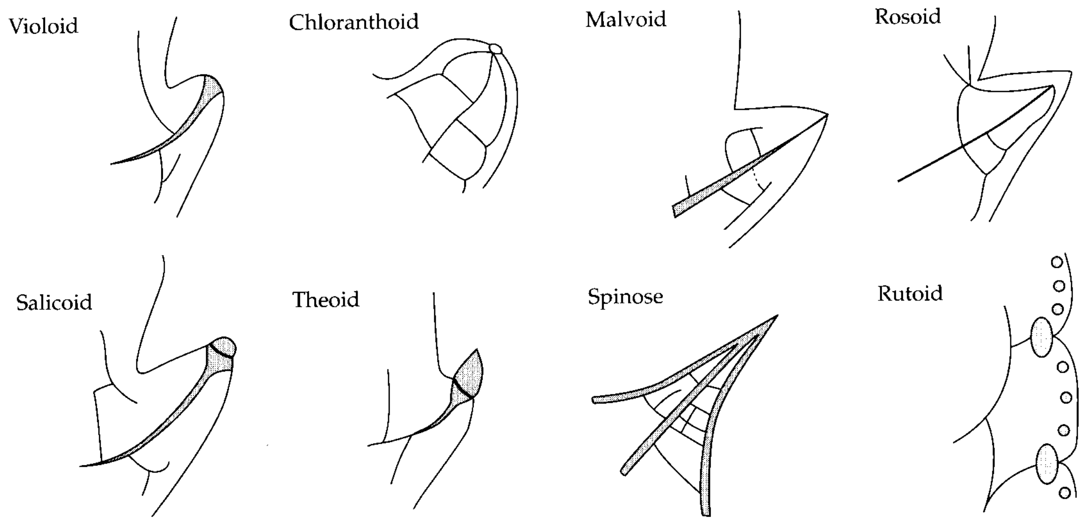


Figure 4.13 Some major tooth types.

hispid having stiff or rough hairs; bristly
lanate woolly, with long intertwined, somewhat matted hairs
pilose having scattered, long, slender, soft hairs
puberulent having minute, short hairs
scabrous rough
sericeous silky, with usually long, thin, appressed hairs
strigose having stiff hairs, all pointing in one direction
tomentose having densely matted soft hairs
velutinous velvety
villous covered with long, fine, soft hairs

We strongly recommend that the kinds of hairs occurring on a plant, along with their distribution and density, be carefully observed under a dissecting (or compound) microscope. Characters derived from such observations usually will be more useful (and consistently applicable) than the indumentum terms listed here.

Hairs may be **unicellular** or **multicellular**, **nonglandular** or **glandular**, and borne **singly** or in **tufts**, with surrounding cells of the epidermis modified or not. The shape of the individual hairs can be described in detail: Are they **branched** or **simple**? How are they branched; that is, are they **dendritic**, **stellate**, or **T-shaped**? Do they have a **flattened** or **globose** head, and is the stalk **uniseriate** (with one row of cells), **biseriate** (with two rows of cells), or **multiseriate** (with several rows of cells)? These terms are illustrated in Figure 4.15.

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** (singular **domatium**)—literally, "tiny homes"—may contain organisms, usually mites or ants. Domatia occur on the leaves of many angiosperms (Pemberton and Turner 1989; 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 and are usually at vein junctions. They may be bowl-, volcano-, or pocket-shaped, formed by axillary hair tufts or by a revolute margin. Various glandular structures may also occur on leaves. These structures usually secrete nectar and attract ants, which protect against herbivory (Bentley 1977).

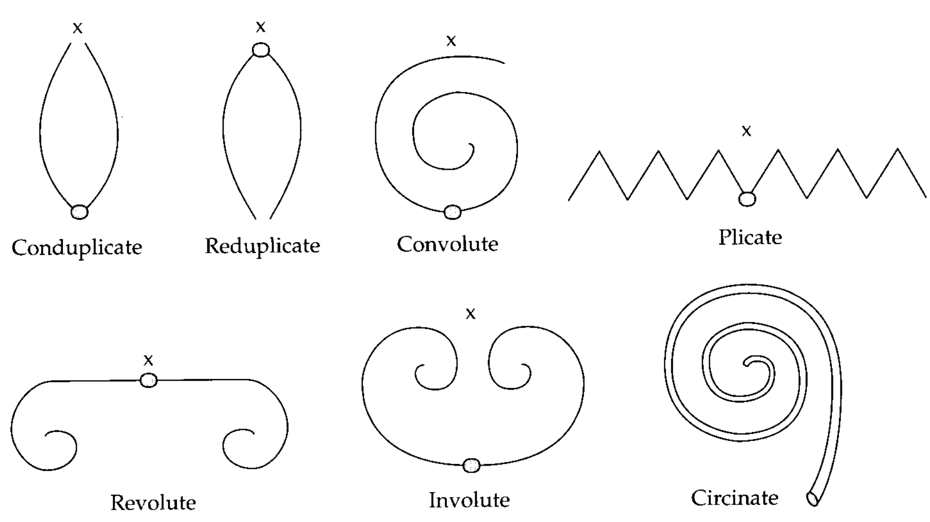


Figure 4.14 A few ptyxis terms. All patterns are shown in cross-section except circinate. An "X" indicates the position of the branch bearing the leaf.

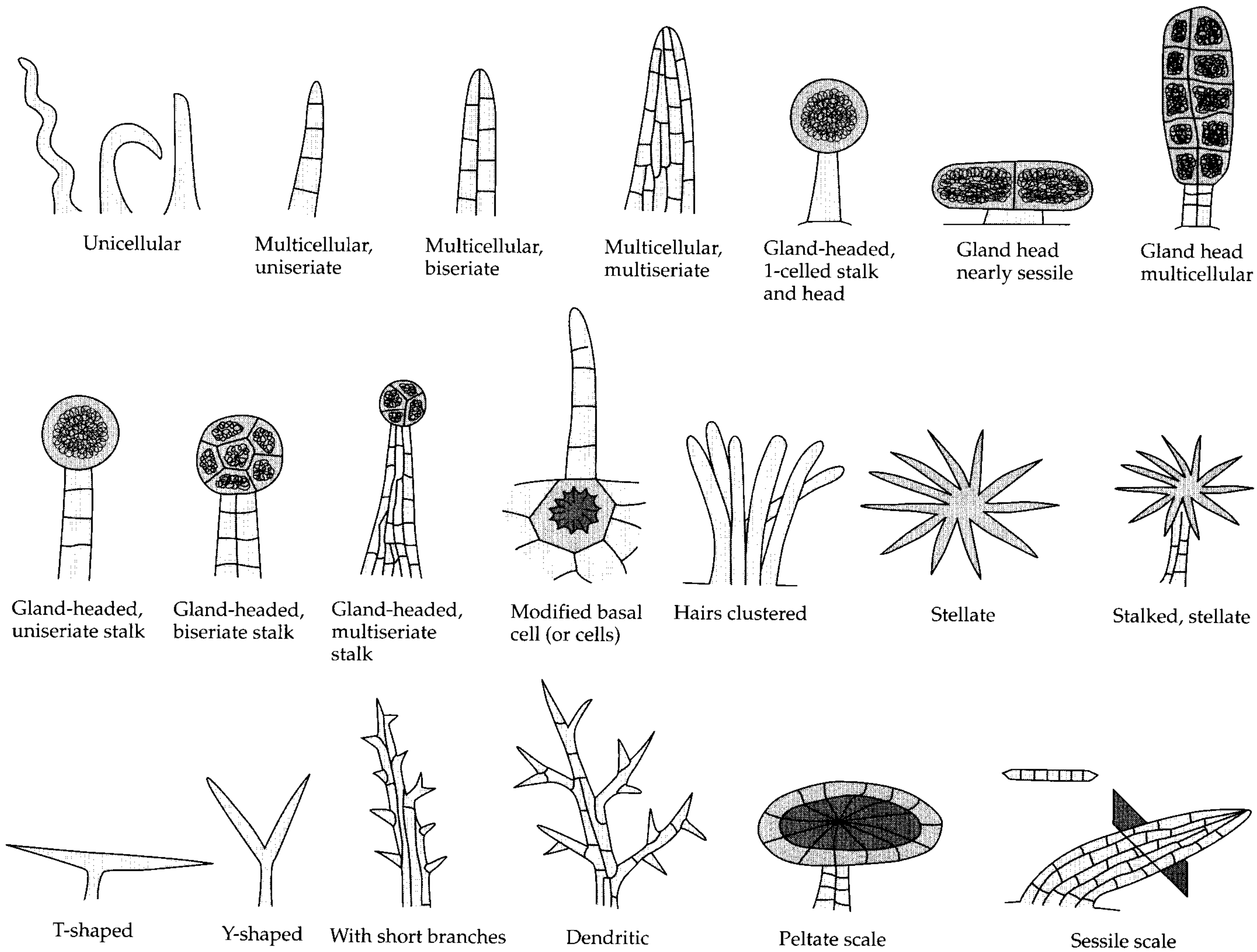


Figure 4.15 Selected features of hairs.

FLORAL MORPHOLOGY

The reproductive structures of angiosperms are called flowers. In our discussion of plant reproductive parts, we will focus on angiosperms; the specialized reproductive structures of the lycophytes, ferns and their allies, conifers, cycads, ginkgos, and gnetophytes are described in Chapter 8.

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**; 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** (plural **androecia**; pollen-producing structures), and **gynoecium** (plural **gynoecia**; ovule-producing structures). Flowers that have all three of these parts are said to be **complete**. If one or more 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; in **dioecious** species, the staminate and carpellate flowers are borne on separate individual plants. Various intermediate conditions exist, of course. **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 two main parts, in which case it is composed of an outer whorl (or whorls or spirals) of **sepals**, collectively called the **calyx** (plural **calyces**), and an inner

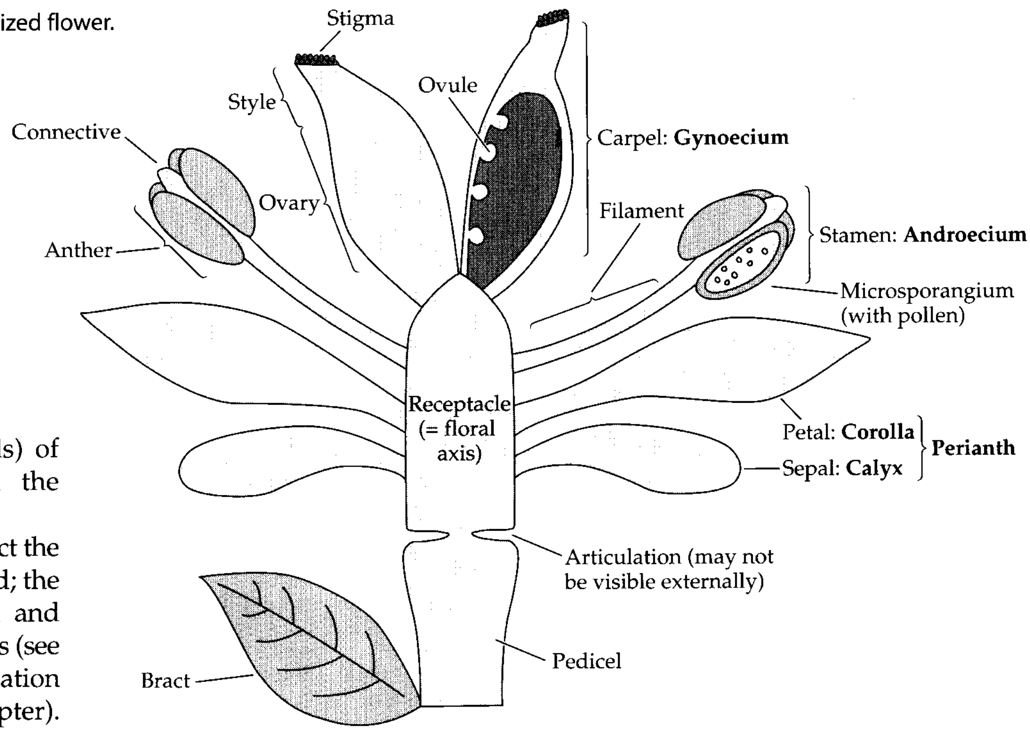


Figure 4.16 Parts of a generalized flower. Collective terms are in boldface.

whorl (or whorls or spirals) of **petals**, collectively called the **corolla**.

The sepals typically protect the inner flower parts in the bud; the petals are usually colorful and assist in attracting pollinators (see also the section on pollination biology later in this chapter). Corollas have evolved independently in various groups of angiosperms; in some families it is clear that the petals are showy, sterile stamens; in others the petals are modified sepals.

It is important to remember that although these perianth terms are useful in descriptions and 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 (singular *microsporangium*], 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 (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**; those that shed pollen toward the periphery are **extrorse**.

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 collects and facilitates 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 either wet or dry.

Each ovule contains the megagametophyte (the 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** (plural **funiculi**) or funicle. The gynoecium is often called the "female part" of the flower, although, as noted already, 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 they are extremely diverse in form and function. (For a detailed discussion of the diversity of these and 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 asymmetry 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 they are also called **actinomorphic** or **regular** (Figure 4.18A). (A few radial flowers have only two planes of symmetry; these are sometimes called **biradial**.)

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** (Figure 4.18B).

A few flowers have no plane of symmetry and are **asymmetrical** (Figure 4.18C). In determining the symmetry of a flower, the position of the more conspicuous

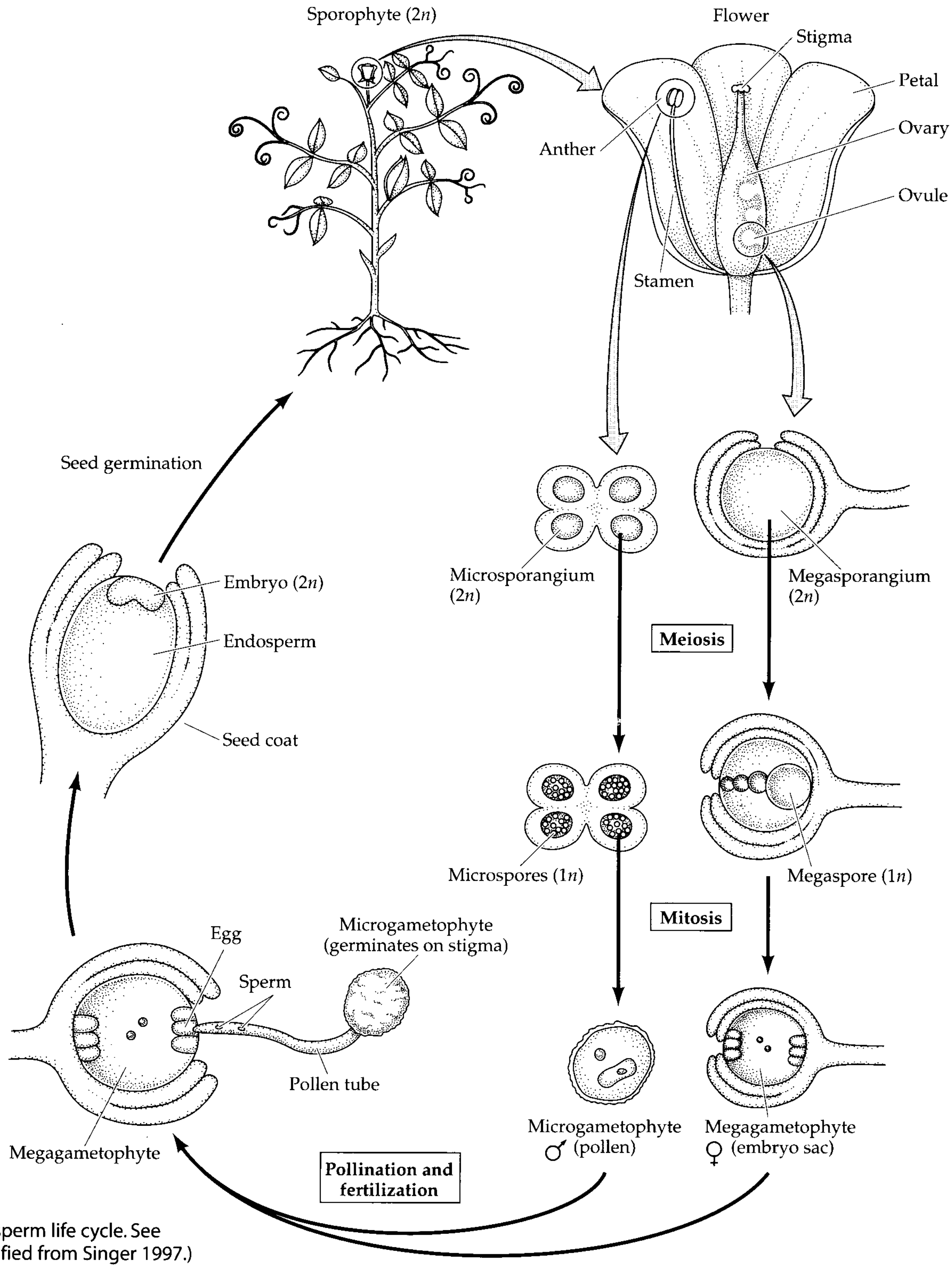


Figure 4.17 Angiosperm life cycle. See also Figure 4.40. (Modified from Singer 1997.)

BOX 4A *Floral Formulas and Diagrams*

A **floral formula** is a convenient shorthand method of recording floral symmetry, number of parts, connation and adnation, insertion, and ovary position. The formula consists of five symbols, as in the following example:

*, 5 , 5 , ∞ , 10

The first symbol indicates either radial symmetry (*), bilateral symmetry (X), or asymmetry ($). The second item is the number of sepals (here 5); the third item the number of petals (also 5); the fourth, the androecial item, is the number of stamens (here numerous—the symbol for infinity is generally used when the number of stamens is more than about 12), and the last item is the number of carpels (here 10). The line below the carpel number indicates the position of the ovary with respect to other floral parts (here superior, and the flower hypogynous). If the ovary were inferior (and the flower epigynous), the line would have been drawn above the carpel number.

Connation is indicated by a circle around the number representing the parts involved. For example, in a flower with five stamens that are monadelphous (i.e., connate by their filaments), the androecial item of the floral formula would be indicated as

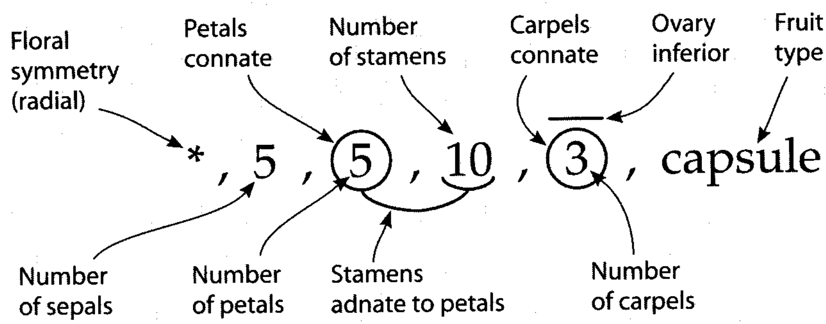
(5)

The plus symbol (+) may be used to indicate differentiation among the members of any floral part. For example, a flower with five large stamens alternating with five small ones would have the androecial item recorded as

5 + 5

Adnation is indicated by a line connecting the numbers representing different floral parts. Thus, a flower that has a sympetalous corolla with epipetalous stamens—for example, two stamens adnate to the four connate petals—would have the numbers representing the corolla and androecium parts indicated as

(4), 2



A sample floral formula.

The presence of a hypanthium (as in perigynous flowers) is indicated in the same fashion as adnation.

X , (5) , (5) , 10 , 5

Sterile stamens (staminodes) or sterile carpels (carpellodes or pistillodes) can be indicated by placing a dot next to the number of these sterile structures. Thus a flower with a syncarpous gynoecium composed of five fertile carpels and five sterile ones would be represented in the formula as

(5 + 5•)

Variation in the number of floral parts within a taxon is indicated by using a dash (–) to separate the minimum and maximum numbers. For example, the formula

* , 4 – 5 , 4 – 5 , 8 – 10 , (3)

would be representative of a taxon that has flowers with either 4 or 5 sepals and petals and from 8 to 10 stamens. Variation within a taxon in either connation or adnation is indicated by using a dashed (instead of a continuous) line:

* , 3 , (3) , 6 , 1

The lack of a particular floral part is indicated by placing a zero (0) in the appropriate position in the floral formula. For example, the floral formula

* , 3 , 3 , 0 , (2)

represents a carpellate flower.

Flowers in which the perianth parts are not differentiated into a calyx and corolla, (that is, flowers with a perianth of tepals) have formulas in which the second and third items (those representing sepals and petals) are combined into a single item (representing tepals). A hyphen (-) is placed before and after this item to indicate that the calyx and corolla categories have been combined. For example, an actinomorphic flower with 5 tepals, 10 stamens, and 3 connate carpels, with a superior ovary, would be represented as

* , -5- , 10 , (3)

The fruit type is often listed at the end of the floral formula:

* , -5- , 10 , (3), capsule

A floral formula is by no means an end in itself; it is merely a convenient means of recording the information needed to identify a plant. Floral formulas also can be useful tools for remembering characteristics of the various angiosperm families. They are used extensively in this text (see Chapter 9). Their construction requires careful observation of individual flowers and of variation among the flowers of the same or different individuals.

Floral diagrams are stylized cross-sections of flowers that represent the floral whorls as viewed from above. Rather like floral formulas, floral diagrams are used to show symmetry, number of parts, their relationships of the parts to each other, and degree of connation and/or adnation. Such diagrams cannot easily show ovary position. For more information of floral diagrams, see Rendle (1925), Porter (1967), Correll and Correll (1982), Zomlefer (1994), and Walters and Keil (1995).

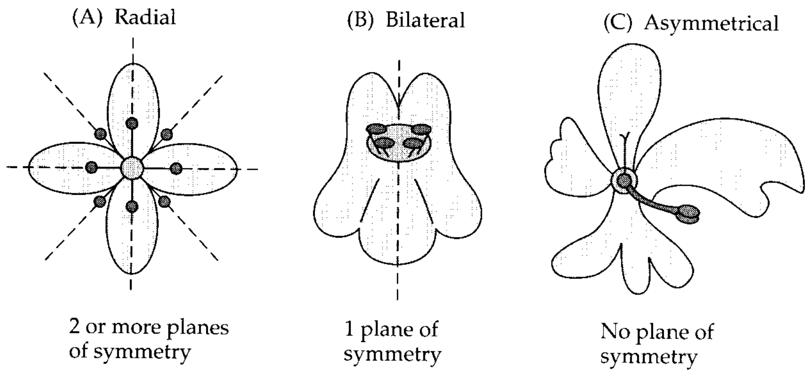


Figure 4.18 Patterns of floral symmetry.

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 here.

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
syngenesious stamens connate by their anthers
synsepalous sepals connate
syntepalous tepals connate

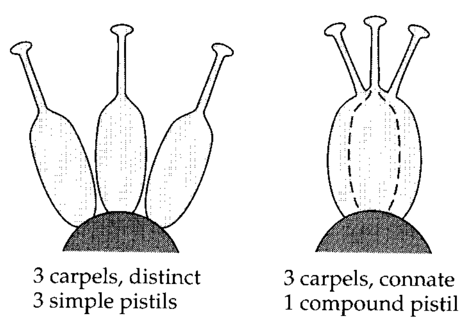


Figure 4.19 The difference between the terms *carpel* and *pistil*.

The corolla shape, especially when sympetalous, may be valuable in identification, and specialized terms are applied to distinctive corolla shapes, including rotate (wheel- or disk-shaped), campanulate (bell-shaped), urceolate (urn-shaped), salverform (with slender tube and abruptly flaring limb), funnelform (funnel-shaped), tubular, and bilabiate (2-lipped).

Carpel versus pistil The term **pistil** is sometimes used for the structure(s) in the center of the flower that contain(s) the ovules. How does this term differ from *carpel*, the term introduced earlier 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, and variation between different flowers of the same plant or closely related species is common. Often it is possible to count fused carpels by counting the number of styles, stigmas, or stigmatic lobes (Figure 4.20). Placentation

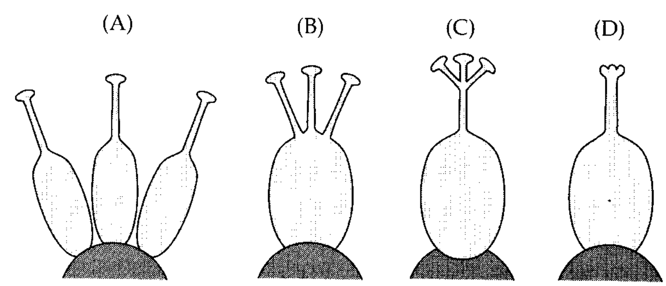


Figure 4.20 Three carpels, variously connate. (A) Three ovaries, styles, and stigmas. (B) One ovary, three styles and stigmas. (C) One ovary and style, the latter apically branched, and three stigmas. (D) One ovary and style, and three stigmas (or stigmatic lobes).

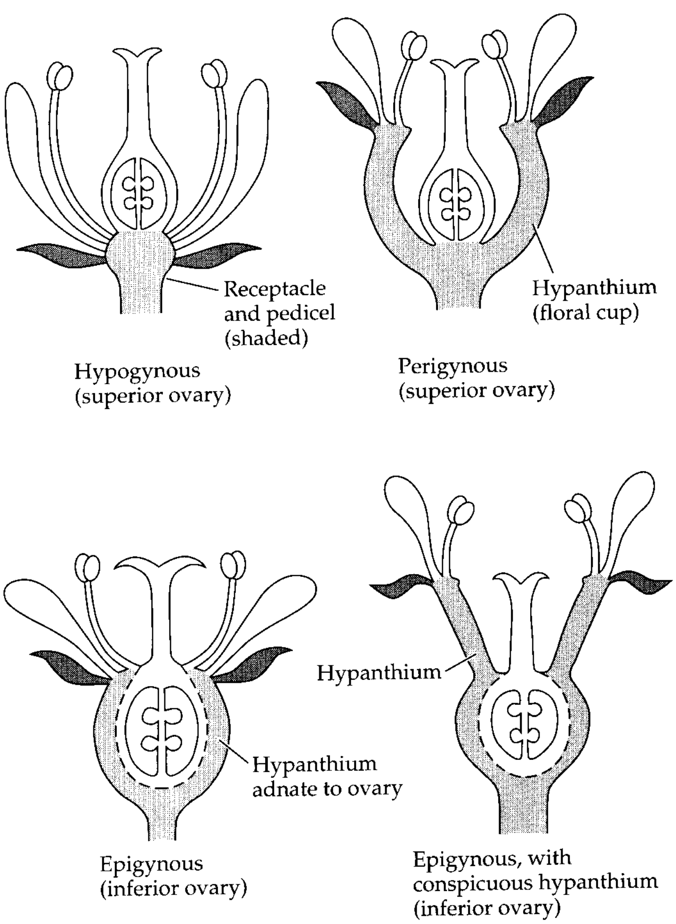


Figure 4.21 Insertion types.

(which will be discussed shortly) 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, but without being adnate to it, are called **perigynous.** In such flowers the perianth and androecium are attached to the rim of this structure, which is called the **hypanthium** (plural **hypanthia;** or **floral cup** or **floral tube**). The ovary of such flowers is also superior.

Hypanthia 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 in a longitudinal section of the flower.

Floral parts making up adjacent whorls normally alternate with each other, so 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 the androecium and gynoecium, occasionally are borne on stalks (the **androgynophore** and **gynophore,** 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 **placenta** (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 placentae, 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 placentae usually equals the carpel number.

Miscellaneous floral terms The following list defines a few other floral terms commonly encountered in plant descriptions.

basifixed referring to 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 periphery
centripetal developing first at the periphery 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

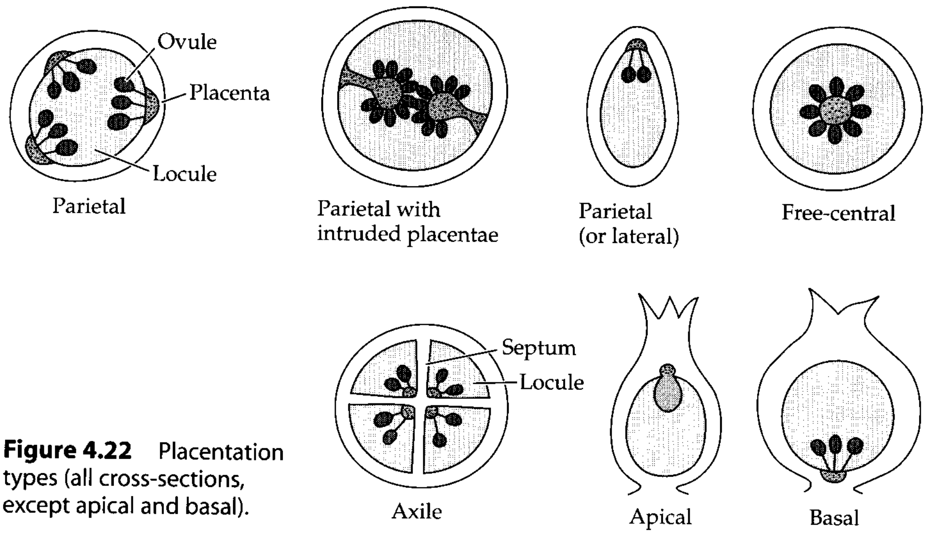


Figure 4.22 Placentation types (all cross-sections, except apical and basal).

pistillode a sterile pistil
staminode a sterile stamen
tetradynamous having four long and two short stamens
versatile referring to a structure, such as an anther, that is attached at its midpoint

Inflorescences, Fruits, and Seeds

An **inflorescence** can be defined as "the shoot system which serves for the formation of flowers and which is modified accordingly" (Troll 1964, trans. Weberling 1989: 201). The arrangement of flowers on a plant (the inflorescence form and position) is important in routine identification, as well as in the determination of phylogenetic relationships. Inflorescence categories have often been confused, however, because of the arbitrary separation of flower-bearing and vegetative regions of the plant (Figure 4.27).

Two quite different inflorescence types occur in angiosperms. In **determinate** (or **monotelic**) inflorescences, the main axis of the inflorescence ends in a flower; in **indeterminate** (or **polytelic**) inflorescences, the growing point produces only lateral flowers or partial inflorescences (groups of flowers). Typical determinate and indeterminate inflorescences are shown in Figure 4.28 (see also Weberling 1989).

The flowering sequence of determinate inflorescences usually begins with the terminal flower at the top (or center) of the cluster of flowers. In indeterminate inflorescences, the flowering sequence usually starts at the base (or outside) of the cluster. Determinate inflorescences are generally ancestral to indeterminate ones, and transitional forms are known. Various kinds of determinate and indeterminate inflorescences, based on pattern of branching, have been described.

One of the more common types of determinate inflorescences is the **cyme** (or determinate thyrse), the lateral branches of which are composed of usually numerous three-flowered units, usually showing opposite branching. Cymes can be of many different shapes because of differences in their branching patterns. If the inflorescence branches are initially monopodial—that is, producing several internodes before ending in a terminal flower—a panicle-like cyme results, and through reduction a racemelike cyme is formed.

The lateral branches (paraclades) of typical cymes or panicle-like cymes may be either alternately or oppositely arranged. **Scorpioid** and **helicoid** cymes are especially distinctive because of their coiled form, resulting from the abortion of one of the flowers within each three-flowered inflorescence unit (Figure 4.29).

The most common types of indeterminate inflorescences are racemes, spikes, corymbs, and panicles. A **raceme** is an inflorescence with a single axis bearing pedicellate flowers; a **spike** is similar, but the flowers are sessile (lacking a pedicel or stalk). In contrast, a **corymb** is a raceme with the pedicels of the lowermost flowers elongated, bringing all flowers to approximately the same level. A **panicle** is merely a compound raceme—that is, an indeterminate inflorescence that has two or more orders of branching, and each axis bears flowers or higher-order axes (Figure 4.30). Axillary racemes or cymes can become reduced in length, resulting in a fascicle.

A **head**, or **capitulum**, is a dense terminal cluster of sessile flowers. This inflorescence type can result through aggregation of the flowers of either an indeterminate or determinate inflorescence. In an indeterminate head, the peripheral flowers open first; in a determinate head the central flowers open first (compare Figures 4.29 and 4.30). An umbel is an inflorescence in which all the

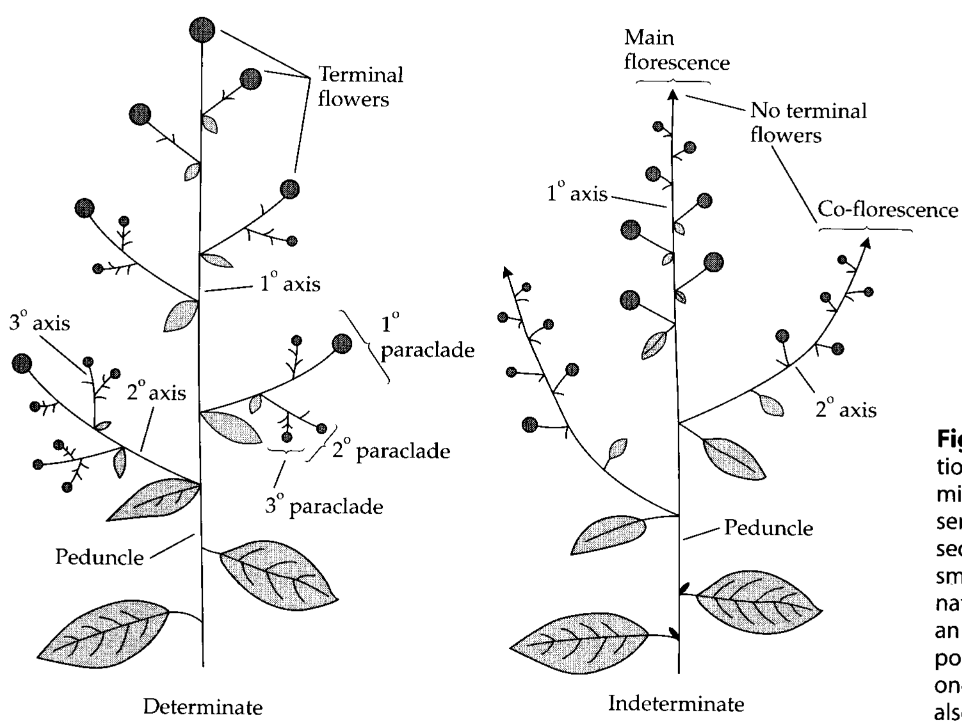


Figure 4.28 Diagrammatic representation of typical determinate and indeterminate inflorescences. The circles represent flowers; their size indicates the sequence of opening (from large to small). The individual units of determinate inflorescences are called paraclades; an indeterminate inflorescence is composed of the main florescence and secondary florescenses (coflorescences). (See also Weberling 1989.)

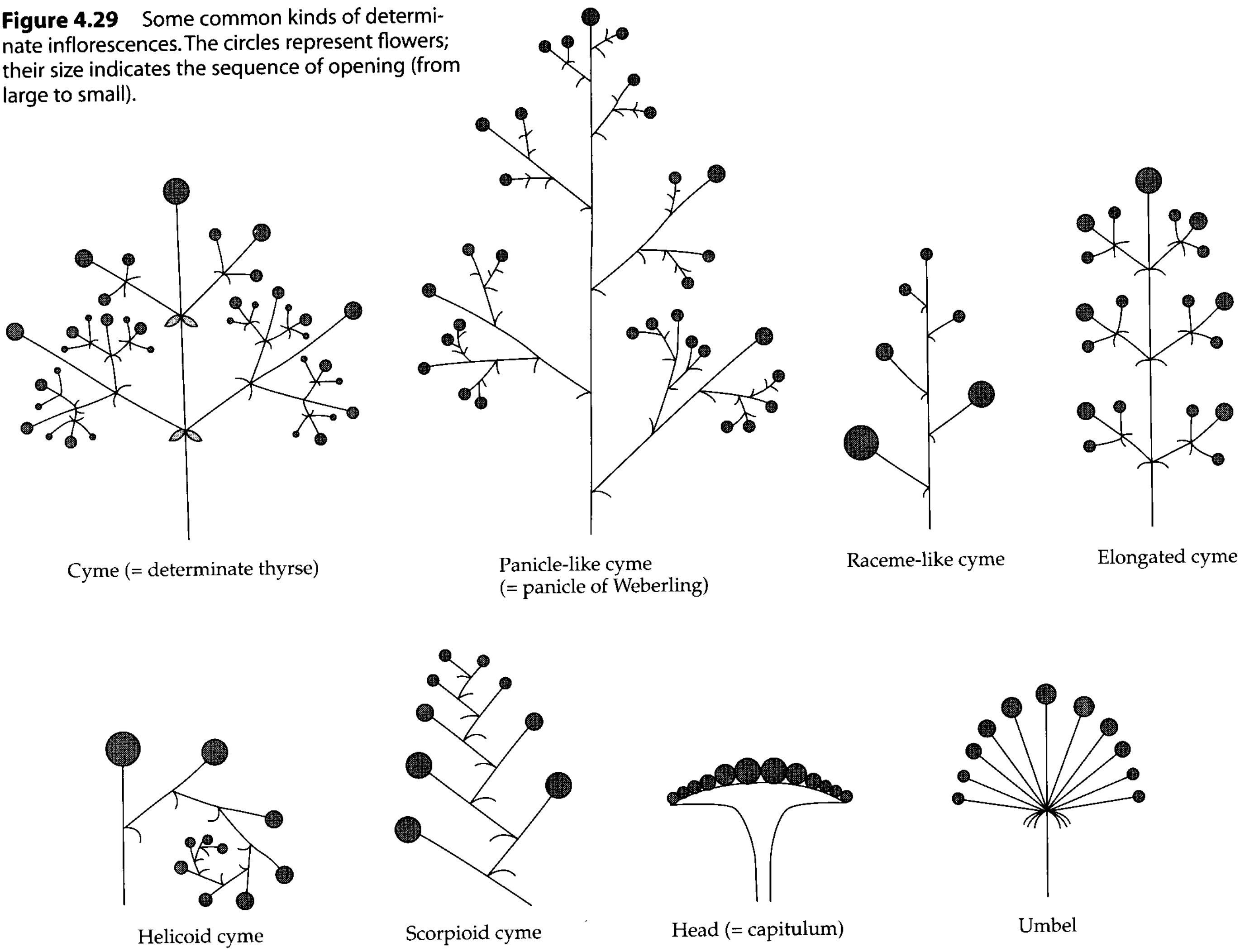


Figure 4.29 Some common kinds of determinate inflorescences. The circles represent flowers; their size indicates the sequence of opening (from large to small).

flowers often have pedicels of approximately equal length that arise from a single region at the apex of the inflorescence axis. Umbels are often indeterminate but may also be determinate (see Figures 4.29 and 4.30).

Simple inflorescences, such as racemes, spikes, umbels, and heads, have only a single axis (i.e., one branch order). Compound inflorescences (e.g., compound racemes, compound umbels, cymes, thyrses, and panicles) have two or more orders of branches.

The term **catkin** or **ament** is used for any elongated inflorescence composed of numerous inconspicuous, usually wind-pollinated flowers. These terms are nonspecific with regard to order of branching and floral arrangement: Aments may be either simple or compound, and they may be determinate or indeterminate structures.

Most inflorescences and solitary flowers are borne on young shoots, but some are borne on leaves (producing **epiphyllous** flowers or inflorescences) or on older stems and/or trunks (producing **cauliflorous** flowers or inflorescences). Epiphylly often (but not always) results from ontogenetic displacement of the bud; in early stages of growth the cells below the young bud primordium and adjacent leaf primordium divide actively, and the bud and leaf grow out as a single unit. In contrast, cauliflory is due to the delayed development of the inflorescences, which break out through old wood.

Inflorescences may sometimes be modified for climbing by becoming elongated and twining or developing adhesive pads, thus forming tendrils. (Tendrils, of course, may also evolve from leaves, and twining stems may be tendril-like.)

FRUIT TYPES

A **fruit** is a matured ovary along with fused accessory structures (hypanthium or perianth parts). The great diversity of size, form, texture, means of opening, and anatomy of fruits has long confounded plant systematists, and many different fruit types have been proposed. All systems of fruit classification must deal with several difficulties.

Foremost is the problem of the bewildering and often continuous variation in fruit structure; van der Pijl (1972: 17) concluded that "the fruit is too versatile and has too many aspects to be divided into strict categories." Second, additional complexities come from the extensive

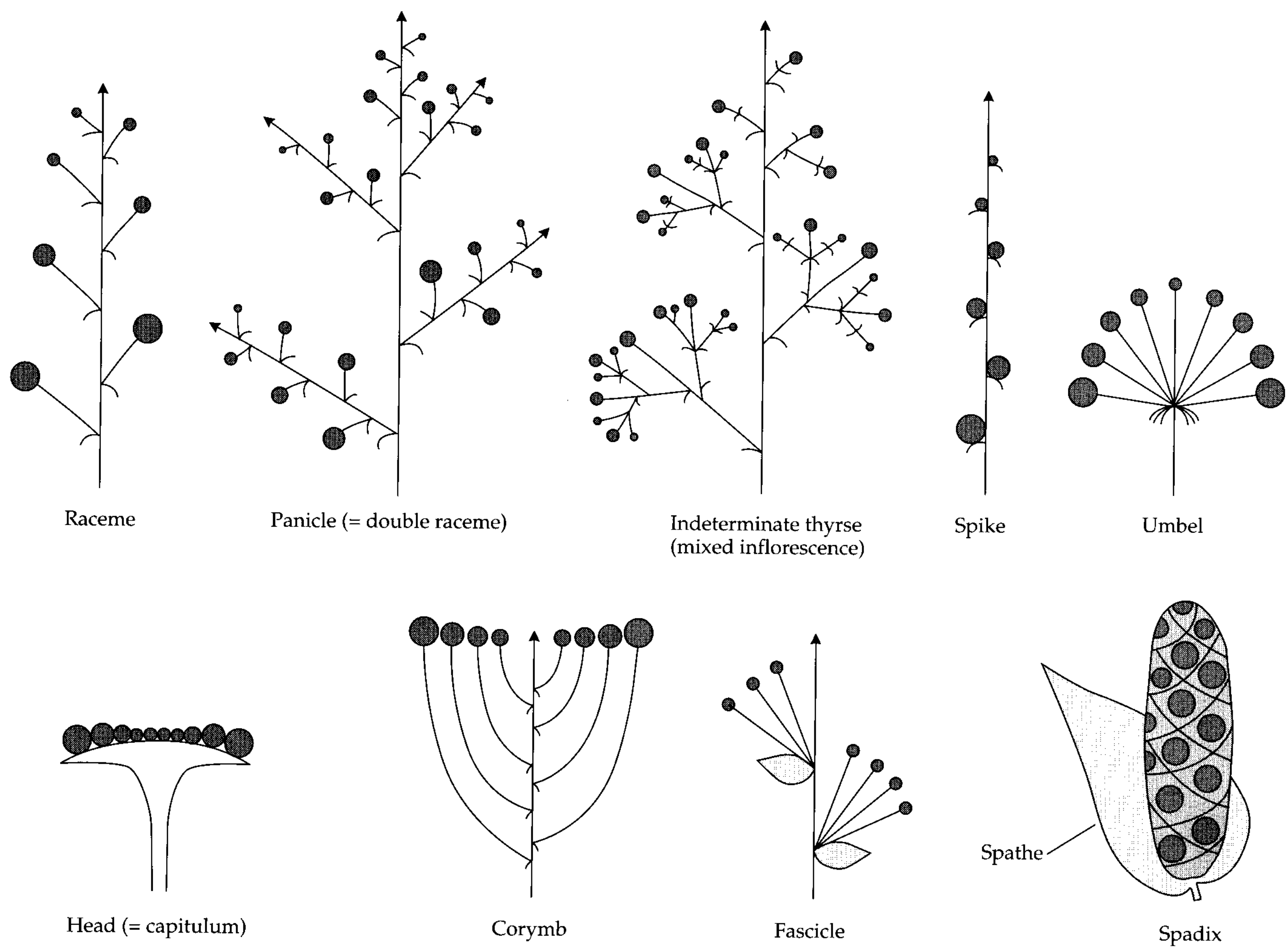


Figure 4.30 Some common kinds of indeterminate inflorescences. The circles represent flowers; their size indicates the sequence of opening (from large to small).

convergent evolution of fruiting structures; functionally similar fruits have arisen independently in different lineages of angiosperms from similar and different gynoecial conditions. Third, other parts of the flower (and even associated vegetative structures), in addition to the matured gynoecium, may form a functional part of the fruit. Examples of such **accessory structures** include the expanded fleshy receptacle of strawberries (*Fragaria*, Rosaceae), the fleshy perianth of seagrape fruits (*Coccoloba*, Polygonaceae), the winglike calyx of dipterocarp fruits (*Dipterocarpus*, Dipterocarpaceae), and the fleshy inflorescence axis of figs (*Ficus*, Moraceae). Finally, tropical fruits have been neglected in many traditional fruit classifications.

In this text we employ an artificial system of descriptive fruit terms, based on the traditional fruit classification of Gray (1877). This system has been widely employed. It is based on the texture of the **pericarp**, or fruit wall (fleshy, dry, or hard), the pattern of **dehiscence** or **indehiscence** (type of fruit opening, or lack thereof), the shape and size of the fruit, and the carpel and ovule number.

Simple fruits (those resulting from a single flower) are divided into two categories: (1) those formed from a single carpel or several fused carpels, and (2) those that develop from several separate carpels of a single gynoecium (**aggregate fruits**). The individual units of an aggregate fruit may be any of the basic fruit types given in the list following this discussion. For example, the fruit of *Magnolia* (Magnoliaceae) is an aggregate of follicles, that of *Annona* (pawpaw, Annonaceae) is an aggregate of berries, and that of *Rubus* (blackberry, Rosaceae) an aggregate of drupes.

If a fruit is the product of the gynoecia of several closely clustered flowers, it is termed a **multiple fruit**. As with aggregate fruits, the individual fruits composing the cluster may consist of any of the basic fruit types outlined in the list that follows this discussion. For example, the fruit of *Ananas* (pineapple, Bromeliaceae) is a multiple of berries, that of *Morus* (mulberry, Moraceae) a multiple of drupes, and that of *Platanus* (sycamore, Platanaceae) a multiple of achenes.

The use of modifying terms (e.g., drupaceous schizocarp, winged or samaroid schizocarp, one-seeded fleshy

A Key to Fruit Types

1. Fruit the product of a single flower 2
1. Fruit the product of several flowers clustered in one mass .... **Multiple fruit** [go to 3 and key based on an individual unit]
2. Single fruit (carpel solitary or several and fused) .... **Simple fruit** [go to 3]
2. Several distinct fruits (carpels several and distinct) .... **Aggregate fruit** [go to 3 and key based on individual units]
3. Fruit not opening (indehiscent) 4
3. Fruit opening or breaking apart (dehiscent) 13
4. Fruit fleshy (at least in part) 5
4. Fruit dry 8
5. Texture of fruit ± homogeneous (except for seeds), fleshy throughout .... **Berry**
5. Texture of fruit heterogeneous 6
6. Outer part of fruit firm, hard, or leathery; inner part softer .... **Berry**
6. Outer part of fruit ± soft; inner part papery, cartilaginous, or hard 7
7. Center of fruit with 1 or more hard pits (pyrenes) enclosing seeds; ovary inferior or superior .... **Drupe**
7. Center of fruit with papery or cartilaginous structures enclosing seeds; ovary inferior .... **Pome**
8. Fruit with several to many seeds .... **Indehiscent pod**
8. Fruit usually 1-seeded 9
9. Fruit winged .... **Samara**
9. Fruit wingless 10
10. Pericarp thick and bony; fruit generally large .... **Nut**
10. Pericarp thin; fruit smaller 11
11. Pericarp loose and free from seed .... **Utricle**
11. Pericarp firm, close-fitting or fused to seed 12
12. Pericarp firm, close-fitting, but free from seed .... **Achene**
12. Pericarp adnate (fused) to seed .... **Caryopsis (grain)**

capsule) is encouraged. This classification is presented by means of a key to a series of definitions. Although this system is admittedly arbitrary, the key and descriptions have proved useful in teaching and floristics. (For more information on fruit types, see Judd 1985, Weberling 1989, and Spjut 1994.)

achene a fairly small, indehiscent, dry fruit with a thin and close-fitting wall surrounding a single seed; includes the **cypsela**. Examples: *Bidens, Carex, Ceratophyllum, Clematis, Cyperus, Ficus, Fragaria, Helianthus, Medicago* (some), *Ostrya, Petiveria, Polygonium, Ranunculus, Rhynchospora, Rosa* (achenes enclosed in a fleshy hypanthium), *Rumex, Sagittaria, Taraxacum, Trifolium* (some), *Vernonia*. (See Figures 9.17, 9.58, 9.80, and 9.146.)

berry an indehiscent, fleshy fruit with one or a few to many seeds. The flesh may be ± homogeneous throughout, or the outer part may be hard, firm, or leathery; septa are present in some, and the seeds may be arillate (having a fleshy outgrowth of the funiculus) or with a fleshy testa (seed coat). Examples: *Actinidia, Aegle, Annona, Averrhoa, Cananga, Citrus, Cucurbita, Eugenia, Litchi, Miconia, Musa* (some), *Opuntia, Passiflora, Phoenix, Punica, Sideroxylon, Smilax, Solanum, Tamarindus, Vaccinium, Vitis*. (See Figures 9.12, 9.48, 9.63, 9.52, 9.100, 9.108, and 9.121.)

capsule a dry to (rarely) fleshy fruit from a two- to many-carpellate gynoecium that opens in various ways to release the seeds. Such fruits may have from one to many locules; if 2-locular, then the partition is not persistent. Examples: *Aesculus, Allium, Antirrhinum, Argemone, Aristolochia, Begonia, Blighia, Campsis, Clusia, Echinocystis, Epidendrum, Eucalyptus, Euonymus, Hibiscus, Hypericum, Ipomoea, Justicia, Lachnanthes, Lagerstroemia, Lecythis, Lyonia, Momordica, Oxalis, Papaver, Portulaca, Rhododendron, Swietenia, Tri-*

13. Fruit from a single carpel 14
13. Fruit from a 2- to many-carpellate gynoecium 16
14. Fruit dehiscing along a single suture (slit) .... **Follicle**
14. Fruit dehiscing by two longitudinal sutures, or breaking up by transverse sutures 15
15. Sutures longitudinal .... **Legume**
15. Sutures transverse, the fruit breaking into 1-seeded segments .... **Loment**
16. Fruit with a dry/fibrous to leathery or fleshy outer husk that early to tardily breaks apart; center of fruit with hard pit(s) enclosing seed(s) .... **Dehiscent drupe**
16. Fruit lacking hard pit(s) enclosing seed(s); splitting open or into 1-seeded segments 17
17. Fruit splitting into 1- or few-seeded segments (mericarps) .... **Schizocarp**
17. Fruit splitting open and releasing seeds 18
18. Fruit 2-locular, the two valves splitting away from a persistent thin partition around the rim of which the seeds are attached .... **Silique**
18. Fruit 1- to several-locular, the partition not persistent if the fruit 2-locular .... **Capsule** [Go to 19]
19. Dehiscence circumscissile (splitting transversely), the top coming off like a lid .... **Circumscissile capsule (pyxis)**
19. Dehiscence not circumscissile 20
20. Fruit opening by pores, flaps, or teeth 21
20. Fruit opening longitudinally or irregularly 22
21. Fruit opening by a series of apical teeth .... **Denticidal capsule**
21. Fruit opening by pores or flaps (often near the top) .... **Poricidal capsule**
22. Fruit opening irregularly .... **Anomalicidal capsule**
22. Fruit opening longitudinally 23
23. Valves breaking away from the septa (partitions between the locules) .... **Septifragal capsule**
23. Valves remaining attached to the septa (at least in part) 24
24. Fruit splitting at the septa .... **Septicidal capsule**
24. Fruit splitting between the septa and into the locules of the ovary, or fruit 1-locular .... **Loculicidal capsule**

odanis, *Viola*. (See Figures 9.32, 9.51, 9.55, 9.62, 9.71, 9.73, 9.109, 9.115, 9.116, 9.131, and 9.134.)

caryopsis (pl. caryopses) **(grain)** a small, indehiscent, dry fruit with a thin wall surrounding and more or less fused to a single seed. Examples: most Poaceae. (See Figures 9.39 and 9.40.)

dehiscent drupe a fruit with a dry or fibrous to fleshy or leathery outer husk that early to tardily breaks apart (or opens), exposing one or more nutlike pits enclosing the seed(s). Examples: *Carya*, *Rhamnus* (some), *Sageretia*. (See Figure 9.96.)

drupe an indehiscent, fleshy fruit in which the outer part is more or less soft (to occasionally leathery or fibrous) and the center contains one or more hard pits (**pyrenes**) enclosing seeds. Examples: *Arctostaphylos*, *Celtis*, *Clerodendrum*, *Cocos*, *Cordia*, *Cornus*, *Ilex*, *Juglans*, *Licania*, *Melia*, *Myrsine*, *Nectandra*, *Prunus*, *Psychotria*, *Roystonea*, *Rubus*, *Sabal*, *Scaevola*, *Syagrus*, *Terminalia*, *Toxicodendron*. (See Figures 9.13, 9.82, 9.95, 9.113, 9.130, and 9.137.)

follicle a dry to (rarely) fleshy fruit derived from a single carpel that opens along a single longitudinal suture; the seeds may be arillate or with a fleshy testa. Examples: *Akebia*, *Alstonia*, *Aquilegia*, *Asclepias*, *Caltha*, *Grevillea*, *Magnolia*, *Nerium*, *Paeonia*, *Sterculia*, *Zanthoxylum*. (See Figures 9.47, 9.61, 9.126, and 9.127.)

indehiscent pod an indehiscent, fairly dry fruit with few to many seeds. Examples: *Adansonia*, *Arachis*, *Bertholletia*, *Cassia* (some), *Crescentia*, *Kigelia*, *Medicago* (some), *Thespesia* (some).

legume a dry fruit derived from a single carpel that opens along ± two longitudinal sutures. Examples: many Fabaceae. (See Figures 9.74, 9.75, and 9.76.)

loment a dry fruit derived from a single carpel that breaks transversely into one-seeded segments. Examples: *Aeschynomene*, *Desmodium*, *Sophora*.

nut a fairly large, indehiscent, dry fruit with a thick and bony wall surrounding a single seed. Examples: *Brasenia, Castanea, Corylus, Dipterocarpus, Fagus, Nelumbo, Quercus, Shorea*. (See Figure 9.91.)

pome an indehiscent, fleshy fruit in which the outer part is soft and the center contains papery or cartilaginous structures enclosing the seeds. Examples: most Rosaceae, subfamily Maloideae. (See Figure 9.81.)

samara a winged, indehiscent, dry fruit containing a single (rarely two) seed(s). Examples: *Ailanthus, Betula, Casuarina, Fraxinus, Liriodendron, Myroxylon, Ptelea, Stigmaphyllon, Ulmus*. (See Figures 9.85 and 9.93.)

schizocarp a dry to rarely fleshy fruit derived from a two- to many-carpellate gynoecium that splits into one-seeded (or few-seeded) segments (**mericarps**). If desired, the mericarps may be designated as samaralike, achenelike, drupelike, and so on. Examples: *Acer, Apium, Cephalanthus, Croton, Daucus, Diodia, Erodium, Euphorbia, Glandularia, Gouania, Heliconia, Heliotropium, Lamium, Lycopus, Malva, Ochna, Oxypolis, Salvia, Sida, Verbena*. (See Figures 9.67, 9.68, 9.112, 9.125, 9.135, and 9.139.) Fruits that show late-developmental fusion of their apical parts are not considered schizocarps—for example, *Asclepias* (follicles), *Sterculia* (follicles), *Ailanthus* (samaras), *Simarouba* (drupes), *Pterygota* (samaras).

silique a fruit derived from a two-carpellate gynoecium in which the two halves of the fruit split away from a persistent partition (around the rim of which the seeds are attached); includes the **silicle**. Examples: many Brassicaceae. (See Figure 9.102.)

utricle a small, indehiscent, dry fruit with a thin wall (bladderlike) that is loose and free from a single seed. Examples: *Amaranthus* (some), *Chenopodium, Lemna, Limonium*. (See Figure 9.54.)

SEEDS

A **seed** is a matured ovule that contains an embryo and often its nutritive tissues (endosperm, perisperm). The **endosperm** is usually triploid tissue derived from the union of two cells of the female gametophyte (the polar nuclei) and one sperm nucleus (see the section on embryology later in this chapter). Endosperm may be **homogeneous** (uniform in texture) or **ruminate** (dissected by partitions that grow inward from the seed coat). It may contain starch, oils, proteins, oligosaccharides, and/or hemicellulose, and it may be hard to soft and fleshy. The **perisperm** is a specialized, diploid nutritive tissue derived from the megasporangium.

The seed is surrounded by a **seed coat**, which develops from the integument(s). The details of seed coat anatomy are quite variable. The **testa** (plural **testae**) develops from the outer integument and the **tegmen** (plural **tegmina**) from the inner integument. The prefixes *exo-*, *meso-*, and *endo-* refer to tissues developing from the outer epidermis, the middle portion, and the inner epidermis, respectively, of each of the two integuments. The seed may be variously sized and shaped, and it may be associated with a wing or a tuft of hairs. The testa varies in surface texture due to the pattern and outgrowths of the individual cells composing its surface, and it is sometimes colorful and fleshy.

Some seeds are associated with a hard to soft, oily to fleshy, and often brightly colored structure called an **aril**. The aril is usually an outgrowth of the funiculus or the outer integument, although sometimes this term is restricted to structures derived from the funiculus, with those derived from the outer integument called **caruncles**. The seed bears a scar, called the **hilum** (plural **hila**), at the point where it was attached to the funiculus.

The embryo consists of an **epicotyl**, which will develop into the shoot; a **radicle**, which will develop into the primary root and usually gives rise to the root system; a **hypocotyl**, which connects the epicotyl and radicle; and usually one or two **cotyledons** (seedling leaves), which may be leaflike, fleshy, or modified as nutrient-absorptive structures.

FRUIT AND SEED DISPERSAL

Most fruit types may be dispersed by a variety of agents. Different parts of the fruit, seed, or associated structures (pedicel, perianth) may be modified for similar dispersal-related functions. For example, wind dispersal may be accomplished by (1) a tuft of hairs on the seeds, as in *Asclepias* (Apocynaceae), which has follicles that open to release hairy seeds; (2) wings on the fruits, as in *Fraxinus* (Oleaceae), which has samaras; (3) hair tufts on the fruits, as in *Anemone* (Ranunculaceae), which has an achene with a persistent style bearing elongated hairs; (4) a winglike perianth, as in *Dipterocarpus* (Dipterocarpaceae), which has nuts associated with elongated, winglike sepals; (5) association of the infructescence (mature inflorescence, with fruits) with an expanded, winglike bract, as in *Tilia* (Malvaceae), in which the fruits are nuts; or (6) a tumbleweed habit, as in *Cycloloma* (Amaranthaceae), in which the entire plant is blown across the landscape, dispersing its small fruits as it rolls.

Bird dispersal may be enhanced by (1) a colorful, fleshy seed coat, as in *Magnolia* (Magnoliaceae), which has an aggregate of follicles that open to reveal the fleshy seeds; (2) fleshy, indehiscent fruits, as in *Solanum* (Solanaceae), which has berries, *Prunus* (Rosaceae), which has drupes, or *Amelanchier* (Rosaceae), which has pomes; or (3) association of the fruit (or fruits) with fleshy accessory structures, as in *Coccoloba* (Polygonaceae), which has achenes surrounded by fleshy perianth, *Fragaria* (Rosaceae), which has achenes borne on an expanded, colorful, fleshy receptacle, or *Hovenia* (Rhamnaceae), which has drupes associated with fleshy pedicels and inflorescence axes.

It is easy to see that similarly functioning fruiting structures may be derived from very different floral parts. Convergence is common in fruits, and similar fruits have evolved independently in many different angiosperm families. (For additional information on fruit dispersal, see van der Pijl 1972 and Weberling 1989.)

Some heavy fruits or seeds simply drop from the plant, land on the ground, and stay there. This is not very common, however, and may be characteristic only of species that have lost their primary dispersal agent, as possibly in osage orange (*Maclura pomifera*, Moraceae).

Dispersal by the plant itself usually occurs through some kind of explosive discharge of seeds, fruits, or portions of fruits by means of swelling of seed mucilage, turgor pressure changes, or hygroscopic tissues. This category also includes passive movement of seed containers by wind, rain, or animals, and creeping dispersal units whereby the fruit or seed moves itself by hygroscopic movements of bristles.

Adaptations for transport by wind include small, dustlike seeds; seeds with a balloonlike, loose testa; inflated utricles, calyces, or bracts; or a pericarp with air spaces. Wind dispersal may be facilitated by a plume formed from a persistent style, long hairy awns, a modified perianth (such as a pappus), placental outgrowths, outgrowths of the funiculus, elongation of the integument, a wing that splits apart, or hair tufts. Wings for wind dispersal may be present on fruits or seeds, or developed from accessory parts (perianth, bracts). In tumbleweed dispersal, a large part of the plant or inflorescence breaks off and is blown around.

Dispersal by water occurs when seeds or fruits are washed away by rainfall or carried in water currents. Such seeds or fruits are often small, dry, and hard, and they may have spines or projections as anchoring structures (water burs), a slimy covering, an unwettable surface layer, or low density and thus the ability to float.

Adaptations for transport on the outside surface of animals include small seeds or fruits with spines, hooks, or sticky hairs that easily detach from the plant and are placed near ground level. This category also includes small and hard fruits or seeds that stick with mud to the feet of waterfowl, as well as trample burs that become caught in the feet of large grazing mammals. Many sticky fruits attach to the feathers of birds.

Fruits and seeds may also be transported either within an animal (after ingestion) or in its mouth. These cases can be divided into subtypes by the kind of animal carrying the fruit or seed:

- *Fish* disperse some fleshy fruits or seeds of plants of riversides or inundated areas.
- Transport by *turtles* or *lizards* characterizes some fleshy fruits that have an odor. Such fruits are sometimes colored and often are borne near the ground or dropped from the plant at maturity. Some have a hard skin; others are hard but contain arillate seeds or seeds with fleshy testae.
- *Birds* may disperse nuts or seeds by carrying them in their bills or by hiding and burying them. Some viscid seeds stick to birds' bills. Bird-dispersed fruits or seeds often have an attractive edible part. The seeds of some fleshy fruits are protected from ingestion by a bony wall, bitter taste, or toxic compounds, and when mature, these fruits have signaling colors that attract birds (often red contrasting with black, blue, or white). These fruits have no odor and no closed hard rind (or in hard fruits, the seeds are exposed or dangling), and they remain attached to the plant. Some have colorful hard seeds that mimic the colorful fleshy fruits of other bird-dispersed species.
- Transport by *mammals* is often associated with their stockpiling of fruits (especially nuts) or seeds. Mammal-dispersed fruits often have a high oil content, and are frequently fleshy, with hard centers or leathery to hard skins that can be opened to reveal fleshy inner tissues, arillate seeds, or seeds with fleshy testae. The seeds may be toxic, bitter, or thick walled. Odor is very important in attracting mammals, but color is not essential. The fruits often drop from the plant.
- Fruits transported by *bats* share many of the characters listed in the previous entry, for mammals, but usually they are borne in an exposed position (e.g., outside the dense crown of a tree). They have drab colors, a musty, sourish, or rancid odor; they are often large, fleshy, easily digested; and they remain attached to the plant.
- Some seeds contain small, nutritious arils (or elaiosomes) and are dispersed by *ants*.

Modes of fruit and/or seed dispersal are noted for most of the families treated in Chapters 8 and 9.