4

CHAPTER

Taxonomic Evidence: Structural and Biochemical Characters

*T*axonomic evidence consists of the characters used in phylogenetic analyses upon which plant classifications are based, along with 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, and palynology, secondary plant compounds, and proteins. Nucleic acids (DNA and RNA) provide an increasingly important source of taxonomic characters, and 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 most of the characters used for practical plant identification and many of those used for hypothesizing phylogenetic relationships. These features have been used for a longer time than anatomic or molecular evidence and have constituted the primary source of taxonomic evidence since the beginnings of plant systematics. Morphological characters are easily observed and find practical use in keys and descriptions. Phylogenetically informative characters may be 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 below, although the reproductive terms strongly emphasize the angiosperms, since 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 7.) Many, if not all, of the terms outlined below should be considered merely convenient points

along a continuum of variation in form. Thus, 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.

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**), while 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 or stops growing; a series of such axillary branches comprise a **sympodial shoot**.
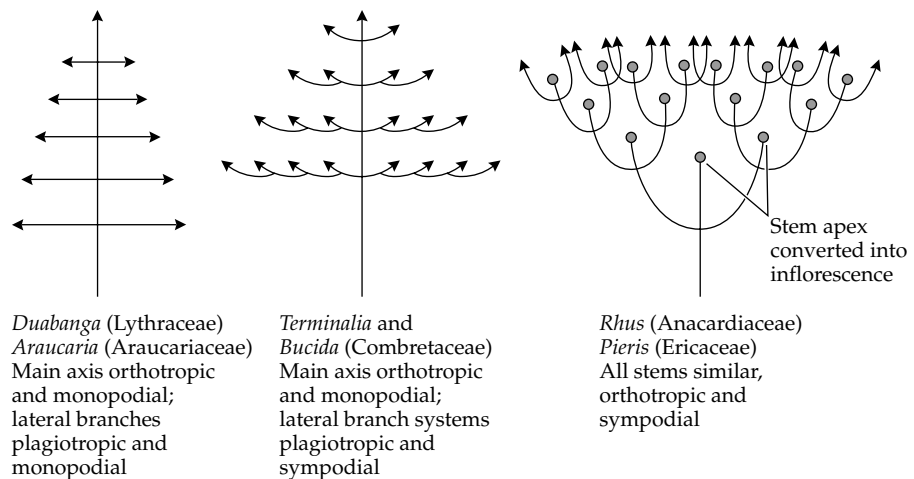
Stems are provided with **buds**, which are small embryonic shoots, often protected by modified leaves (bud scales) or hairs. Buds may show a period of dormancy, and when they eventually grow out, may leave scars at the base of the new shoot. Such shoots are called **proleptic**. On the other hand, buds may develop and elongate at the same time as the shoot on which they are borne, in which case the new shoot usually lacks bud-scale 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. Finally, all shoots on a plant may be the same, or there may be two or more kinds of 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.

ROOTS

Roots usually branch irregularly. Lateral roots are initiated internally (in the endodermis and pericycle, the cell layers surrounding the conducting tissues) and erupt through the cortex (although those of the lycopodiophytes 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 (a central region with more or less isodiametric cells). Roots also lack the nodes and internodes that characterize stems (see below), and they are usually found underground. The primary functions of roots are holding the plant in place, absorbing water and minerals, and storing water and carbohydrates. Some roots are specialized for other functions, such as photosynthesis (as in some reduced epiphytic Orchidaceae), penetrating the tissues of a host species (as in parasitic species such as mistletoes, Viscaceae), constricting the trunks of supporting trees (as in strangler figs, Moraceae), or providing 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

Duabanga (Lythraceae)
Araucaria (Araucariaceae)
Main axis orthotropic and monopodial; lateral branches plagiotropic and monopodial

Terminalia and *Bucida* (Combretaceae)
Main axis orthotropic and monopodial; lateral branch systems plagiotropic and sympodial

Rhus (Anacardiaceae)
Pieris (Ericaceae)
All stems similar, orthotropic and sympodial

Stem apex converted into inflorescence

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

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. A few important terms relating to roots are listed below.

adventitious   developing from any plant part other than the embryonic root (radicle) or another root
aerial   growing in the air
fibrous   with all portions of the root system being of more or less equal thickness, often well branched
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. Some, however, may be photosynthetic (as in asparagus, Asparagaceae, and many cacti, Cactaceae), store water or carbohydrates (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). In addition to terms already mentioned, some important stem-related vocabulary is listed below.

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 at the end of the growing season
internode   the part of the stem between two adjacent nodes
lenticels   wartlike protuberances 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   area of the stem where the leaf and bud are borne
pith   soft tissue in center of stem, usually consisting of more or less isodiametric cells
rhizome   a horizontal stem, often underground or lying along the surface of the ground, bearing scalelike 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
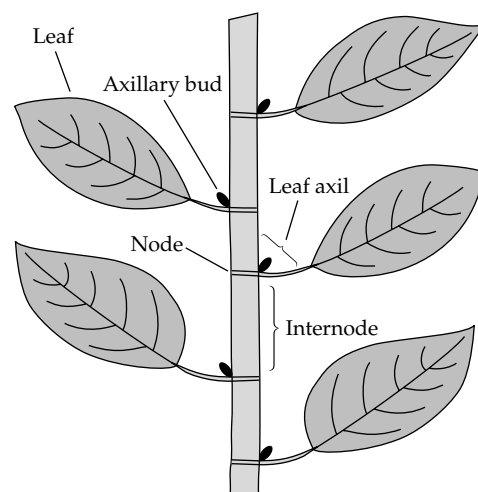
Figure 4.2   A generalized angiosperm stem showing nodes and internodes, leaves, leaf axils, and axillary buds.

scar   the remains of a point of attachment, as in leaf scar, stipule scar, bud-scale scar
short shoot   a stem with short 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

BUDS

Buds are short embryonic stems. They may be protected by bud scales (modified leaves), stipules, a dense covering of hairs, or a sticky secretion. In angiosperms they 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) and may also terminate the stem. They are especially useful for identifying twigs in winter condition. Some common terms pertaining to buds are listed below.

accessory bud   an extra bud (or buds) produced on either side of or above the 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 or stipules
pseudoterminal bud   an axillary bud that has taken over the function of a terminal bud (in sympodial shoots)
superposed bud   bud(s) located above the axillary bud
terminal bud   a bud at the apex of a stem (in monopodial shoots)

Figure 4.3   Parts of a generalized angiosperm leaf.
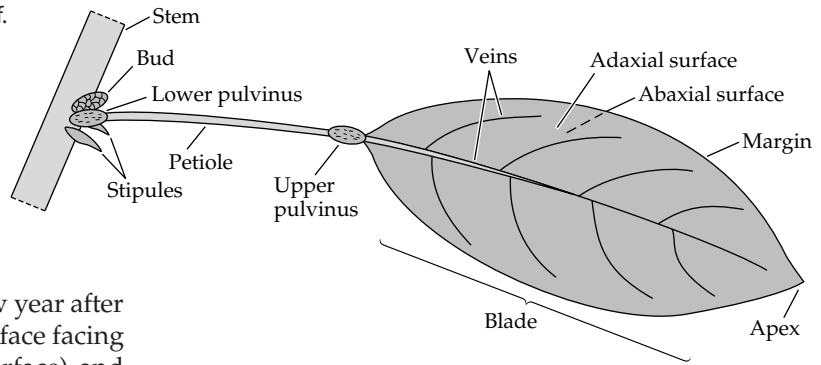
LEAVES

Leaves are the major photosynthetic parts of most plants. They are borne at the nodes of a stem, usually below a bud (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 (**adaxial** or upper surface) and another surface facing away from the stem axis (**abaxial** or lower surface). Most leaves are **bifacial,** having a definite adaxial and abaxial surface, but sometimes they are **unifacial** and lack such differentiation. Leaves are homologous structures among the angiosperms, but not among vascular plants as a whole (see Chapter 7). In addition to their obvious function in photosynthesis, leaves may be modified for protection (forming sharp-pointed structures called **spines**), water storage (as in many succulents), climbing (as in vines or lianas with tendril leaves), capturing insects (as in carnivorous plants), or providing homes for ants or mites (forming domatia, as 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 petiole is almost always broadly sheathing at the base, and taxa such as grasses (Poaceae) and gingers (Zingiberaceae) have an adaxial flap or **ligule** at the junction of the sheath and blade. A leaf that lacks a petiole is said to be **sessile**. A **lower pulvinus** is usually present and is involved in leaf movement; an **upper pulvinus** is sometimes present, as in prayer plants (Marantaceae).
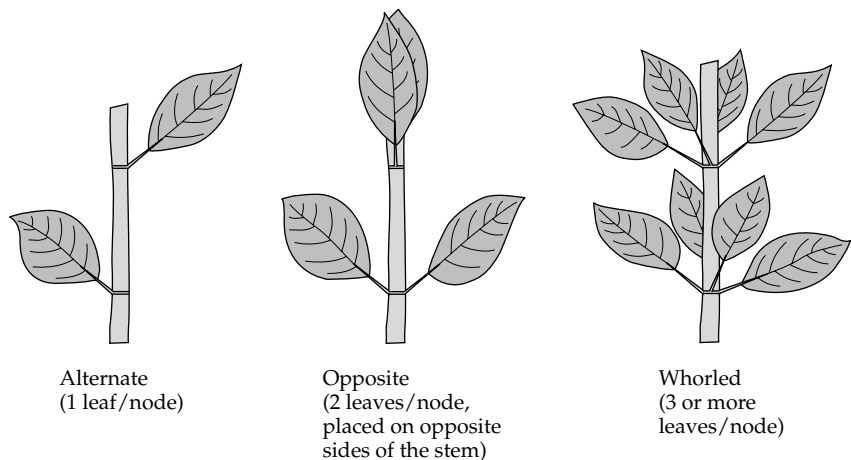
Stipules are usually paired appendages located on either side of (or on) the petiole base. Stipules are sometimes single, and are then borne between the petiole and stem. They may be leaflike, scale-like, tendril-like, spine-like, glandular, very reduced, or completely lacking. They have various functions, but most often help in protecting the young leaves. Stipules are not always homologous.
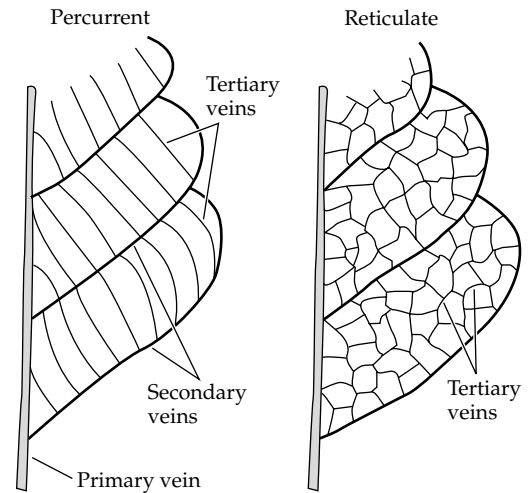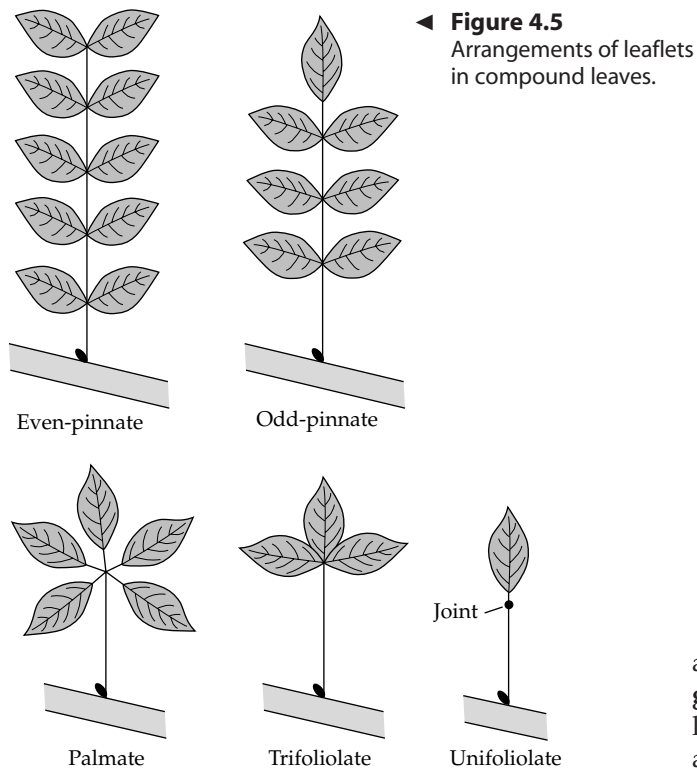
Leaf arrangement   Leaves may be arranged in one of three major patterns (Figure 4.4). **Alternate** leaves are borne singly and are usually arranged in a spiral pattern along the stem. Various kinds of spirals occur, and these can be evaluated by determining the angle around the stem between the points of insertion of any two suc-

cessive 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, 2-ranked, or **decussate** (the leaves of adjacent nodes rotated 90°); the last is the most common condition among temperate 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**, while a leaf with two or more blades (**leaflets**) is said to be **compound**. The distinction between simple and compound leaves may be made by locating an axillary bud, which is subtended by the entire leaf and not 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

Alternate
(1 leaf/node)

Opposite
(2 leaves/node,
placed on opposite
sides of the stem)

Whorled
(3 or more
leaves/node)

Figure 4.4   The three major patterns of leaf arrangement.

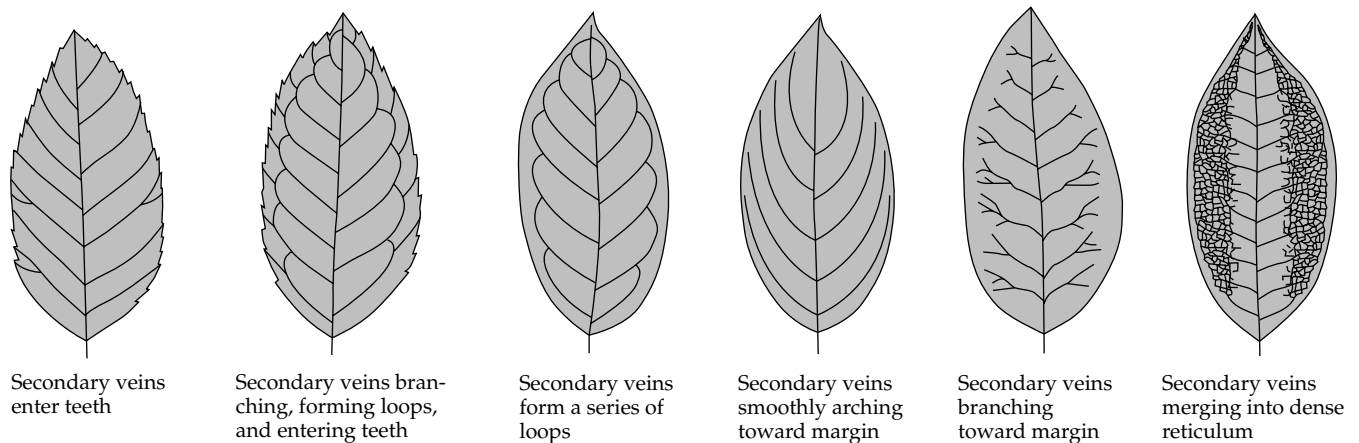◄ **Figure 4.5** Arrangements of leaflets in compound leaves.

Figure 4.6 Two patterns of tertiary veins.

abscised) at the end of the growing season, while **evergreen** plants are leafy throughout the year. Some leaves, such as those of many members of Fagaceae, are **marcescent**; they wither but do not fall off during the winter or dry season.
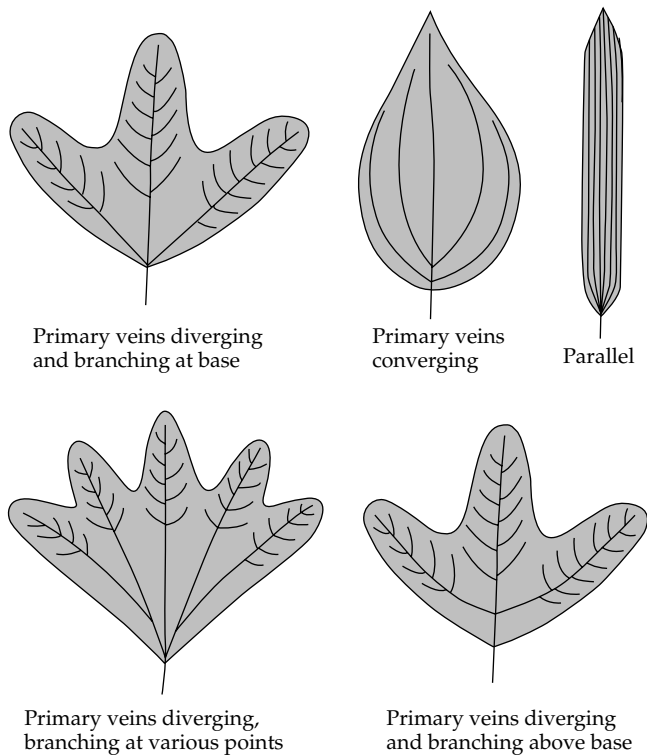
Venation types If there is one most prominent vein in a leaf, it is called the midvein or primary vein; branches from this vein are called secondary veins. Tertiary veins usually link the secondaries, forming a ladderlike (**percurrent**) or netlike (**reticulate**) pattern (Figure 4.6).

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 4.8)

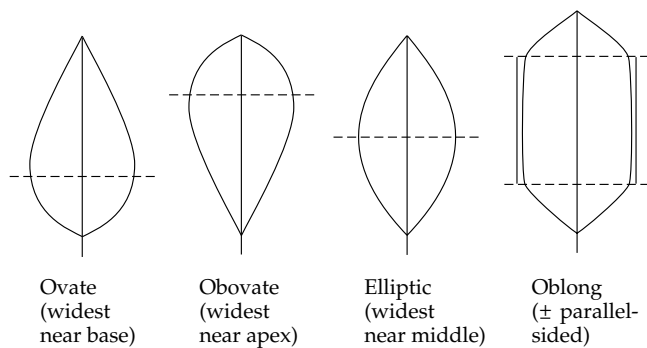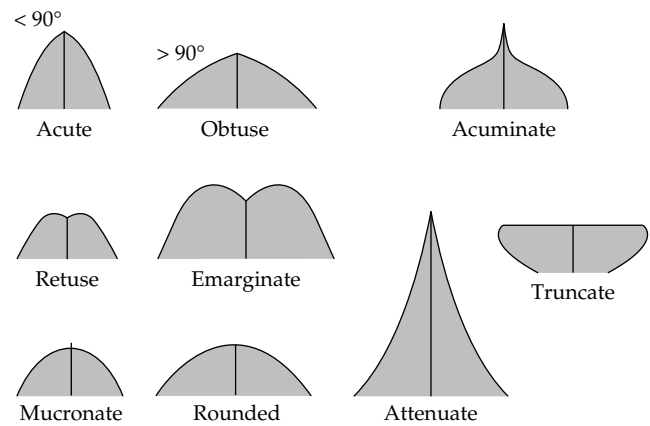**Figure 4.7** Some kinds of pinnate venation. (After Hickey 1975.)

Primary veins diverging and branching at base

Primary veins converging

Parallel

Primary veins diverging, branching at various points

Primary veins diverging and branching above base

Figure 4.8   Some kinds of palmate venation and parallel venation. (After Hickey 1973.)

< 90°   Acute

> 90°   Obtuse

Acuminate

Retuse

Emarginate

Truncate

Mucronate

Rounded

Attenuate

Figure 4.10   Leaf apex shapes.

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 4.8).

Leaf shapes   The leaf may be considered to have one of four major shapes (**ovate**, **obovate**, **elliptic**, **oblong**) depending upon where the blade is the widest (Figure 4.9; Hickey 1973). The meaning 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 so that the leaf and its stalk form an "umbrella," the leaf is termed **peltate**, and such leaves
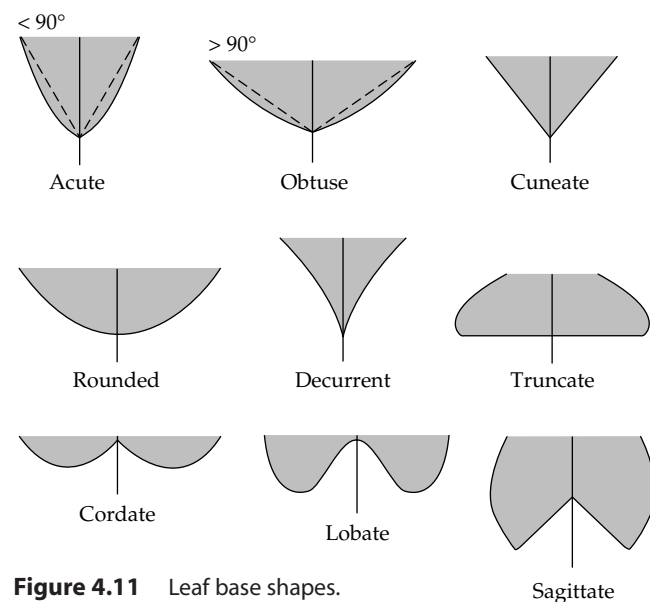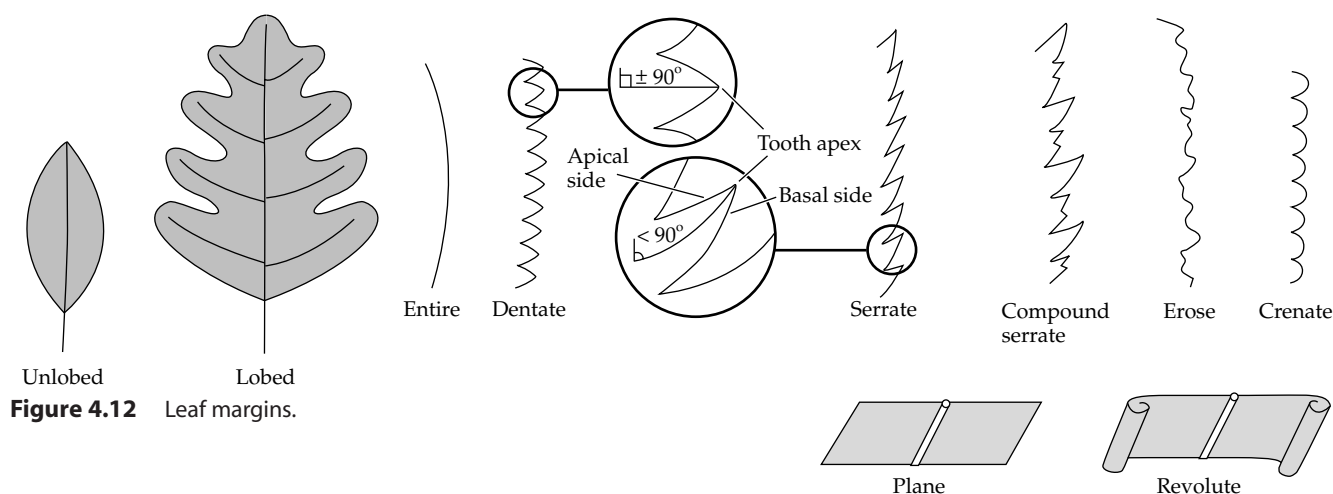
may be any of a number of different shapes. Various other specialized shape terms are sometimes employed, such as **linear** (for a long and very narrow leaf) or **scale-like** (for a very small leaf), but the use of such terms is avoided as much as possible here. The blade of a leaf may be symmetrical 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 shown in Figure 4.10; those relating to the shape of the leaf base are illustrated in Figure 4.11.

< 90°   Acute

> 90°   Obtuse

Cuneate

Rounded

Decurrent

Truncate

Cordate

Lobate

Sagittate

Figure 4.11   Leaf base shapes.

Ovate (widest near base)

Obovate (widest near apex)

Elliptic (widest near middle)

Oblong (± parallel-sided)

Figure 4.9   Leaf shapes.

Figure 4.12   Leaf margins.

Leaf margin   The leaf blade may be **lobed** or **unlobed**. These and other marginal conditions are illustrated in Figure 4.12. Various kinds of marginal teeth may be defined by using anatomic 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 8 (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, while **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 8 (in the discussion of particular families). A few ptyxis terms are illustrated in Figure 4.14 (see also Cullen 1978).

Indumentum   An **indumentum**, or covering of hairs (or trichomes), on the surface of an angiosperm gives that surface a particular texture. Most terms describing plant surfaces 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 below; we will not use them in this text, but, unfortunately, you may encounter them, as well as many others, in botanical keys and descriptions.

arachnoid   having a cobwebby appearance
canescent   gray hairy
hirsute   having long, often stiff, hairs
hispid   having stiff or rough hairs
lanate   woolly
pilose   having scattered, long, slender, soft hairs
puberulent   having minute, short hairs
scabrous   rough
sericeous   silky
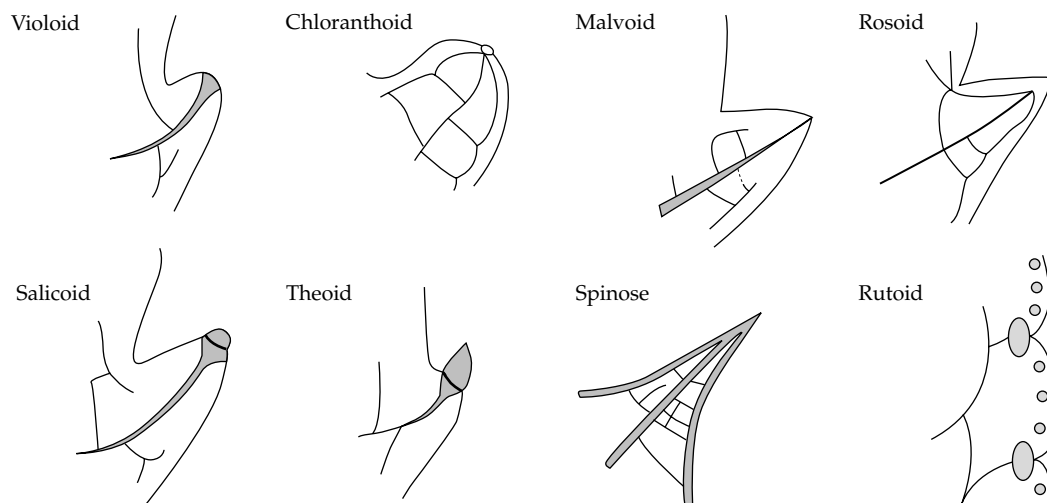
Figure 4.13   Some major tooth types.

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

Conduplicate   Reduplicate   Convolute   Plicate

Revolute   Involute   Circinate
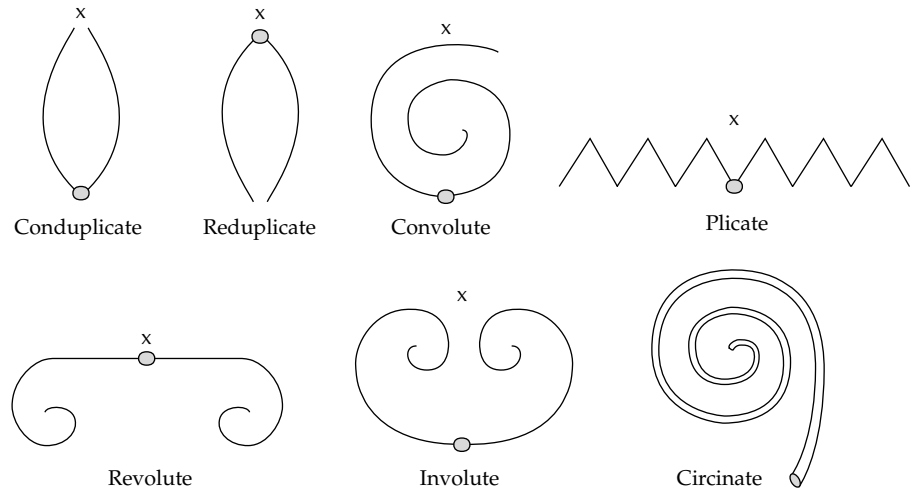
strigose   having stiff hairs, all pointing in one direction
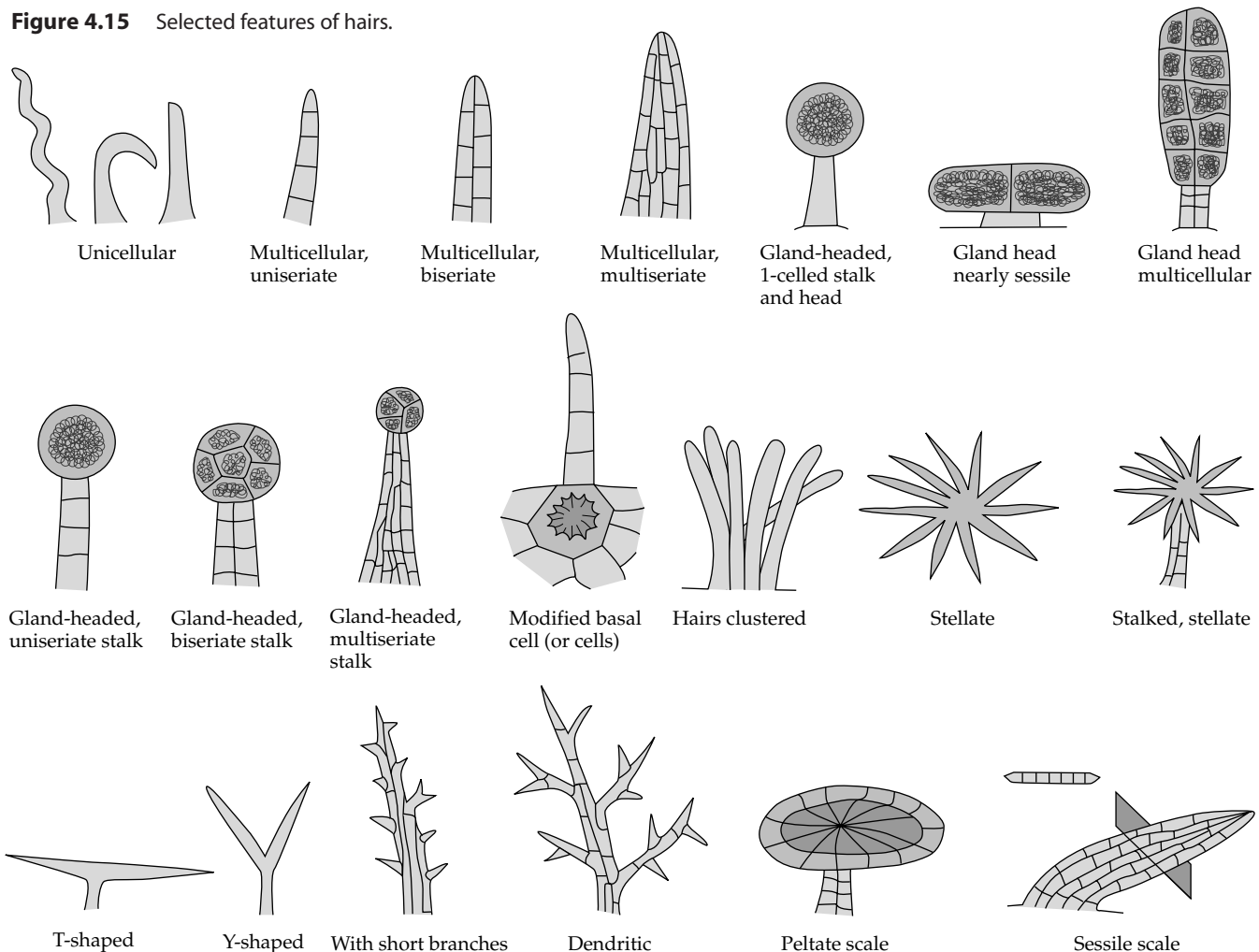**tomentose**   having densely matted soft hairs
velutinous   velvety
villous   covered with long, fine, soft hairs.

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

Figure 4.15   Selected features of hairs.

Unicellular   Multicellular, uniseriate   Multicellular, biseriate   Multicellular, multiseriate   Gland-headed, 1-celled stalk and head   Gland head nearly sessile   Gland head multicellular

Gland-headed, uniseriate stalk   Gland-headed, biseriate stalk   Gland-headed, multiseriate stalk   Modified basal cell (or cells)   Hairs clustered   Stellate   Stalked, stellate

T-shaped   Y-shaped   With short branches   Dendritic   Peltate scale   Sessile scale

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
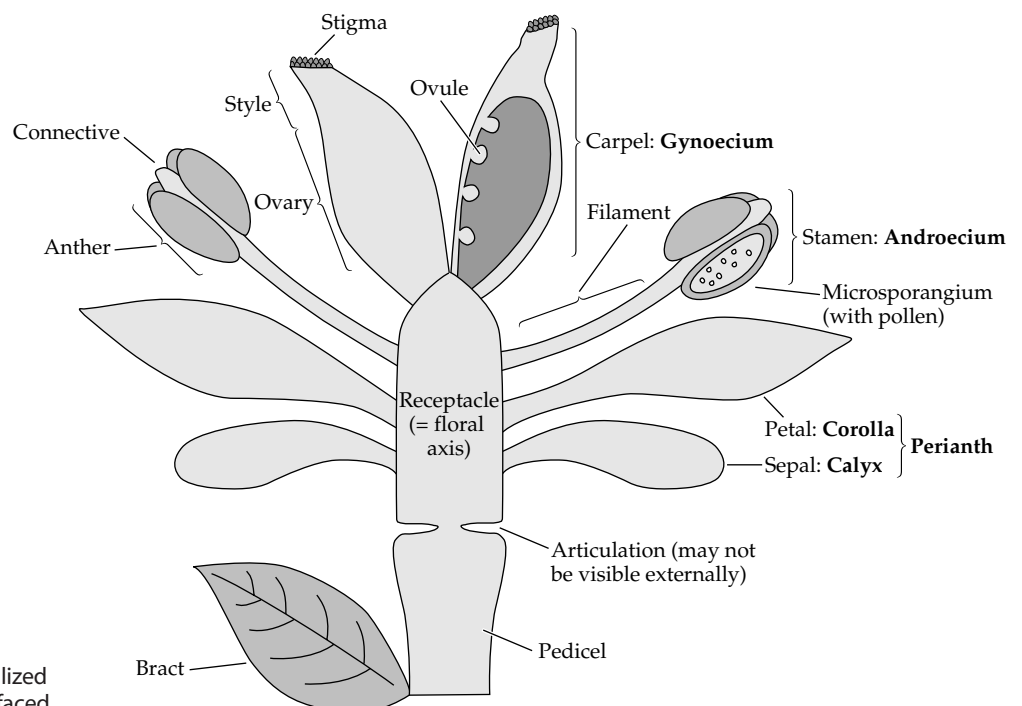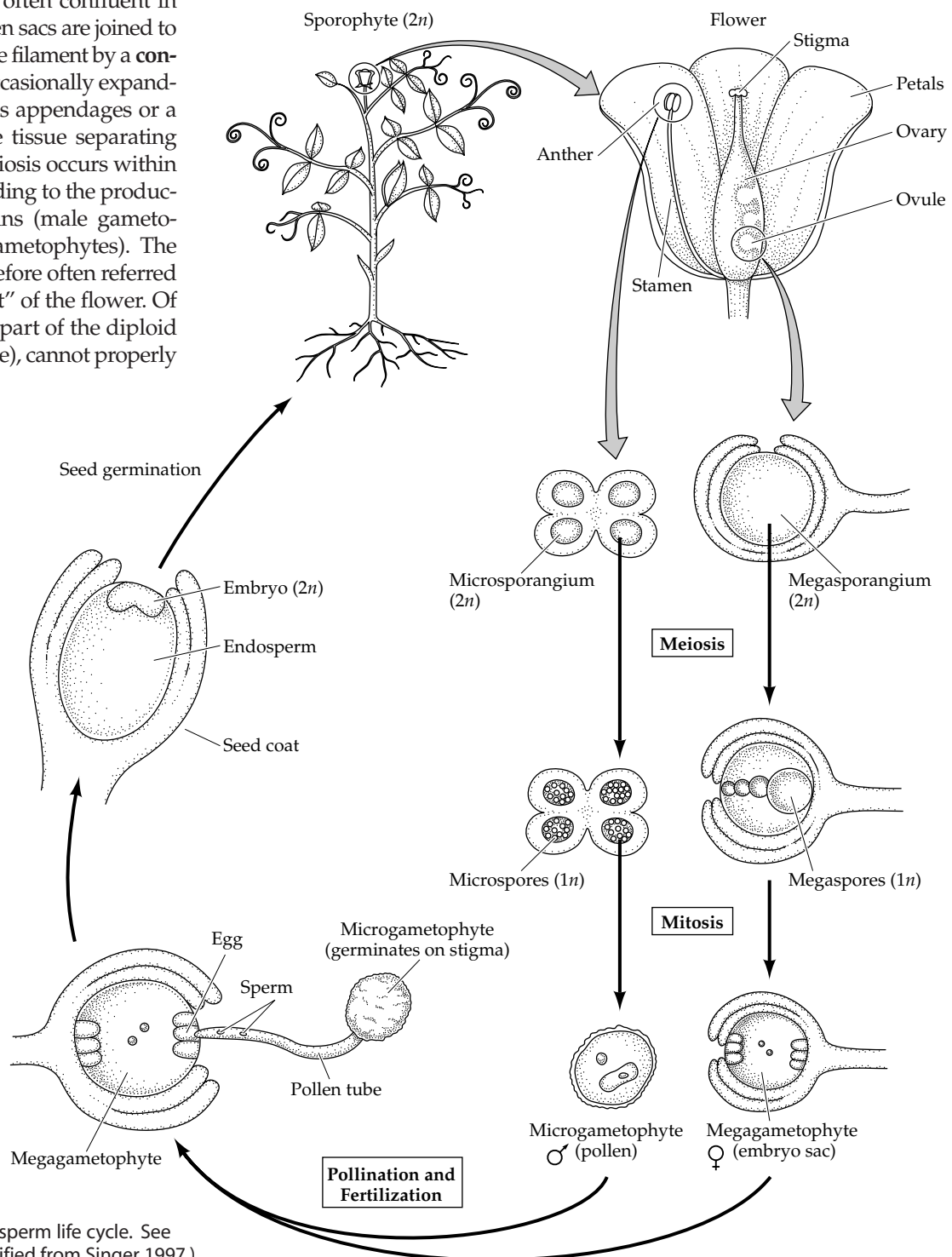

Figure 4.16   Parts of a generalized flower. Collective terms are boldfaced.
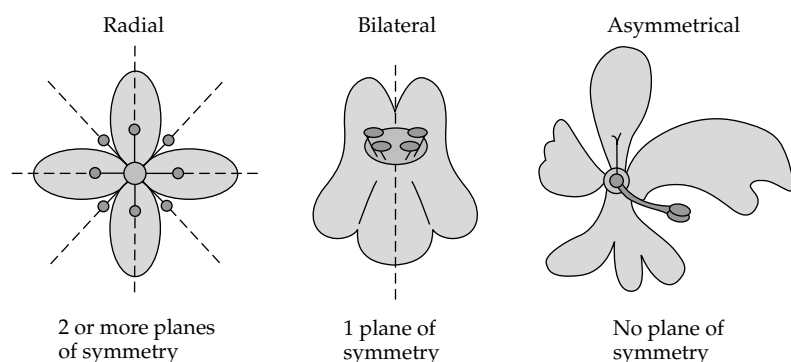
important to remember that although these perianth terms are useful in practical identification, they need to be used with caution in phylogenetic studies. Homology should not be assumed merely on the basis of a general similarity of form and function.

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.)

Radial   Bilateral   Asymmetrical

2 or more planes   1 plane of   No plane of
of symmetry   symmetry   symmetry

Figure 4.18   Patterns of floral symmetry.

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.
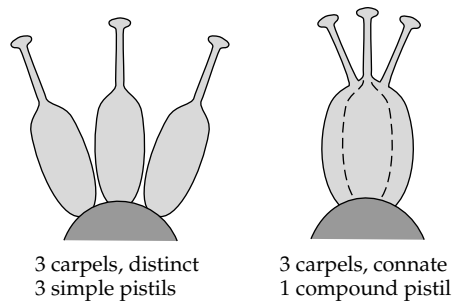
Fusion of floral parts   Floral parts may be fused together in various ways. Fusion of like parts (e.g., petals united to petals) is called **connation**. When like parts are not fused, they are said to be **distinct**. Fusion of unlike parts (e.g., stamens united to petals) is called **adnation;** the 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
syngenesious   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. How 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).

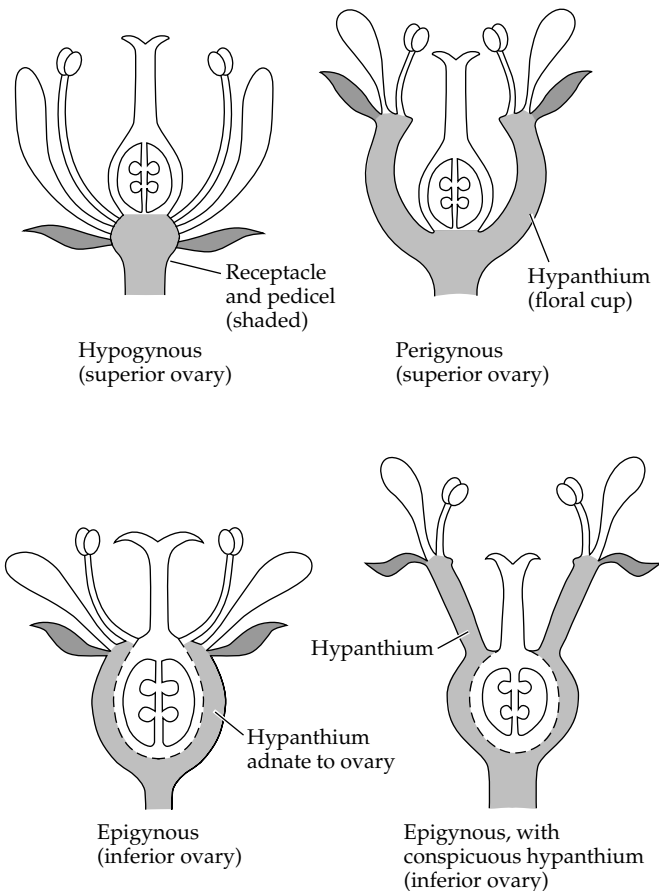***Number of parts***   Flowers differ in numbers of sepals, petals, stamens, and carpels. The number of parts is usually easily determined by counting, but extreme connation, especially of the carpels, may cause difficulties. Fused carpels often can be counted by using the number of styles, stigmas, or stigmatic lobes (Figure 4.20). Placentation (see below) may also be useful in determining carpel numbers.

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

3 carpels, distinct
3 simple pistils

3 carpels, connate
1 compound pistil

Receptacle
and pedicel
(shaded)

Hypanthium
(floral cup)

Hypogynous
(superior ovary)

Perigynous
(superior ovary)

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. 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

Hypanthium

Hypanthium
adnate to ovary

Epigynous
(inferior ovary)

Epigynous, with
conspicuous hypanthium
(inferior ovary)

Figure 4.21   Insertion types.

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 **placenta** (plural **placentae**) is the part of the ovary

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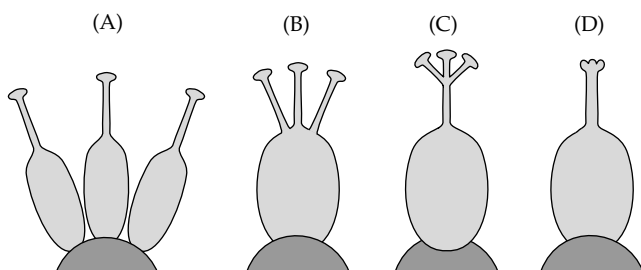
Figure 4.20   Three carpels, variously connate. (A) Three ovaries, styles, and stigmas. (B) One ovary, three styles and stigmas. (C) One ovary and style, the latter apically branched, and three stigmas. (D) One ovary and style, and three stigmas (or stigma lobes).

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:

$$*, 5, 5, \infty, \underline{10}$$

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 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:

$$\boxed{5}$$

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:

$$\boxed{4}, 2$$
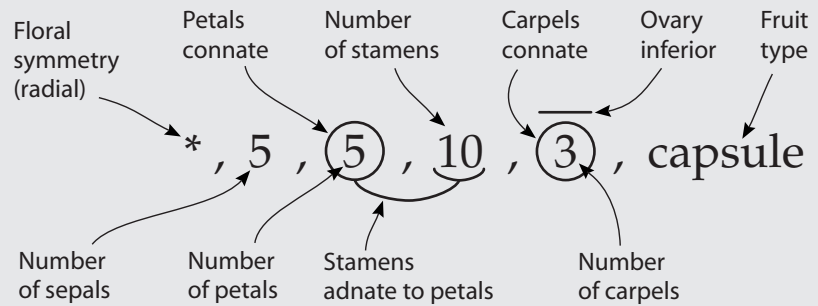
A sample floral formula.

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

$$X, \boxed{5}, \boxed{5}, \underline{10}, \underline{5}$$

Sterile stamens (staminodes) or sterile carpels (carpellodes or pistillodes) can be indicated by placing a dot by 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:

$$\boxed{5 + 5\bullet}$$

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

$$*, 4 - 5, 4 - 5, 8 - 10, \underline{3}$$

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:

$$*, 3, \boxed{3}, \underline{6}, \underline{1}$$

If a particular floral part is lacking, this is indicated by placing a zero (0) in the appropriate position in the floral formula. For example, the floral formula

$$*, 3, 3, 0, \underline{2}$$

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 indicated as:

$$*, -5-, 10, \underline{3}$$

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

$$*, -5-, 10, \underline{3}, \text{capsule}$$

A floral formula is by no means an end in itself; it is merely a convenient means of recording the information needed when identifying 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 8). 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 relationship 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).

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

basifixed   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 polli-
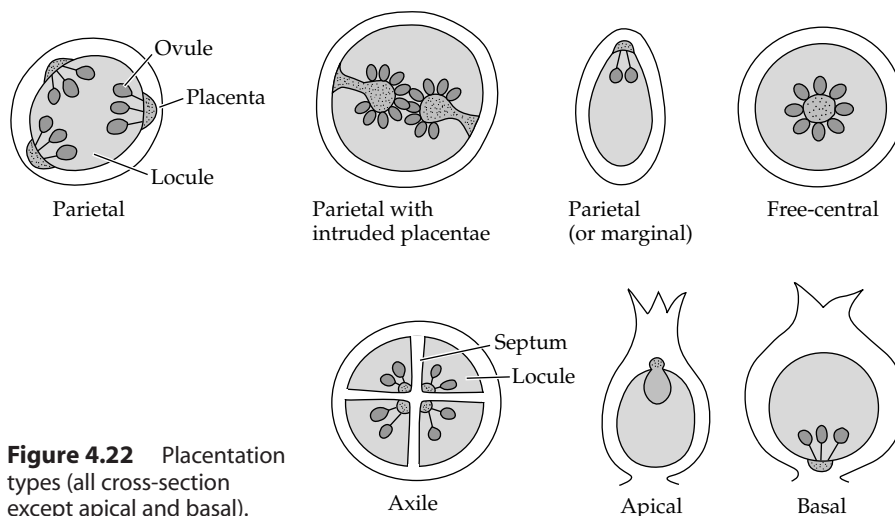
nation occurs largely via wind. Most flowering plants are animal-pollinated, although wind pollination predominates in some large and ecologically dominant families and occurs sporadically in many others. Water pollination is rare.

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 examples, illustrations of Betulaceae, Cyperaceae, 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

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

Parietal

Parietal with intruded placentae

Parietal (or marginal)

Free-central

Axile

Apical

Basal

Ovule
Placenta
Locule
Septum
Locule

the density of the pollen grain and make it float better. The pollen-receptive surface of conifers and wind-pollinated angiosperms is either a sticky or a netlike trap for airborne pollen.

Wind pollination is unusual in the tropics, especially in lowland rainforests. Temperate forests, in contrast, are dominated by wind-pollinated trees—oaks (*Quercus*, Fagaceae), beeches (*Fagus*, Fagaceae), chestnuts (*Castanea*, Fagaceae), hickories (*Carya*, Juglandaceae), walnuts (*Juglans*, Juglandaceae), and birches (*Betula*, Betulaceae) in the Northern Hemisphere and southern beeches (*Nothofagus*, Nothofagaceae) in the Southern Hemisphere. Pollen shed in wind-pollinated temperate species occurs at the beginning of the growing season, before or as leaves develop. A leafless forest has fewer obstacles to interrupt pollen flow. Pollen shed is also timed to avoid high humidity, which prevents drying out of the pollen and therefore reduces its buoyancy, and rain, which carries pollen down out of the air currents.

Corn (*Zea mays*, Poaceae) illustrates another common feature of wind pollination: unisexual flowers. The pollen is borne in staminate flowers in the corn "tassel," at the top of the plant, and the stigmas are the familiar "silk" that emerges, plumelike, from the top of the ear. Many people are unhappily aware of wind pollination from hay fever, an allergic reaction to proteins in the exterior pollen wall of some wind-pollinated species such as ragweed (*Ambrosia*, Asteraceae).

Water pollination is limited to about 150 species in 31 genera and 11 families (Cox 1988). Almost half are marine or grow in brackish water, and 9 of the families are monocots. Pollen may be transported above, on, or below the water surface. Plants that pollinate underwater often have filamentous or eel-shaped pollen borne in mucilaginous strands. One of the longest known and most fascinating examples of water pollination is *Vallisneria* (Hydrocharitaceae). In this genus, plants grow submersed. Their staminate flowers are released from the plant and float to the water surface, where they open and float about. At the same time, carpellate flowers rise to the surface on long peduncles and create a slight depression in the water surface, into which staminate flowers fall and are captured. Pollination follows this capture.

Animal pollination   Animal pollination is thought to be an important factor in the evolutionary success of angiosperms. Animals are often more efficient transporters of pollen than wind, can be found where there is little wind (such as within a dense tropical forest), and promote cross-pollination by moving between plants. Animal pollination has driven diversification in many groups, and evolution associated with pollination is nowhere more evident than in the Orchidaceae, as we shall see below. This family contains more species than any other, apparently due to floral reproductive isolation.

We are all familiar with bees buzzing about brightly colored flowers on warm summer days. In an apple orchard, bees fly from flower to flower, collecting pollen in special pollen baskets on their legs and drinking the flowers' sugary nectar. Back at their hive, the bees convert the nectar into honey and feed their young the protein-rich pollen. In return for these rich rewards, the bees pollinate the apple flowers. As a bee drinks nectar and collects pollen, some pollen becomes stuck to its body hairs. That pollen is removed from its body by the stigmas of the next flower it visits. Without bees, there would be no or few fruits.

In essence, bees and apples have a contract: apples are pollinated, and bees are rewarded with nectar and pollen. A plant's part of this contract consists of adaptations to attract pollinators, exploit their morphology and behavior to effect pollination, and ensure that they will return to its flowers by rewarding them. Many, though not all, flowers pollinated by one of the major kinds of animal pollinators have characteristic suites of floral adaptations (Table 4.1).

Flowers attract their pollinators with color and scent. Insects do not see the same spectrum of light that we do; they are less sensitive to red and able to see shorter wavelengths, down into the ultraviolet. Bee-pollinated flowers often have ultraviolet-reflecting or absorbing patterns that attract the insects to the flower and then direct them to the nectar. Flowers open and emit scents when their pollinators are active. Moths and bats, for example, are active at night. The flowers they visit are white and emit their scents at night, and are therefore easier to locate in the darkness.

Flowers are built to fit their pollinators physically and to provide an appropriate reward. The corollas of many bee-pollinated flowers have nectar guides, lines or marks that direct bees to the nectar source. The corolla may form a landing platform that orients pollinators toward the nectar and/or pollen and forces them to perform the movements required for pollination. The pollen of many animal-pollinated flowers is covered with minute projections that stick to animal hair or feathers (see Figure 4.47 E–H). Bees consume both nectar and pollen, while butterflies, moths, and birds are rewarded by nectar alone. In some cases pollinators are not rewarded, but rather deceived into pollinating a flower, as we shall see below.

Plant species may specialize for one pollinator or may be served by a wide range of pollinators; the latter species are called **generalists**. *Acer saccharum* (sugar maple, Sapindaceae), for example, is both wind- and animal-pollinated.

COEVOLUTION BETWEEN PLANT AND POLLINATOR

One of the most fascinating cases of pollination is that of the yucca (*Yucca*, Agavaceae) and the yucca moth (*Tegiticula*). The white yucca flowers open at night and attract the female yucca moth. Once inside the flower, the moth pollinates it. She carries pollen from another yucca plant

TABLE 4.1 *Floral pollination syndromes.*

Pollinator	Floral characteristics				
	Color	Scent	Time of flowering	Corolla	Reward
Bee	Blue, yellow, purple	Fresh, strong	Day	Bilateral landing platform	Nectar and/or pollen
Butterfly	Bright; often red	Fresh, weak	Day	Landing platform; sometimes nectar spurs	Nectar only
Moth	White or pale	Sweet, strong	Night or dusk	Dissected; sometimes nectar spurs	Nectar only
Fly (reward)	Light	Faint	Day	Radial, shallow	Nectar and/or pollen
Fly (carrion)	Brownish, purplish	Rotten, strong	Day or night	Enclosed or open	None
Beetle	Often green or white	Various, strong	Day or night	Enclosed or open	Nectar and/or pollen
Bird	Bright; often red	None	Day	Tubular or pendant; ovary often inferior	Nectar only
Bat	Whitish	Musky, strong	Night	Showy flower or inflorescence	Nectar and/or pollen

in special tentacles under her head, and she stuffs this pollen into the stigmatic cavity (Figure 4.23). She then uses her ovipositor to penetrate the ovary wall and lay eggs among the ovules. Finally, just prior to leaving the flower, she climbs the filament, stabilizes herself by laying her tongue over the top of the filament, and collects pollen with her tentacles. She takes no food from the flower, as adult yucca moths do not eat; all consumption in the species is by the larvae. The moth eggs hatch inside the fruit at about the time the seeds ripen, and the larvae consume some, but not all, of the developing seeds. When they have eaten enough, the larvae bore out of the fruit, fall to the ground, and burrow into the ground to overwinter as pupae.

Coevolution is evident in the adaptations of yucca and moth that facilitate pollination. The plant produces stout, club-shaped filaments that the moth can easily climb to collect pollen. The anthers are positioned on top of the filament where they are readily accessible to the moth. Her tentacles are an adaptation for collecting and transporting pollen and placing it in stigmatic cavities. The moth's pollination behavior ensures a food supply for her young as well as reproduction by the plant that her species absolutely depends upon.

Another tight coevolutionary relationship exists between figs (*Ficus*, Moraceae) and their fig wasp pollinators. Like the *Yucca* and its moth, figs and wasps are completely dependent upon each other. There are about 750 species of figs, each with its own species of fig wasp pollinator.

DECEPTION IN ORCHID POLLINATION

Of the 19,500 species of orchids, about 8000 offer no food reward to their pollinators. Instead, they deceive their pollinators into pollinating them. Some orchids, like some species in other families, bear flowers that resemble rotting flesh in their scent and purplish color. These flowers, which are called carrion flowers (see Table 4.1), attract flies that lay their eggs in the flower because they are tricked by its odor and color into perceiving it as a source of food for their offspring. In the process of laying eggs, the fly moves within the flower and pollinates it.

Far more bizarre methods of trickery have evolved in some tropical orchids. Many New World tropical orchids are pollinated by male euglossine bees. After emerging from the nest, male euglossines fly through the forest, feeding on the nectar from various flowers and sleeping on the underside of a leaf or in a tubular flower. They are strongly attracted by the fragrant chemicals of certain orchids that do not produce nectar. They scratch at the source of the odor, and in the process of transferring the chemicals to their hind tibiae, involuntarily follow a path in the flower that leads to pollination. In some species of the orchid genera *Gongora* and *Stanhopia*, the bee is
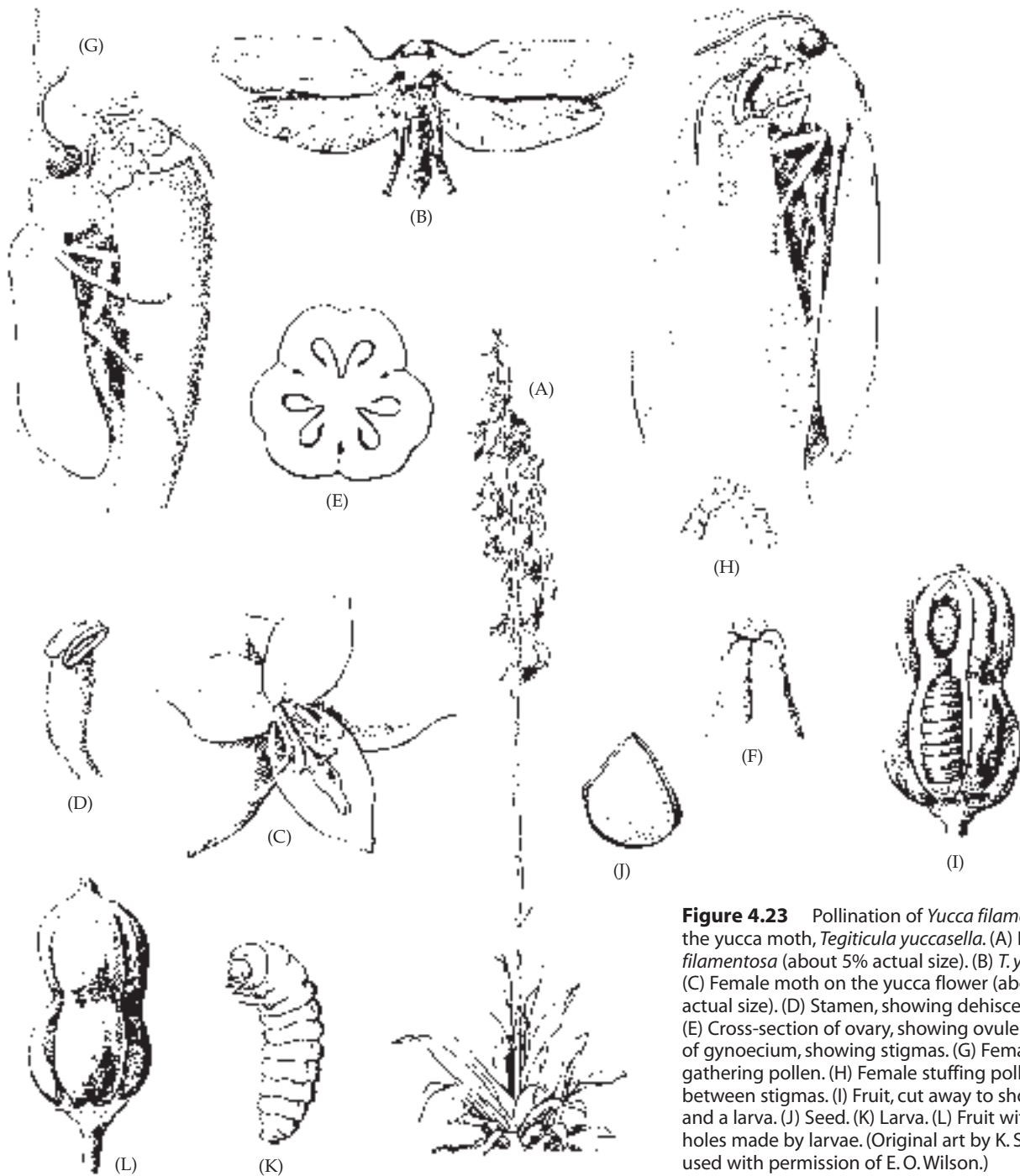
Figure 4.23   Pollination of *Yucca filamentosa* by the yucca moth, *Tegiticula yuccasella*. (A) Habit of *Y. filamentosa* (about 5% actual size). (B) *T. yuccasella*. (C) Female moth on the yucca flower (about 75% actual size). (D) Stamen, showing dehisced anther. (E) Cross-section of ovary, showing ovules. (F) Apex of gynoecium, showing stigmas. (G) Female moth gathering pollen. (H) Female stuffing pollen between stigmas. (I) Fruit, cut away to show seeds and a larva. (J) Seed. (K) Larva. (L) Fruit with exit holes made by larvae. (Original art by K. S. Velmure; used with permission of E. O. Wilson.)

turned upside down and slides down the flower in such a way that it picks up the pollinium (Figure 4.24; see the discussion of Orchidaceae in Chapter 8 for a description of the pollinium). The bee flies to another flower of the same species and eventually slides past the stigma, where the pollinium is deposited. The male euglossines use the floral fragrances they gather to attract females.

We see another example of orchid pollination deception in Chapter 6, in the flowers of *Ophrys* (Orchidaceae), which trigger mating behavior in male bees and wasps and provide no food reward. The Orchidaceae are an encyclopedia of pollination syndromes. In addition to pseudocopulating bees and wasps, carrion flies, and euglossine bees, orchid species are pollinated by beetles, bugs, moths, butterflies, mosquitoes, and birds.

SELF-INCOMPATIBILITY

Pollination may occur within an individual (**self-pollination** or **selfing**) or between individuals (**cross-pollination**). It has long been known (Darwin 1876) that many plants avoid self-pollination and thus the possible harmful consequences of inbreeding depression. Such avoid-
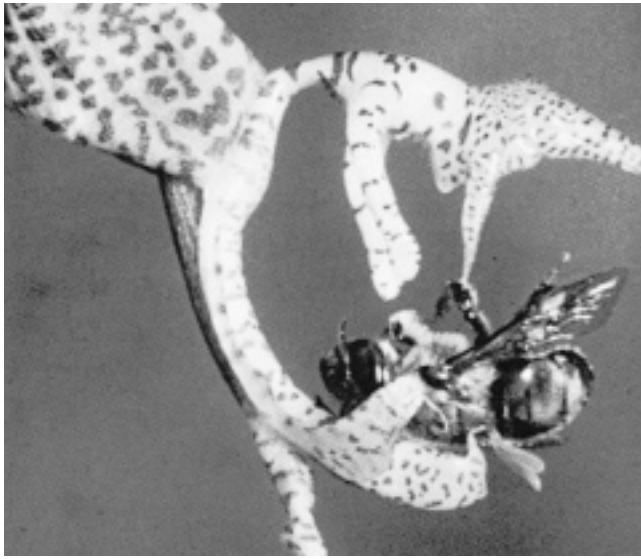
Figure 4.24   Male *Euglossa hemichlora* falling and sliding through the flower of *Gongora grossa*. In this posed photograph, the pollinia are attached to the bee as it slides past the apex of the column. (From Van der Pijl and Dodson 1966.)

ance may be achieved by separating female and male gametes in space or time. Spatial separation may be through dioecy or monoecy. To achieve temporal separation, the stigmas may be receptive before the pollen is shed in a bisexual flower or monoecious individual (**protogyny**), or the anthers may shed pollen before the stigmas are receptive (**protandry**). The arrangement of stamens and stigmas and the movement of pollinators may also limit selfing.

Another mechanism for avoiding self-pollination is **self-incompatibility**, the inability of a bisexual plant to produce zygotes with its own pollen. Self-incompatibility is genetically controlled in many species by multiple alleles of a gene labeled simply *S*. Even though a diploid individual has only two of these alleles, there may be hundreds of other alleles in other individuals of the species. If a pollen grain has the same *S* allele as the carpellate plant, then mating will not be successful. Self-fertilization therefore will not occur, but with many different *S* genotypes possible, most matings with other individuals will be at least partially successful. Note that this mechanism will prevent not only selfing, but also matings between individuals that happen to have the same *S* alleles, regardless of how genetically different they are otherwise.

Monomorphic self-incompatibility   In **monomorphic self-incompatibility**, there are no morphological differences between the flowers of incompatible individuals. Monomorphic self-incompatibility may be gametophytic or sporophytic. In **gametophytic self-incompatibility**, the genotype of the pollen determines what matings will be successful. If two individ-

uals have the same two self-incompatibility alleles, then no pollinations between them will be successful (Figure 4.25). If one or both self-incompatibility alleles differ, however, then some or all matings will produce zygotes. The genetic difference between pollen parent and potential ovulate parent is most often recognized within the style, where the pollen tube with a matching self-incompatibility allele simply stops growing.

In **sporophytic self-incompatibility**, the sporophyte genotype determines the fate of pollen grains. This form of self-incompatibility occurs in the Asteraceae and the Brassicaceae and a small number of other families, and is not as widespread as gametophytic self-incompatibility.

Heterostyly   **Heterostyly**, or **heteromorphic self-incompatibility**, is a sporophytic self-incompatibility system that also involves floral morphological differences. The existence of two kinds of flowers in *Primula* (Primulaceae) was recognized long ago. One kind of flower has a long style and short stamens and is called **pin**, due to the resemblance of the long style to a pin. The other kind has a short style and long stamens that project out of the top of the corolla tube. This morph is called **thrum**, referring to the resemblance of the stamens to pieces of thread coming out of the end of a shirtsleeve (Figure 4.26A). Darwin (1877) demonstrated that this heteromorphy is associated with self-incompatibility: only pollinations between different morphs are successful. The heteromorphism is governed by a supergene, a series of genes closely spaced or linked on a chromosome. Thrum individuals are heterozygous (*Ss*) and pins are homozygous recessive (*ss*), so that the cross pin × thrum gives equal numbers of thrum and pin offspring.

Heterostyly is relatively infrequent. It is known from 24 families and is especially common in the Rubiaceae, where it has been documented in about 90 genera. It
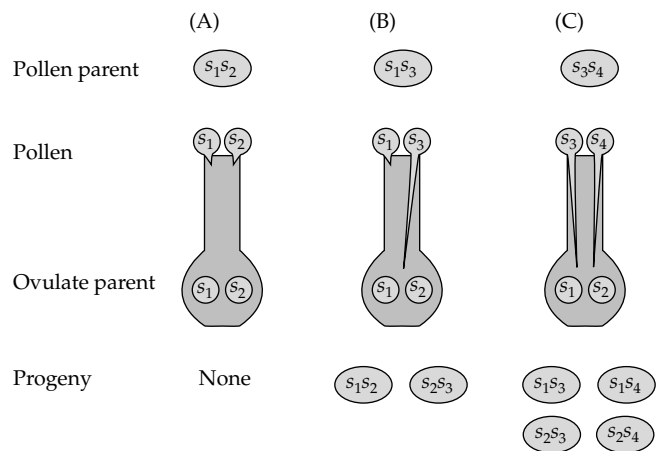
Figure 4.25   The consequences of a gametophytic self-incompatibility system on the production of progeny and the genetic variability of those progeny. (After Lewis 1949.)

(A)

Pin

Thrum

(B)

Long

Mid

Short
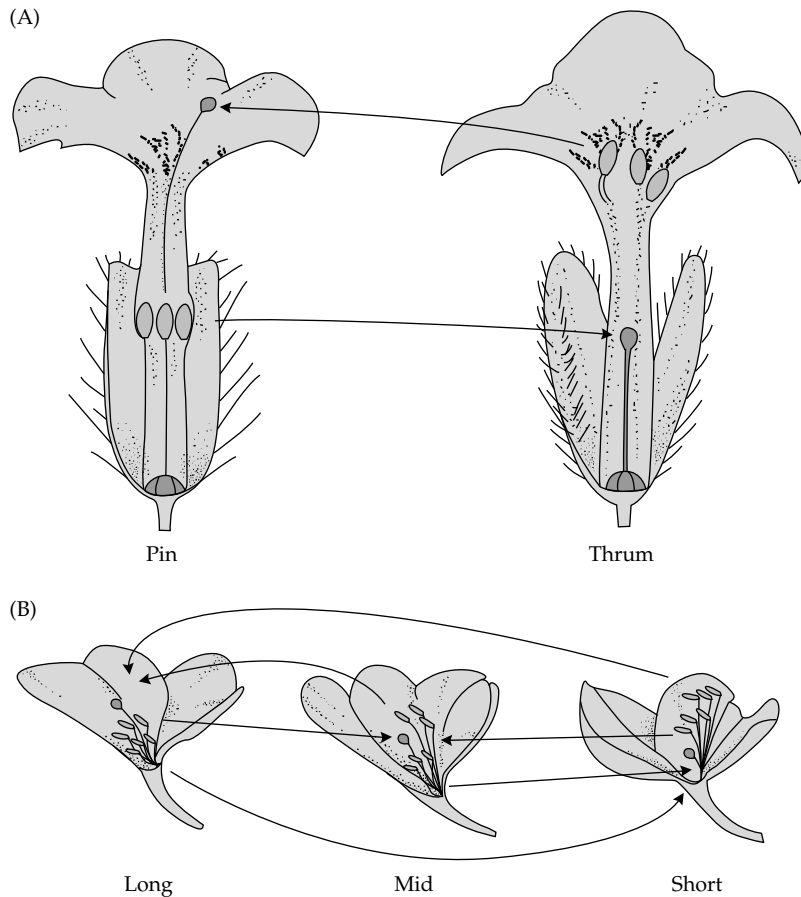
Figure 4.26 Heterostyly. (A) Reciprocal anther and stigma positions in pin and thrum morphs of a distylous plant. (B) The three forms of a tristylous plant. Anthers and stigma are positioned at three levels. The arrows indicate the directions of compatible pollinations. (After Ganders 1979.)

is important in routine identification as well as the determination of phylogenetic relationships. Inflorescence categories have often been confused, however, due to the arbitrary separation of flower-bearing and vegetative regions of the plant (see 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, while 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). In determinate inflorescences, the flowering sequence 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 have been described, based on their pattern of branching.

One of the more common types of determinate inflorescence 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 due to differences in their branching patterns. If the inflorescence
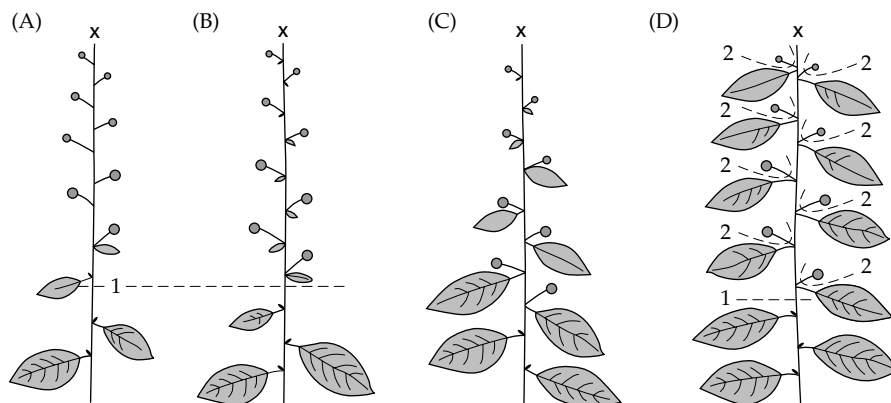
may be expressed as either two (distyly, Figure 4.26A) or three (tristyly) floral morphs (Figure 4.26B). Distyly, as in *Primula* and many Rubiaceae, is far more common than tristyly, which is known only from three families (Lythraceae, Oxalidaceae, and Pontederiaceae).

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). The arrangement of flowers on a plant (the inflorescence form and position)

(A) (B) (C) (D)

Figure 4.27 Inflorescences (in this case, racemes) with various types of subtending leaves or bracts. (A) Ebracteate raceme. (B) Bracteate raceme. (C) Leafy-bracted raceme. (D) Leafy raceme. Ebracteate and bracteate forms are frequently called terminal racemes due to the arbitrary delimitation of inflorescences from vegetative region at 1. Leafy racemes (D) are often considered to have solitary, axillary flowers due to the arbitrary delimitation of inflorescences from vegetative region at 2.

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

Determinate
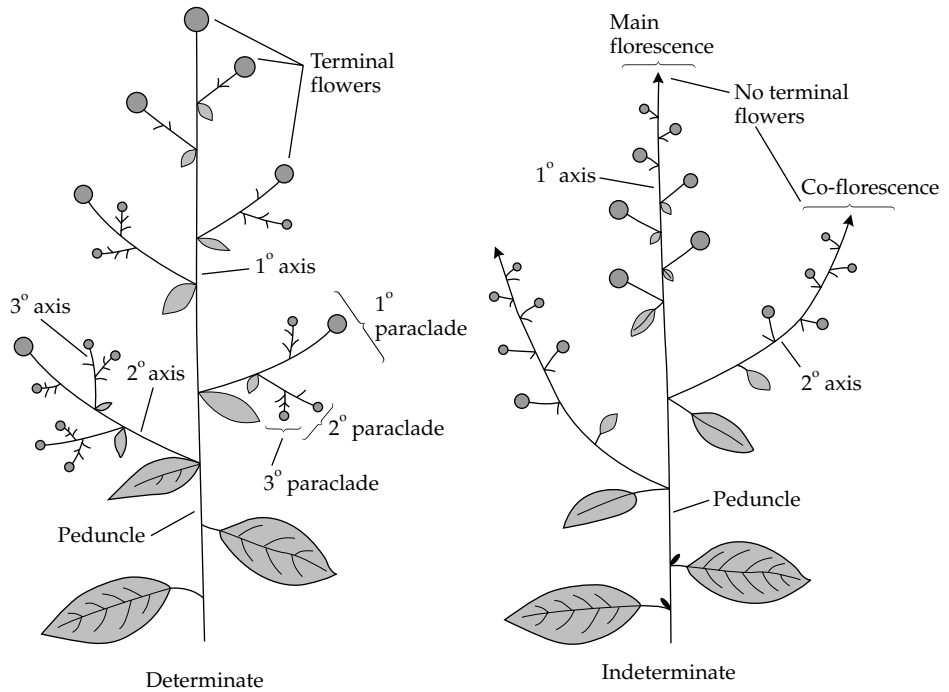
Indeterminate

Figure 4.29 Some common kinds of determinate inflorescences. The circles represent flowers; their size indicates the sequence of opening.

Cyme (= determinate thyrse)

Panicle-like cyme (= panicle of Weberling)

Raceme-like cyme

Elongated cyme

Helicoid cyme

Scorpioid cyme

Head (= capitulum)

Umbel
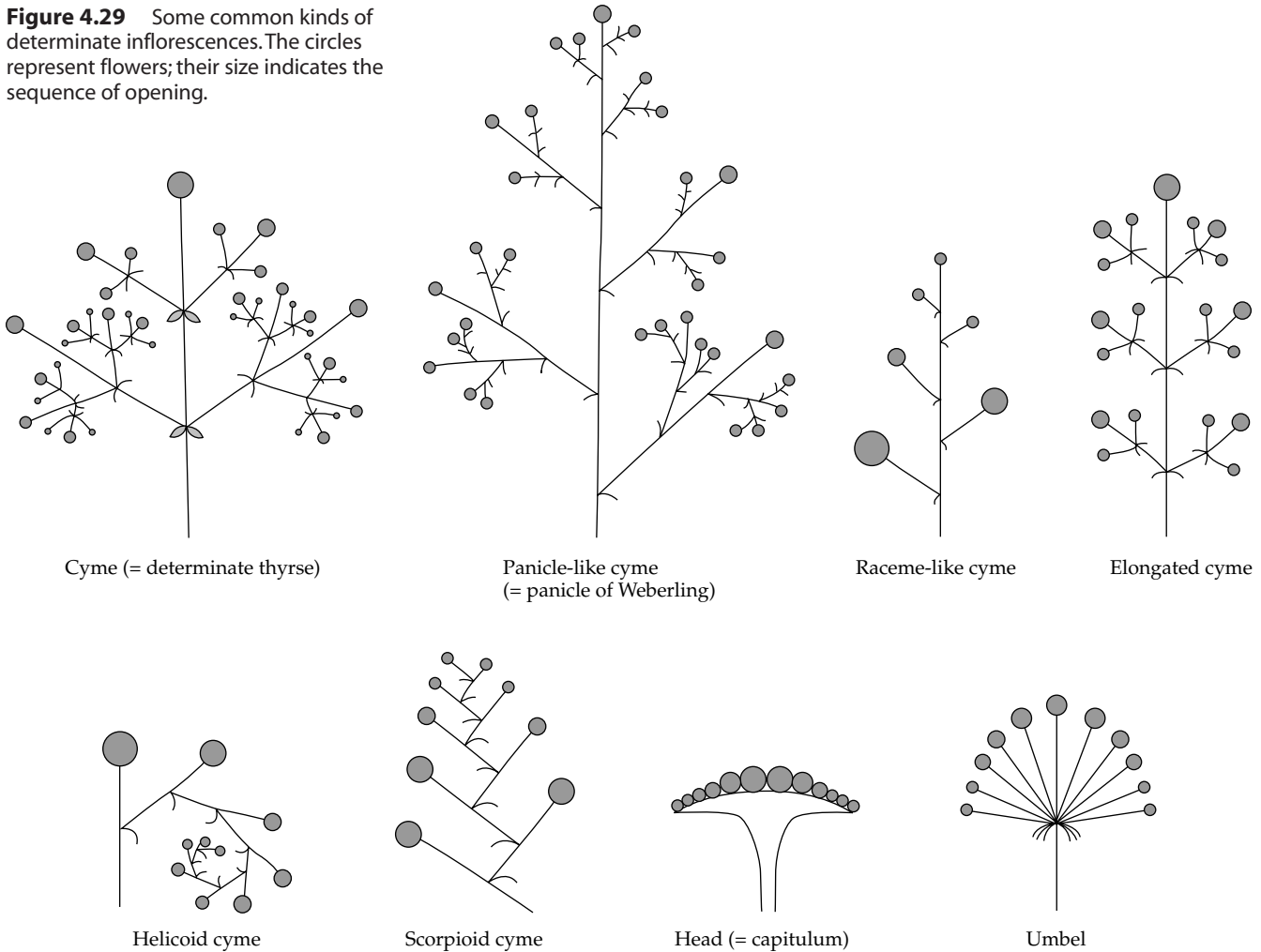
branches are monopodial (producing several internodes before ending in a terminal flower), a **panicle-like cyme** results, and through reduction a **raceme-like cyme** is formed. The paraclades (lateral branches) of typical cymes or panicle-like cymes may be either alternately or oppositely arranged. **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 (i.e., 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. Axillary racemes or cymes can become reduced in length, resulting in a **fascicle**. 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).
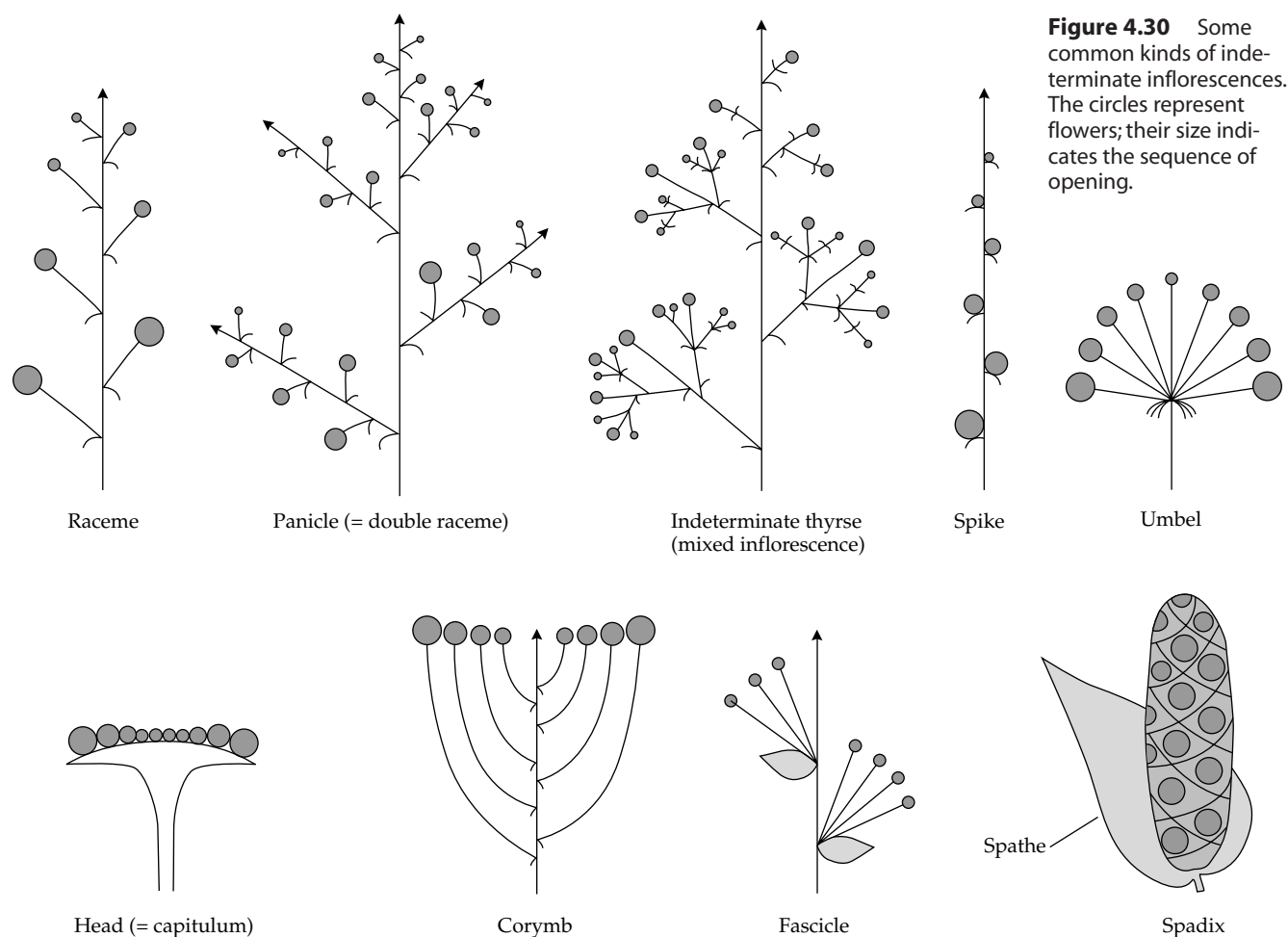
A **head**, or **capitulum**, is a dense terminal cluster of sessile flowers. This inflorescence type can result through aggregation of the flowers of either an indeterminate or determinate inflorescence. In an indeterminate head, the peripheral flowers open first, while in a determinate head the central flowers open first. An **umbel** is an inflorescence in which all the flowers 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), while **compound inflorescences** (e.g., double racemes, double umbels, cymes, thyrses, and panicles) have two or more orders of branches.

The term **ament** (or catkin) is used for any elongated inflorescence composed of numerous inconspicuous, usually wind-pollinated flowers. This term is unspecific in regard to order of branching and floral arrangement, and aments may be either simple or compound, and 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

Figure 4.30 Some common kinds of indeterminate inflorescences. The circles represent flowers; their size indicates the sequence of opening.

Raceme

Panicle (= double raceme)

Indeterminate thyrse (mixed inflorescence)

Spike

Umbel

Head (= capitulum)

Corymb

Fascicle

Spadix

Spathe

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, 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 systema-

tists, and many different fruit types have been proposed. All systems of fruit classification must deal with several difficulties. The problem of the bewildering and often continuous variation in fruit structure is the foremost; 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 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

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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 . . . . **Berry**
6. Outer part of fruit ± soft 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)**

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 carpel and ovule number. **Simple fruits** (those resulting from a single flower) are divided into two categories: first, those formed from a single carpel or several fused carpels, and second, 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 following list. 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 be of any of the basic fruit types outlined below. 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 capsule) is encouraged. This classification is presented by means of a key to a series of definitions. Although this system is admittedly

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 by pores or flaps (often near the top) . . . . **Poricidal capsule**

21. Fruit opening by a series of apical teeth . . . . **Denticidal capsule**

21. Fruit opening longitudinally or irregularly 22

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**

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 8.13, 8.51, 8.72, and 8.129.)

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 8.37, 8.41, 8.43, 8.45, 8.90, 8.97, and 8.109.)

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, Euononymous, Hibiscus, Hypericum, Ipomoea, Justicia, Lachnanthes, Lagerstroemia, Lecythis, Lyonia, Momordica, Oxalis, Papaver, Portulaca, Rhododendron, Swietenia, Triodanis, Viola*. (See Figures 8.26, 8.44, 8.48, 8.54, 8.62, 8.64, 8.98, 8.104, 8.105, 8.116, and 8.119.)

caryopsis (= 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 8.30 and 8.31.)

dehiscent drupe   a fruit with a dry/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 8.87.)

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 8.38, 8.74, 8.86, 8.102, 8.115, and 8.122.)

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 8.40, 8.53, 8.113, and 8.114.)

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 8.66, 8.67, and 8.68.)

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 8.82.)

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 8.73.)

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 8.77 and 8.84.)

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, achene-like, drupelike, etc. Examples: *Acer, Apium, Cephalanthus, Croton, Daucus, Diodia, Erodium, Euphorbia, Glandularia, Gouania, Heliconia, Heliotropium, Lamium, Lycopus, Malva, Ochna, Oxypolis, Salvia, Sida, Verbena*. (See Figures 8.58, 8.59, 8.101, 8.112, 8.120, and 8.124.) Fruits that show late-developmental fusion of their apical parts are not considered schizocarps, e.g., *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 8.92.)

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 8.47.)

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 below). 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 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** develops from the outer integument and the **tegmen** 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 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 is sometimes colorful and fleshy. 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. 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**, at the point where it was attached to the funiculus.

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; or hair tufts on the fruits, as in *Anemone* (Ranunculaceae), which has an achene with a persistent style bearing elongated hairs; (3) a winglike perianth, as in *Dipterocarpus* (Dipterocarpaceae), which has nuts associated with elongated, winglike sepals, (4) association of the infructescence (mature inflorescence, with fruits) with an expanded, winglike bract, as in *Tilia* (Malvaceae), in which the fruits are nuts, or (5) 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; (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 1982 and Weberling 1989.)

Dispersal by weight characterizes heavy fruits that drop from the plant, land on the ground, and stay there. This category is not very common, and may be characteristic only of species that have lost their primary dispersal agent.

Dispersal by the plant itself usually occurs through some kind of explosive liberation 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 balloon-like 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 up, 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 may have spines or projections as anchoring structures (water burrs), 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, which 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 burrs that get 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 with an odor. They 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 a fleshy testa.
- *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, no closed hard rind (or in hard fruits, the seeds are exposed or dangling), and 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 often fleshy, with hard centers or leathery to hard skins that can be opened to reveal fleshy inner tissues, arillate seeds, or seeds with a fleshy testa. 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, but are usually borne in an exposed position (e.g., outside the dense crown

of a tree). They have drab colors, a musty, sourish, or rancid odor, and are often large, fleshy, easily digested, and remain attached to the plant.
- Some seeds contain small, nutritous arils (or elaiosomes) and are dispersed by *ants*.

Anatomy

Characteristics related to the internal structure of plants have been employed for systematic purposes for over 150 years, and are useful in both practical identification and determination of phylogenetic relationships. **Anatomical characters** are investigated by light microscope study. Characters observable with the transmission electron microscope (TEM) are frequently referred to as **ultrastructural**, while those observable with the scanning electron microscope (SEM) are often called **micromorphological**. Some important characters—anatomical, ultrastructural, and micromorphological—are briefly discussed below.

SECONDARY XYLEM AND PHLOEM

Wood (often called **secondary xylem**) is produced by a **vascular cambium**, a cylinder of actively dividing cells just inside the bark of a woody plant. Wood is a complex mixture of water-conducting cells (**tracheids** and/or **vessel elements**), cells with a support function (**fibers**), and living cells that run from the outside to the inside of the stem (**rays**) (Figure 4.31). The water-conducting and support cells are both dead at maturity, which makes sense because cytoplasm would interfere with water transport. These cells have thick walls made up of both cellulose and lignin, the former a long chain of glucose molecules
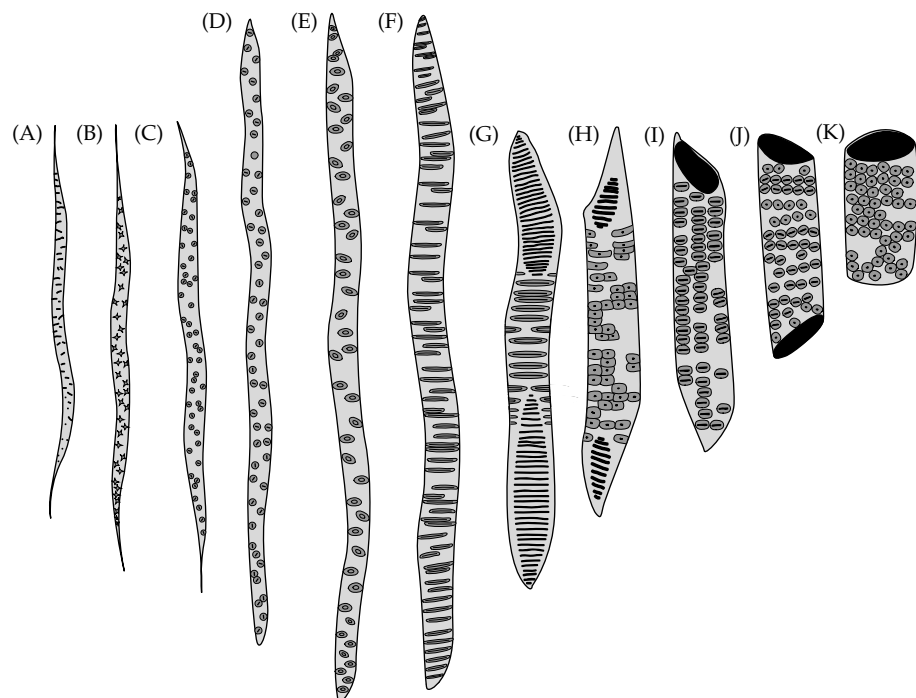
Figure 4.31 Some cell types of the secondary xylem. (A–D) Wood fibers. (E–F) Tracheids. (G–K) Vessel elements. (G) A vessel element type with many-barred scalariform perforation plates (the ladder-like pattern of openings at each end of the cell. (H) This vessel element also has scalariform perforation plates, but the bars are reduced in number. (I) This vessel element is an intermediate between H and J. (J–K) These short, broad, vessel elements have simple perforation plates. (Modified from Radford et al. 1974.)

and the latter a complex polymeric substance composed of phenolic subunits. Conifers and cycads have only tracheids for water conduction, whereas gnetopsids and angiosperms have both tracheids and vessel elements. Angiosperms tend to have short, broad vessel elements with completely open ends that fit together like sewer pipes and conduct large amounts of water rapidly. Many anatomists (e.g., Bailey 1944, 1951, 1957) have considered xylem types in terms of a priori defined trends in vessel element evolution; that is, the progression from tracheids to long, narrow vessel elements with slanted, scalariform perforation plates, to short, broad, vessel elements with simple perforation plates (Figure 4.31E–K). Carlquist emphasized the linkage between xylem structure and its ecological function.

Other important aspects of wood anatomy include growth rings (bands or layers in the wood produced by seasonal variation in cambial activity) and the presence of various specialized cells containing crystals, resins, mucilage, or latex.

Secondary phloem provides fewer taxonomic characters than secondary xylem. There are two major types of carbohydrate-conducting cells in vascular plants: **sieve cells** and the more specialized **sieve tube elements**. The latter possess a distinctive sieve plate and companion cells. Much emphasis has been placed on the structure of the sieve-element plastids of angiosperms (Behnke 1972, 1975, 1977, 1981, 1994) because differences in their structure have been correlated with major clades, such as monocots, Caryophyllales, and Fabaceae. Behnke recognized two major categories of plastids in sieve tube elements, the S-type, which accumulates starch, and the P-type, which accumulates proteins (or proteins and starch) (Figure 4.32).
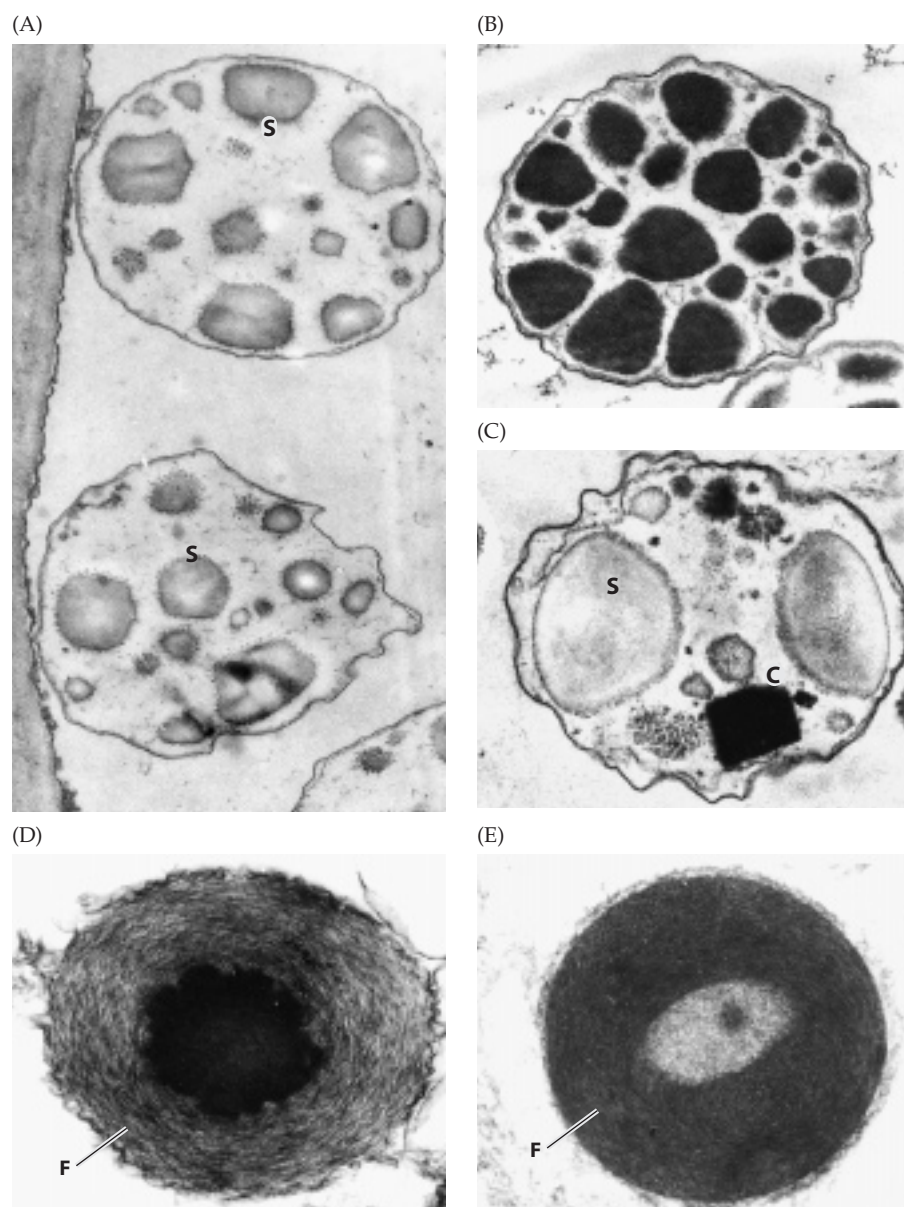
Figure 4.32 A few examples of sieve-element plastids. (A) S-type, with many starch grains (common in many angiosperms). (B) *Dracaena* (Convallariaceae); P-type, with numerous cuneate crystalloids. (C) *Laurus* (Lauraceae); plastid with both proteins and starch. (D) *Petiveria* (Petiveriaceae); P-type, with central protein crystalloid surrounded by protein filaments. (E) *Alternanthera* (Amaranthaceae); P-type, with protein filaments only. C, protein crystalloid; F, protein filaments; S, starch. (From Behnke 1975.)

NODAL ANATOMY

Nodal anatomy describes the various patterns in vascular connections between stem and leaf. The anatomy of the node is quite variable and often of systematic significance. A key feature is the number of **leaf gaps**, or **parenchymatous interruptions**, left in the secondary vascular system of angiosperms by the departure of vascular bundles (**leaf traces**) to the leaves. The configuration of these leaf gaps is used as the basis of nodal types (Figure 4.33). The nodal pattern can be expressed in terms of the number of traces (strands of vascular tissue) and gaps, or **lacunae** (spaces between the vascular strands). For example, a unilacunar node with a single trace would be described as 1:1; a unilacunar node with two traces would be recorded as 2:1; and a trilacunar node with three traces would be 3:3.

LEAF ANATOMY

Leaves are extremely varied anatomically and provide numerous systematically significant characters (Carlquist 1961; Dickison 1975; Stuessy 1990).

The **epidermis** (outer layer of the leaf) varies in the number of cell layers, the size and shape of individual cells, the thickness of cell walls, and the occurrence of papillae (rounded bumps or projections of individual epidermal cells) or various kinds of hairs (trichomes; see "Indumentum," p. 51). Some leaves have a **hypodermis**, which is formed from one or more differentiated layers of cells beneath the epidermis. The **cuticle** is a waxy coating over the epidermis, and it varies in thickness and surface texture. Various wax deposits (**epicuticular waxes**) may also be deposited on top of the cuticle (Figure 4.34; see also Behnke and Barthlott 1983; Barthlott 1990; Barthlott et al. 1998).

The epidermis contains pores, or **stomates** (or stomata), each surrounded by specialized **guard cells** that open or close the pore by means of changes in their internal water pressure. A variety of stomatal forms occur in vascular plants. Stomates are usually classified by the relationships of their **subsidiary cells** (epidermal cells associated with the stomate and morphologically distinguishable from the surrounding epidermal cells) to one another and to the guard cells. It should be noted that the same configuration of subsidiary cells can result
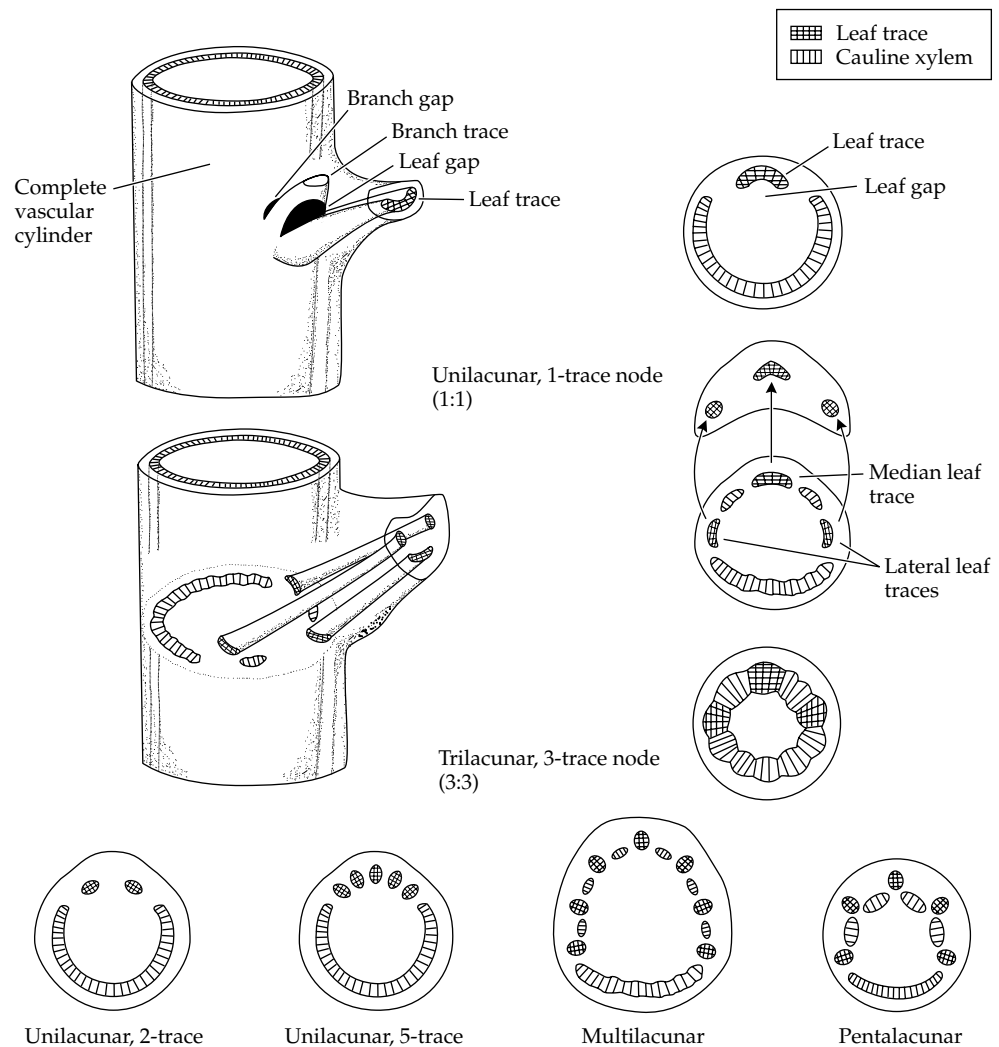
Figure 4.33 Some types of nodal anatomy. (Modified from Radford et al. 1974.)
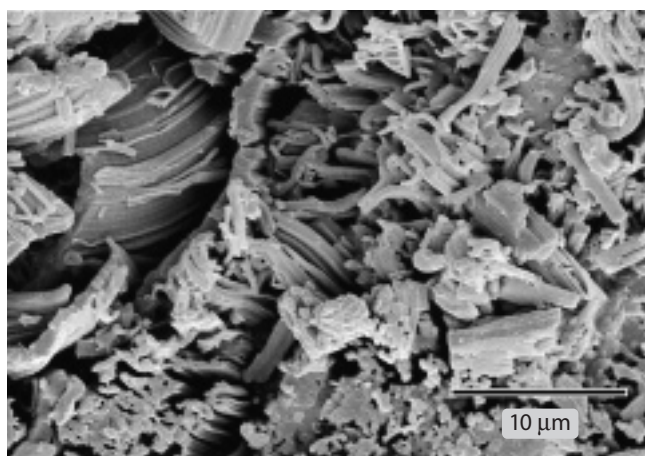
Figure 4.34 *Strelitzia*-type epicuticular waxes—large, massive secretions composed of rodlet-like subunits—in a leaf of *Latania* (Arecaceae). (Photograph by Y. Renea Taylor, used with permission.)

from different developmental pathways; studies of these pathways often aid in the interpretation of the phylogenetic significance of stomatal form. **Anomocytic** stomata are surrounded by a limited number of cells that are indistinguishable in size and shape from those of the remainder of the epidermis; other stomatal types have recognizable subsidiary cells in various arrangements (Figure 4.35). Stomates may be surrounded by a cuticular ridge, various cuticular projections, or may be sunken into crypts or grooves.

Characters relating to the internal tissues of leaves are also important. The **mesophyll** may be differentiated into palisade and spongy layers, and the number of cell layers in each may vary. The distribution and shape of mesophyll cells and the presence or absence of intercellular spaces may also be diagnostic. Internal leaf structure is correlated with the biochemistry of photosynthesis. Leaves associated with C_3 photosynthesis, the most common photosynthetic pathway in green plants, in which compounds with three carbon atoms are the immediate products of carbon dioxide fixation, typically have a distinct chlorenchymatous layer of palisade cells in one to several cell layers below the leaf epidermis. In contrast, leaves associated with the C_4 photosynthetic pathway, in which compounds with four carbon atoms are the immediate products of carbon dioxide fixation, have prominent chlorenchymatous vascular bundle sheaths (**Kranz anatomy**; Rathnam et al. 1976).

Various thick-walled and lignified cells, such as sclereids or fibers, may also be present in mesophyll tissues. **Fibers** are elongated cells that frequently surround and protect the vascular tissue that forms the veins of the leaf. Such fibers vary in their pattern of arrangement and sometimes form girders connecting the vein to the adaxial and/or abaxial epidermis. **Sclereids** are thick-walled cells of various shapes; they are frequently scattered in the mesophyll. Secretory canals or cells in the mesophyll and cells containing various kinds of crystals are often diagnostic for particular taxa (see below).
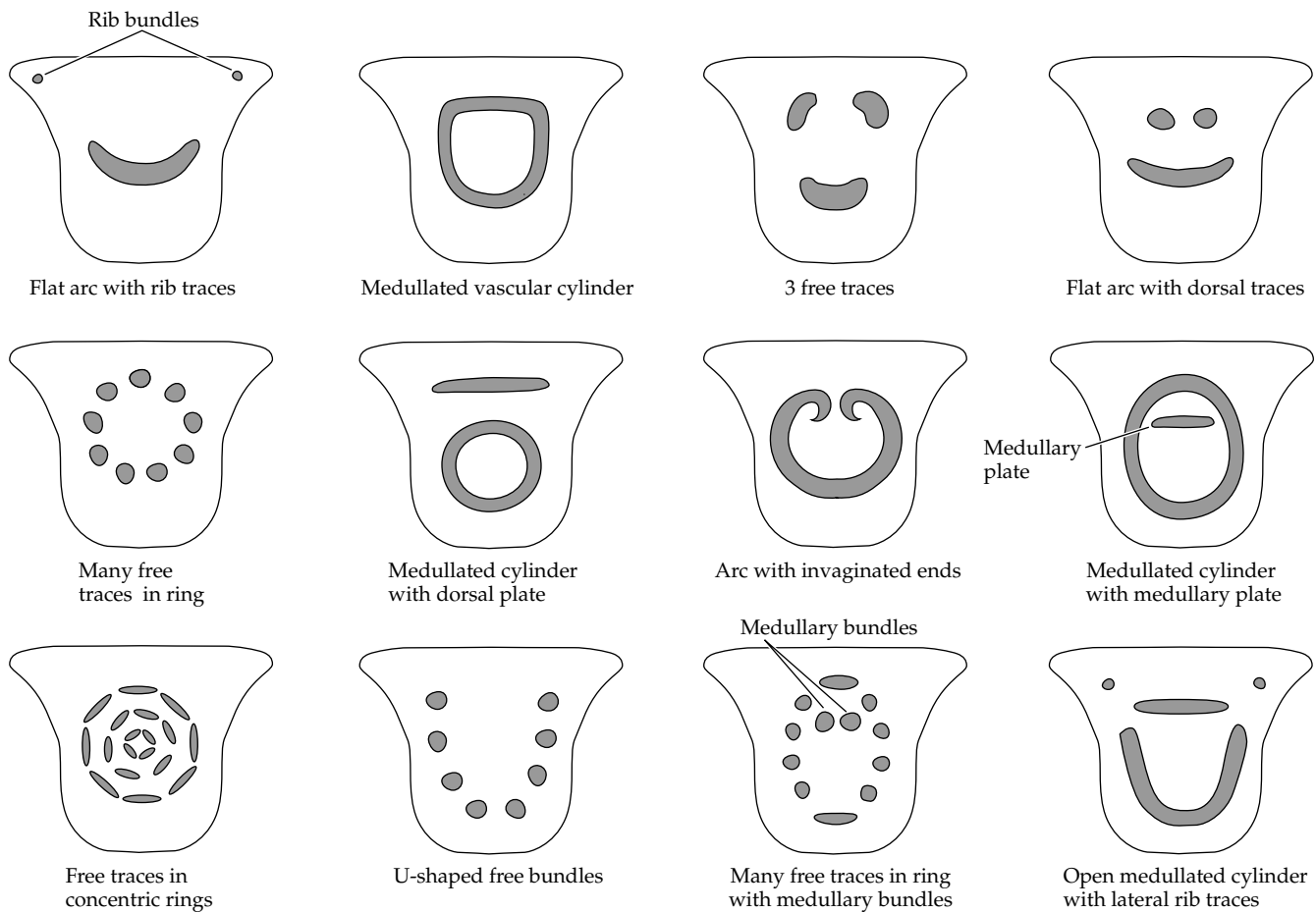
Xylem and phloem may be arranged in various ways in the petiole and midvein of the leaf (Figure 4.36; see Howard 1974 for more detail). Such patterns are best studied by making a series of cross-sections through the petiole; several sections are usually required because the pattern often changes as one moves from the petiole base to its apex and into the leaf midvein.

SECRETORY STRUCTURES

Many plant species contain specialized cells or groups of cells that produce latex, resins, mucilage, or essential oils (Metcalfe 1966; Metcalfe and Chalk 1950). **Latex** is a more or less opaque and milky or colored (usually yellow, orange, or red, but sometimes green or blue) fluid pro-

Figure 4.35 Some important stomatal types.

Anomocytic   Diacytic   Paracytic   Cyclocytic   Anisocytic

Paratetracytic   Pericytic   Amphiparacytic   Polocytic

Rib bundles

Flat arc with rib traces

Medullated vascular cylinder

3 free traces

Flat arc with dorsal traces

Many free traces in ring

Medullated cylinder with dorsal plate

Arc with invaginated ends

Medullary plate

Medullated cylinder with medullary plate

Free traces in concentric rings

U-shaped free bundles

Medullary bundles

Many free traces in ring with medullary bundles

Open medullated cylinder with lateral rib traces

Figure 4.36   Common petiole vascular patterns (diagrammatic transverse sections at base of blade). (Modified from Radford et al. 1994.)

duced by specialized cells called **laticifers**. Laticifers are located in parenchymatous tissues (of any plant part, but especially stems and leaves), and may be solitary or in groups (forming tubes, which may be branched or unbranched). Latex contains a wide variety of secondary compounds in solution and suspension and is important in deterring herbivory. Some species produce clear **resins** (aromatic hydrocarbons that harden when oxidized) or **mucilage** (slimy fluids) in scattered cells, specialized cavities, or canals. **Essential oils** are highly volatile, aromatic organic compounds that are produced by specialized spherical cells scattered in the mesophyll or in cavities created by cellular breakdown or the separation of adjacent cells. Such cells or cavities in leaves cause them to appear **pellucid dotted** when viewed with transmitted light. The presence or absence of latex, resins, mucilage, and essential oils and the form and distribution of laticifers and secretory canals or cavities are often taxonomically significant.

CRYSTALS
Crystals are frequent in vascular plants, usually located in cells, variously shaped (Figure 4.37), and usually composed either of calcium oxalate, calcium carbonate, or silica. **Druses** (spherical crystals), **raphides** (needle-like crystals), and **crystal sand** are the most common. Silica bodies are often taxonomically important in monocots. Calcified bodies called **cystoliths** sometimes occur in specialized cells (called **lithocysts**); these often have systematic significance. The calcareous material in cystoliths is in the form of small amorphous particles.

(A)

(B)

(C)

(D)
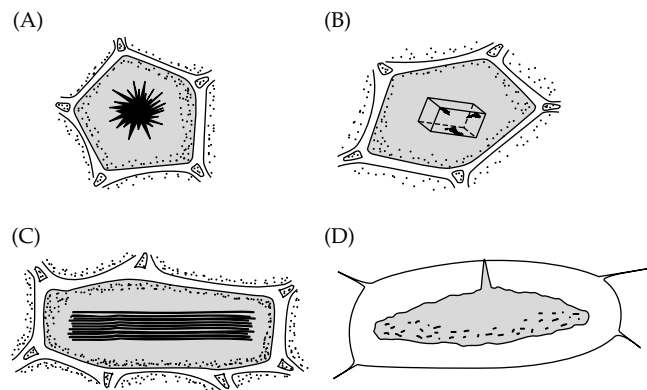
Figure 4.37   Crystal types. (A) Druse. (B) Prismatic form. (C) Raphides. (D) Cystolith.

ARRANGEMENT OF XYLEM AND PHLOEM IN THE STEM

The stems of most seed plants contain a ring of primary xylem and phloem (as seen in cross-section; Figure 4.38). Primary vascular tissues result from the differentiation of cells produced by the **apical meristem** (the zone of dividing cells at the apex of branches). This ring of bundles is called a **eustele**. In woody species, a generative layer, the **vascular cambium**, develops between the xylem and phloem and adds to the thickness of the stem by producing secondary xylem toward its inner side and secondary phloem on the side toward the periphery of the stem. This is the normal pattern of secondary growth in angiosperms (and seed plants in general). Monocots usually lack a vascular cambium and secondary growth; their stems have scattered bundles, each containing xylem and phloem. Some angiosperms have various so-called anomalous patterns of secondary growth, some of which are listed below (and illustrated in Figure 4.38). Anomalous growth patterns are frequently encountered in succulents, where they allow for rapid increases in girth, and in lianas, where they resist damage due to twisting and bending.

axes more or less flattened or furrowed   stem flattened or furrowed due to unequally active cambium

cortical bundles   leaf trace bundles that run longitudinally in the cortex of the stem before joining the vascular system of the stem

fissured xylem   xylem broken up by the development of phloem or parenchyma tissue

included phloem   strands of phloem embedded in the secondary xylem

internal phloem   primary phloem in the form of strands or a continuous ring (as seen in a cross-section of the stem) at the inner boundary of the xylem; thus, the xylem is bounded by phloem on both its inner and outer surfaces. In species lacking secondary growth, development of internal phloem results in the presence of **bicollateral bundles**; that is, the vascular bundles of the stem have phloem on the inner as well as the normal outer side of the xylem.

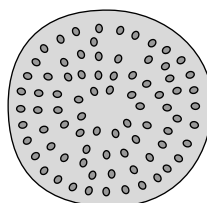**medullary bundles**   supplementary vascular bundles in the pith

xylem and phloem concentrically alternating   layers of phloem and xylem alternate in the stem due to the action of a series of vascular cambia
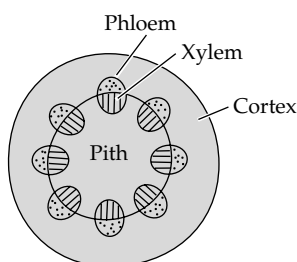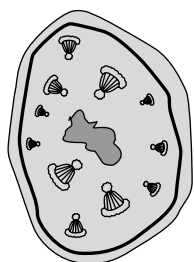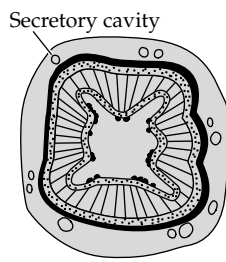

Primary vascular
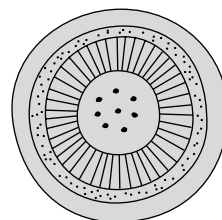system in dicot stem
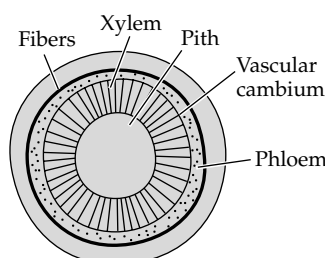
Normal secondary
growth in dicot stem

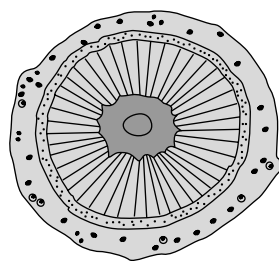Primary vascular
system in monocot stem
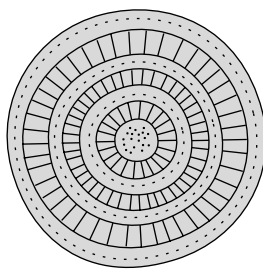
Bicollateral
vascular bundles
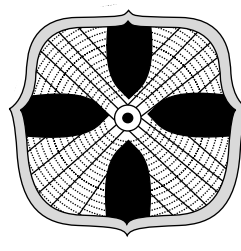
Internal phloem

Medullary
vascular bundles

Cortical vascular bundles

Successive rings
of xylem and phloem

Fissured xylem

Figure 4.38   Various arrangements of xylem and phloem in stems.

FLORAL ANATOMY AND DEVELOPMENT

The pattern of vascular traces in flowers is often useful in understanding vestigial structures and homologies of parts in highly modified flowers. Extreme modification of parts is a particular problem in flowers that are greatly reduced (and often densely clustered together) in association with the evolution of wind pollination, such as the Betulaceae (see Chapter 8). The pattern of vascular traces in the gynoecium usually can be used to indicate the number of carpels, especially in gynoecia that have completely fused carpels with free-central, basal, or apical placentation.

The positioning of floral **primordia** (floral parts or organs in their earliest condition) and their sequence of initiation are also of taxonomic significance (Evans and Dickinson 1996). Developmental studies are important in understanding homologies of various floral parts. For example, some flowers with many stamens have stamen primordia positioned in a spiral, while in other flowers they are clustered into five or ten groups. Additionally, stamen primordia may be initiated **centripetally** (from outside to inside) or **centrifugally** (from inside to outside). Such variation suggests that numerous stamens have evolved many times among angiosperms. Studies of corolla development have also been especially informative. In some sympetalous flowers the corolla develops from a ring primordium, which then develops lobes, while in others the corolla lobes are initiated first. Developmental studies have indicated that some flowers, such as Apiaceae and many Ericaceae, that appear to have separate petals are sympetalous early in development; they are therefore considered to have evolved from sympetalous ancestors.

Embryology

Spores, gametophytes, and gametangia show marked evolutionary trends in tracheophytes (Table 4.2). Sporophytes produce spores in **sporangia** (singular: **sporangium**). Most lycopodiophytes, equisetophytes, psilotophytes, and ferns (see Chapter 7) have only one kind of spore; these plants are **homosporous**. Their gametophytes are completely independent of the sporophyte (see Figure 7.2), bear both kinds of gametes, egg and sperm, and are either large (about 1 cm in diameter), green, and photosynthetic or curious subterranean structures that are saprophytic, acquiring nutrition from dead organisms with the aid of a fungus. Gametes are housed and protected in specialized structures within gametophytes called **gametangia**: eggs in **archegonia** and sperm in **antheridia**.

Heterosporous plants, which include a few genera of lycopodiophytes and ferns and all seed plants, have two kinds of sporangia. **Megasporangia** contain **megaspores** that develop into **megagametophytes** (or female gametophytes, or embryo sacs), and **microsporangia** contain **microspores** that develop into **microgametophytes** (male gametophytes). Heterospory is correlated with three gametophytic adaptations. First, gametophytes are small and develop inside the spore, unlike the relatively large, independent gametophytes of most free-sporing tracheophytes. Second, the two kinds of gametophytes are specialized; the megagametophyte is larger and is invested with a supply of nutrients, and the microgametophyte is small and dispersible. Third, the gametophytes are nutritionally dependent upon the sporophyte. Reduction in gametophyte size continues in seed plants and is associated with

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TABLE 4.2 *General features of spores, gametophytes, and gametangia in major groups of tracheophytes.*

Group[a]	Heterospory	Gametophyte dependence on sporophyte	Gametophyte size (in cells)	Gametangia (antheridia and archegonia)
Lycopodiaceae, Equisetaceae, Psilotaceae, and most leptosporangiate ferns	No	None	Millions (macroscopic)	Present
Selaginellaceae, Isoetaceae, and aquatic leptosporangiate ferns (Azollaceae, Marsileaceae, and Salviniaceae)	Yes	Almost complete	1000s (female); sometimes under 100 (male)	Present
Conifers, cycads, ginkgos, gnetopsids	Yes	Complete	1000s (female); a few (male)	Archegonia only
Angiosperms	Yes	Complete	About 7 (female); 3 or fewer (male)	Absent

[a] See Chapter 7 for more information about groups other than angiosperms and Chapter 8 for angiosperms.

the loss of recognizable antheridia in conifers and related plants and of antheridia and archegonia in angiosperms.

Embryological features of lycopodiophytes, equisetophytes, psilotophytes, ferns, conifers, cycads, ginkgos, and gnetopsids are further discussed in Chapter 7. In this section we focus on angiosperm ovules, megagametophytes, embryos, and endosperm, and on agamospermy.

OVULES AND MEGAGAMETOPHYTES

The **ovule** is a megasporangium surrounded by one or two protective layers (the integuments) and attached to the ovary wall by a stalk (the funiculus). The integuments nearly enclose the ovule, leaving only a small opening, the **micropyle**, through which pollen tubes usually enter the megasporangium. Ovules have been classified by their curvature. In an **orthotropous** ovule the axis of the ovule and funicle are in a straight line, while in an **anatropous** ovule the ovule is inverted almost 180°. In **campylotropous** ovules, the axis of the ovule is curved and the ovule is held at about 90° (Figure 4.39). The ovule develops into a seed, with the integuments becoming the seed coat.

The megasporangium is the site of the meiosis that generates the megaspore. In at least 70% of angiosperms, meiosis yields four haploid megaspores, three of which degenerate. The fourth megaspore undergoes three mitotic divisions to produce a megagametophyte with eight nuclei in seven cells (Figure 4.40). Typically the egg and two other cells (the *synergids*) cluster near the micropyle, and a cell with two nuclei (the *polar nuclei*) ends up near the center. The pollen tube enters the megagametophyte through the micropyle and releases two sperm. One sperm fertilizes the egg to form the diploid **zygote**, the first cell of the next sporophytic generation. The other sperm fuses with one, or usually both, nuclei of the central cell to form the triploid primary endosperm nucleus. This double-fertilization formation of endosperm is unique to angiosperms. The function of the other cells of the megagametophyte is unclear. Other less common types of megagametophytes are restricted to certain genera or families.
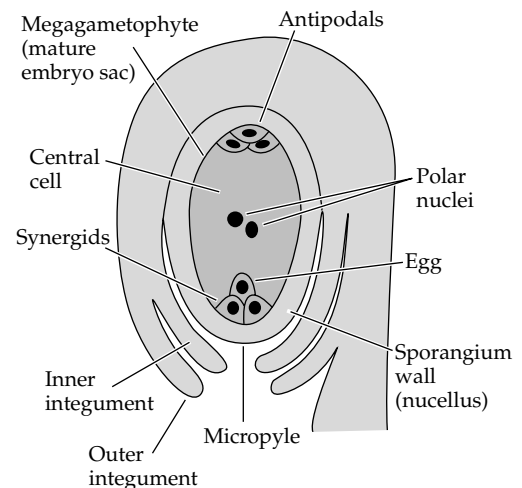
EMBRYO AND ENDOSPERM

Embryo and endosperm are the two major components of angiosperm seeds. The development of embryos varies considerably within angiosperms. Mature embryos consist of an axis, one end of which is the root (radicle) and the other end the shoot (epicotyl; Figures 4.41). When there are two cotyledons, the shoot apex lies between them, as in Figure 4.41. Plants with such embryos are called **dicotyledons** and have long been considered a taxon, but they are acutally a paraphyletic group. In **monocotyledons**, the shoot apex is lateral, lying next to the solitary cotyledon (Figure 4.42). When the seed germinates and the embryo begins growing into a seedling, the cotyledon or cotyledons may enlarge and become green and photosynthetic. Alternatively, they may remain below ground or not develop beyond their embryonic state.

Endosperm is the specialized tissue of angiosperms that supplies nutrients to the developing embryo and in many cases to the seedling as well. Endosperm may be completely absorbed by the cotyledons of the embryo before it matures, as in peas, beans, and walnuts (something you can easily confirm for yourself). The cotyle-
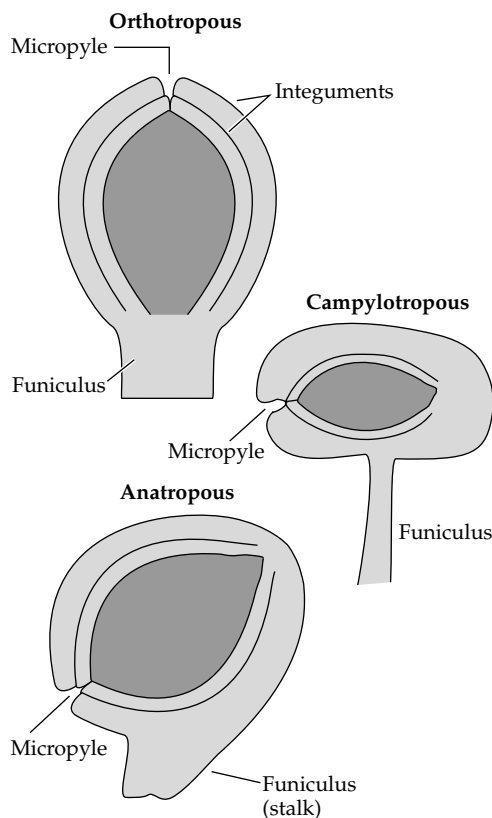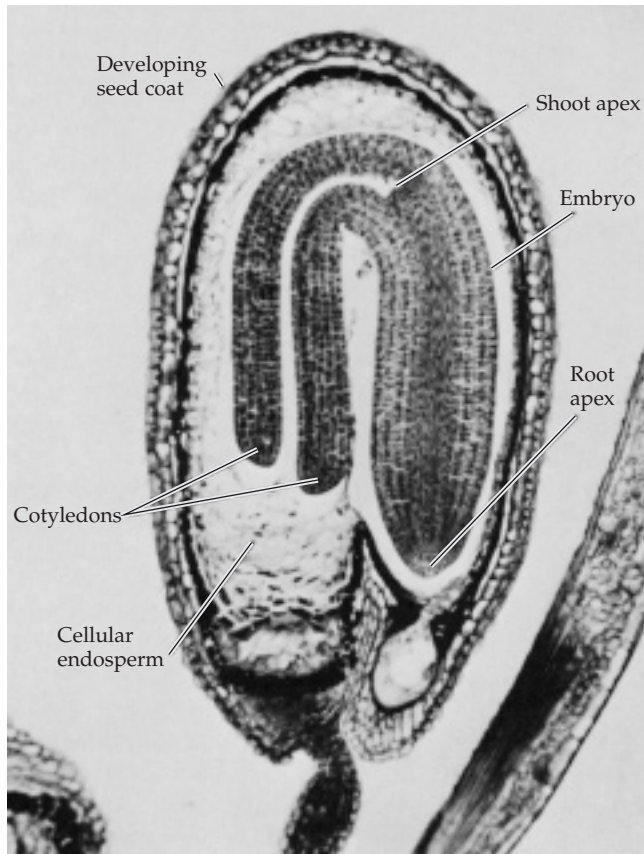
Figure 4.39 Three common types of ovule axes.

Figure 4.40 A mature ovule.

Figure 4.41 Longitudinal section of seed of *Capsella (*Brassicaceae), showing embryo and endosperm. (From Gifford and Foster 1988. Copyright W. H. Freeman; used with permission.)

many times without the formation of cell walls. In most species with this **nuclear type** of endosperm development, cell walls do eventually form. The **cellular type** of endosperm development involves cell wall formation from the start. In the **helobial type** of endosperm development, which characterizes most monocots, the primary endosperm nucleus produces two cells; one divides little while cells derived from the other make up most of the endosperm.

AGAMOSPERMY

Some plant species produce embryos without producing haploid gametes and without fertilization. This phenomenon is referred to as **agamospermy** (*a* = without, *gamo* = gametes, *sperm* = seed). There are two major forms of agamospermy. In the first, a diploid cell functions as a megaspore to produce a gametophyte with the somatic chromosome number. Such megagametophytes are often similar in appearance to sexually derived gametophytes. The egg develops into an embryo without fertilization, a process called **parthenogenesis**. The second form of agamospermy, **adventitious embryony**, is best known in citrus plants (*Citrus*, Rutaceae) and is otherwise rare. Here the embryo develops directly from a somatic cell within the ovule without the formation of a gametophyte. The best method of detecting agamospermy is to study megaspore development to determine whether the megaspores are mitotically or meiotically derived. The taxonomic distribution and systematic significance of agamospermy are discussed in Chapter 6.
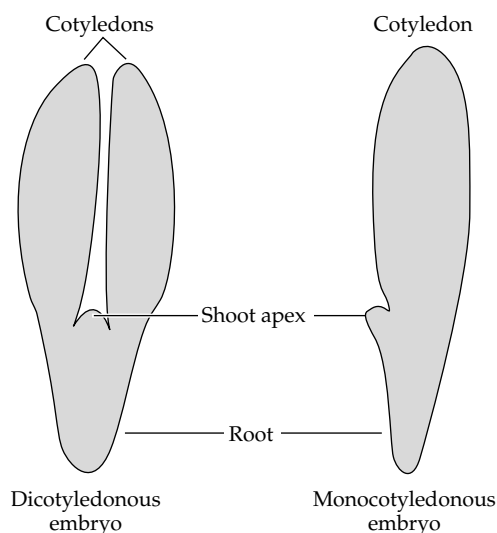
dons of these **exalbuminous** seeds take over the role of the endosperm in nourishing the seedling. Examples of mature seeds with conspicuous endosperm are cereal grains, such as rice, wheat, corn, and oats; and palms. Corn endosperm is the source of popcorn, and endosperm of coconut (*Cocos nucifera*) is the familiar coconut "milk" (endosperm before cell walls have formed) and "meat" (endosperm after cell walls have formed). The primary endosperm nucleus may divide

Chromosomes

Chromosome number by itself may be a useful systematic character. Similar chromosome numbers may indicate close relationship; different chromosome numbers often create some reproductive isolation through reduced fertility of hybrids. Chromosome size, the position of the centromere, special banding patterns, and other features may also be systematically informative.

CHROMOSOME NUMBER

The lowest chromosome number in the somatic cells of a plant is its **diploid** number, often designated as 2*n*. Rice, for example, has a diploid number of 24. The diploid genome consists of two full chromosome sets (or complements), one from the ovulate (maternal) parent and one from the pollen (paternal) parent. One full set is

Figure 4.42 A comparison of "dicot" and monocot embryos. (Modified from Gifford and Foster 1988.)

TABLE 4.3 *Some chromosome number variation in tracheophytes.*

Taxon	Family	2*n*
Asplenium trichomanes	Polypodiaceae	
ssp. *trichomanes*		72
ssp. *quadrivalens*		144
Lycopodium and related genera	Lycopodiaceae	34–36, 44–48, 68, 136, 260, 272
Betula	Betulaceae	28, 42, 56, 70, 84
Lantana	Verbenaceae	18, 22, 24, 27, 33, 44, 48, 72
Vicia	Fabaceae	10, 12, 14, 24, 28
Maloideae	Rosaceae	34, 51, 68
All genera	Pinaceae	24

borne by spores and by gametes–eggs and sperm—which have the **haploid** chromosome number. The haploid number, *n*, of rice is 12. The lowest haploid number in a group of plants, such as a genus or family, is referred to as the **base number** and designated by *x*. In the birches (*Betula*), for example, *x* = 14, and the lowest diploid number in the genus is therefore 2*n* = 28 (Table 4.3).

The chromosome numbers of angiosperms range from 2*n* = 4 (*Happlopappus gracilis*, Asteraceae; and some other species) to 2*n* = ca. 250 [*Kalanchoe* (Crassulaceae)]. Ophioglossaceae and Polypodiaceae (see Chapter 7) show unusually high chromosome numbers, the highest being 2*n* = 1260 in *Ophioglossum reticulatum* (Ophioglossaceae). Knowledge of chromosome numbers is limited in many groups to a minority of species and often comes from a small sample of individuals within species.

The addition or loss of one or two whole chromosomes is referred to as **aneuploidy**. Examples of aneuploidy in *Clarkia* and *Lantana* are discussed below. The presence of three or more whole sets of chromosomes in somatic cells is called **polyploidy**. A familiar polyploid is bread wheat (*Triticum aestivum*), which has six full sets of chromosomes. In *Triticum*, *x* = 7, and the chromosome number of bread wheat is therefore 2*n* = 6*x* = 42. Polyploids are differentiated by the number of chromosome complements they contain. Triploids contain three chromosome complements, tetraploids four (hence *tetra-*), pentaploids five, and hexaploids six.

There are two major forms of polyploidy. **Autopolyploidy** results from the union of three or more chromosome complements from the same (hence *auto-*) species, while **allopolyploidy** results from the union of two or more different (hence *allo-*) genomes. Because they have diverged, chromosomes of different genomes often do not pair with each other. In diploids and allopolyploids, there are two copies of each chromosome, and in meiosis the two homologous chromosomes pair to form a **bivalent**. Autopolyploids contain three or more homologues of each chromosome, and pairing of more than two chromosomes to form **multivalents** is thus a possibility. Mul-

tivalents lead to gametes with unbalanced chromosome numbers and sterility problems.

Chromosomal pairing between genomes from different sources ranges from none (allopolyploids) to complete (autopolyploids), with a full range of intermediate levels corresponding to intermediate levels of genetic divergence. Hence it is best to consider autopolyploidy and allopolyploidy as extremes of a continuum. Some examples of polyploid plants are given in Table 4.4. Autopolyploidy is apparently not as common as allopolyploidy.

The addition of whole chromosome complements can occur in either somatic tissue or gametes. For example, if the nucleus of a cell that gives rise to a flowering branch fails to divide mitotically, then the chromosome number is automatically doubled. More commonly, production of chromosomally unreduced gametes leads to polyploidy. If, for example, an unreduced (2*n*) egg is fertilized by a reduced (1*n*) sperm, the zygote will be triploid (3*n*). If the plant that develops from this triploid zygote produces a triploid egg that is fertilized by a haploid sperm, the offspring will be tetraploid. Evolutionary and systematic aspects of polyploidy are discussed in Chapter 6.

Chromosome number is generally constant within a species, although exceptions to this generality are fairly frequent. Chromosome number may be constant within large groups. Andropogoneae, the large grass tribe that includes *Zea*, *Sorghum*, and many important range grasses, consistently has *x* = 10; the great majority of the approximately 1000 species of the subfamily Maloideae are *x* = 17; and almost all members of Pinaceae are diploids (2*n* = 24).

In some species, chromosome number varies without correlated morphological variation. Autopolyploids, for example, may not differ morphologically from their diploid progenitors and are therefore often placed in the same species. Diploid (2*n* = 14) *Tolmiea menziesii* (Saxifragaceae), which grows in northern California and southern Oregon, and tetraploid (2*n* = 28) *T. menziesii*, which grows from central Oregon to southern Alaska, are mor-

TABLE 4.4   *Examples of plant polyploids and their 2n chromosome numbers.*

Species	Type of polyploid	2*n*
Taraxacum officinale, common dandelion	Allotriploid	21
Nicotiana tabacum, tobacco	Allotetraploid	48
Gossypium barbadense, cotton	Allotetraploid	52
Vaccinium corymbosum, highbush blueberry[a]	Allotetraploid	48
Betula papyrifera, white birch[a]	Allopentaploid	70
Triticum aestivum, bread wheat	Allohexaploid	42
Lythrum salicaria, purple loosestrife[a]	Autotetraploid	60
Phleum pratense, timothy grass[a]	Autohexaploid	42

[a]Other ploidy levels are known for these species.

phologically indistinguishable. In spring beauty (*Claytonia virginica*, Portulacaceae) of eastern North America, aneuploidy is extensive: there are 50 diploid numbers reported for this species, ranging from 12 to about 191.

Differences in chromosome number, when associated with morphological differences, may be recognized taxonomically, as in subspecies of *Asplenium trichomanes* (see Table 4.3). Species within many genera differ in ploidy level. The white-barked birches (*Betula*, Betulaceae) of North America, for example, include diploids (2*n* = 28: gray birch, *B. populifolia*, and mountain paper birch, *B. cordifolia*), tetraploids (2*n* = 56: *B. cordifolia* and paper birch, *B. papyrifera*), pentaploids (2*n* = 70: *B. papyrifera*), and hexaploids (2*n* = 84: *B. papyrifera*).

Differences in chromosome number between species often lead to reduced fertility in hybrids and the creation of a species boundary. *Clarkia biloba* (Onagraceae) is a widespread and variable Californian endemic with *n* = 8. *Clarkia lingulata* (*n* = 9) has apparently arisen from *C. biloba* by the development of one chromosome made up of two chromosomes of *C. biloba*. The two species differ only in petal shape, but hybrids between them show very low fertility. Such aneuploid changes, however, do not always lead to speciation, as *Claytonia virginica* and other species with more than one chromosome number exemplify.

As an example of the taxonomic utility of chromosome number, consider *Lantana* (see Table 4.3). These tropical shrubs are taxonomically confusing due to hybridization, polyploidy, and poorly resolved generic limits. There are two base numbers (11 and 12) and perhaps a third (9) in the genus. Diploid species, with 2*n* = 22 or 24, are the foundations for polyploids, especially tetraploids (2*n* = 44 or 48). Triploids (2*n* = 33 or 36) result from crosses between diploids and tetraploids. The base number 12 characterizes *Lantana* section *Callioreas*, and *x* = 11 is found in *Lantana* section *Camara*, which may have evolved via aneuploidy from *x* = 12. The occurrence of two base chromosome numbers in the genus is co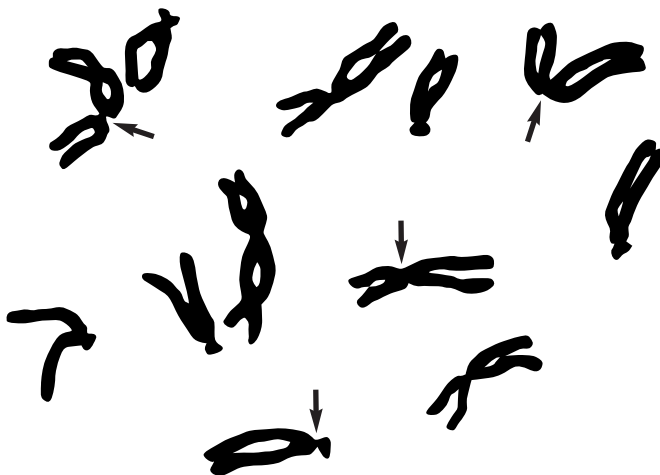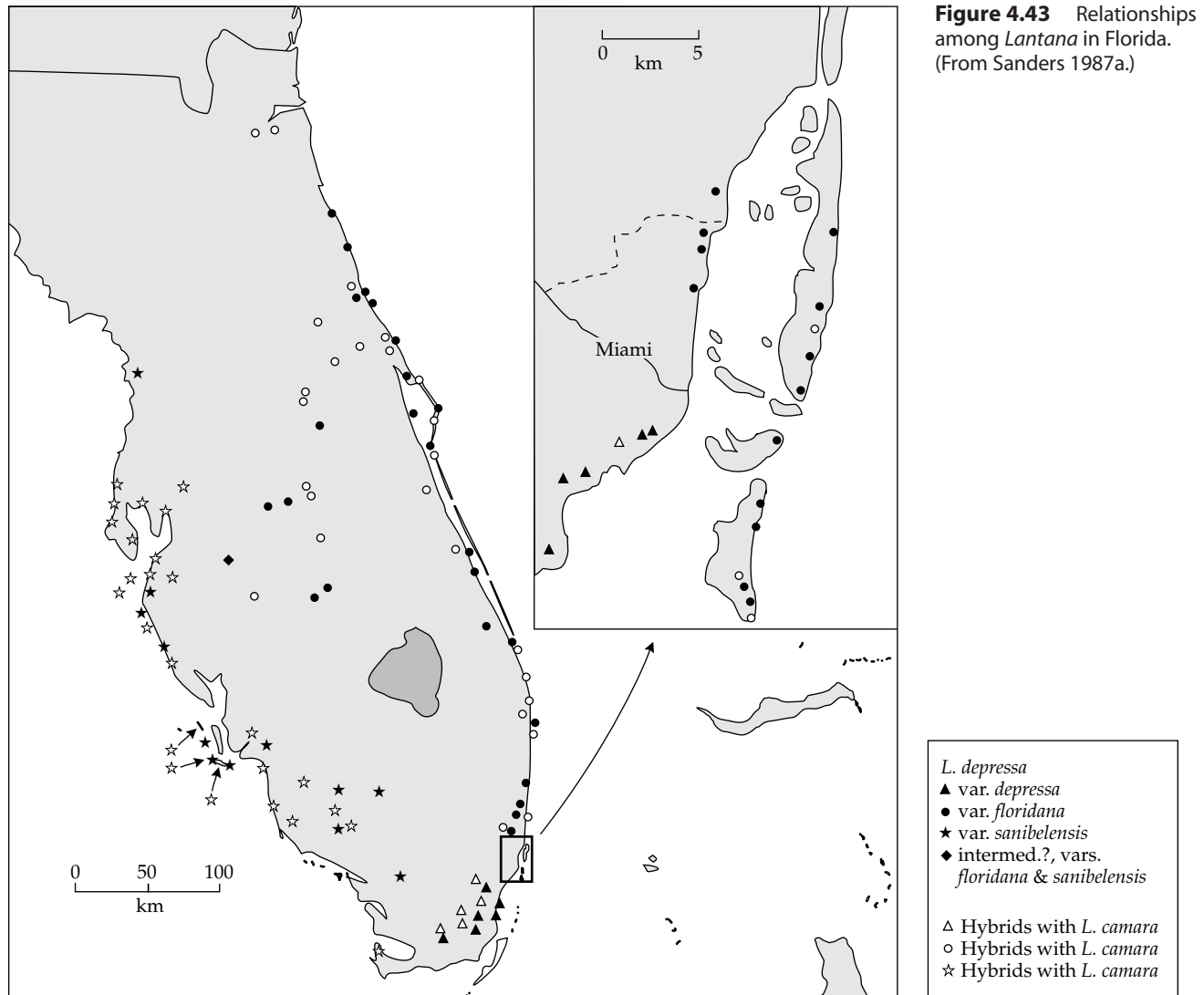nsistent with a polyphyletic origin. Several apparent synapomorphies support section *Camara* as monophyletic, but section *Callioreas* strongly resembles the related large genus *Lippia*. Additional studies are required to unravel the relationships among these groups.

At the species level, chromosome studies have augmented morphological studies in *Lantana*. Most triploids have some chromosomes that do not pair as bivalents in meiosis. Instead, they occur as **univalents**, solitary chromosomes for which there is no homologue, and multivalents. The presence of univalents corroborates the morphologically based hypothesis that many of the triploids are hybrids.

Cytology has played a key role in resolving relationships among Florida *Lantana* sect. *camara* species. Morphologically based studies initially identified two species in the state: native *L. depressa* and the introduced tetraploid *L. camara*. Chromosome studies, coupled with other data, identified three diploid varieties of *L. depressa* in Florida (Figure 4.43), each of which hybridizes with *L. camara*. Chromosome numbers were critical data in resolving this systematic problem.

CHROMOSOME STRUCTURE

Chromosome number, size, and structural features make up what is called the **karyotype**, which may be useful in discriminating taxa. Chromosomes differ not only in overall length, but also in the length of the two chromosomal arms (Figure 4.44). The location of the **centromere**, the point on the chromosome where it is attached to the mechanism that separates chromosomes in cell division, determines whether the arms are more or less equal or unequal in length. The combination of overall chromosome length and centromere location may allow discrimination of many of the chromosomes in a genome. Further distinctions are provided by specialized techniques for staining chromosomal bands (Nogueira et al. 1995). Genome mapping, an exciting approach that may soon have a major impact on systematic studies, is discussed in Chapter 5.

Figure 4.43   Relationships among *Lantana* in Florida. (From Sanders 1987a.)

L. depressa
▲ var. *depressa*
● var. *floridana*
★ var. *sanibelensis*
◆ intermed.?, vars.
   floridana & *sanibelensis*

△ Hybrids with *L. camara*
○ Hybrids with *L. camara*
☆ Hybrids with *L. camara*

Figure 4.44   Chromosomes from *Callisia fragrans* (Commelinaceae), 2*n* = 12. Some of the centromeres are indicated with arrows. (From Jones and Jopling 1972.)

METHODS OF CHROMOSOME STUDY

Determination of chromosome number and other karyotypic features is a routine component of plant systematics. Chromosome number may be studied from mitotic or meiotic cell divisions (Figure 4.45). Mitosis is commonly examined in cells from actively growing root tips, but other tissue (such as expanding petals) may be used. Meiosis is studied most often because it contains more information than mitosis about relationships of genomes. **Microsporocytes**, the cells that give rise to pollen, are the cells of choice for meiotic study because they are easier to work with than **megasporocytes,** and because they are easily removed from the anthers.

Protocols for chromosome study involve staining the cells with a chromosome-specific stain, such as carmine. Softening of the tissue facilitates squashing the cells so that the chromosomes separate from one another and are distinguishable for counting. Successful chromosome study may require considerable patience and skill because the chromosomes may be numerous and small,

Figure 4.45   (A) Mitosis in *Rheo spathacea* (Commelinaceae), 2*n* = 12. Each structure consists of two duplicate DNA molecules (sister chromatids). (From Jones and Jopling 1972.) (B) Meiosis in *Andropogon gyrans* (Poaceae) *n* = 10, × 940; each object is a pair (bivalent) of homologous chromosomes. The partial sphere just above the center is the nucleolus, where ribosomes are made. (From Campbell 1983.)

(A)

(B)

5μm
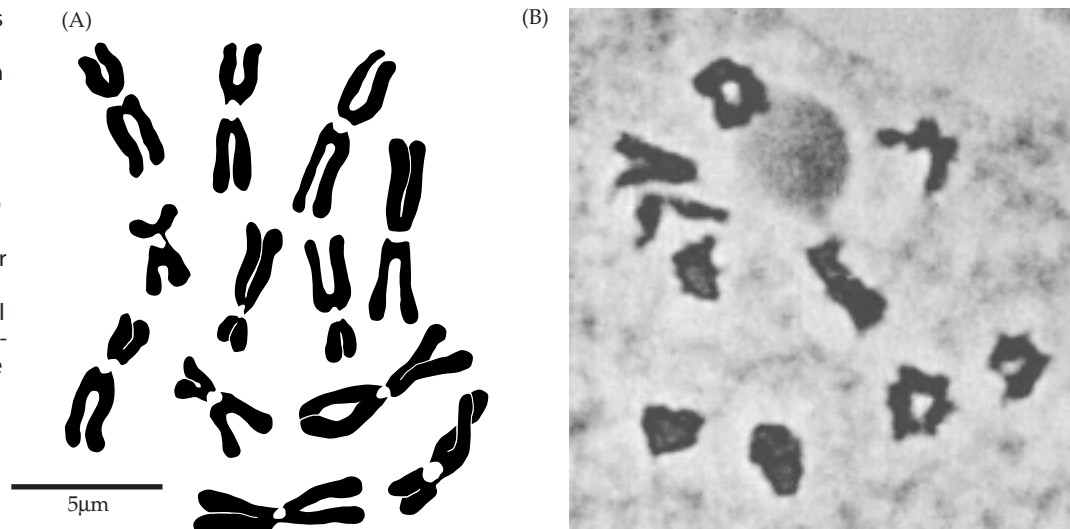
and because it may be difficult to collect material during the correct stage of meiosis. (Methods are outlined in Darlington and La Cour 1975 and Sessions 1990.)

There are now rapid procedures for estimating nuclear DNA content, which often strongly correlates with ploidy. One may therefore survey a large number of individuals for nuclear DNA content and, based on direct knowledge of chromosome number in a smaller sample of individuals, at least infer ploidy (see, for examples, Dickson et al. 1992 and Cox et al. 1998).

Palynology

Palynology is the study of pollen and spores. Pollen and spores are similar, minute particles, but spores are the beginning of the gametophyte generation, whereas pollen grains are mature microgametophytes. The outer layer of pollen and spores often contains a special compound, sporopollenin, which resists degradation by various chemicals, bacteria, and fungi and contributes to the long persistence of pollen in sediments. Pollen, therefore, has been important in paleobotanical studies. Pollen also interests people as a cause of the allergic reaction called hay fever. We will examine the spores of lycopodiophytes, equisetophytes, psilotophytes, and ferns in Chapter 7; here we will focus on pollen. But first we will briefly consider the development of the anther.

DEVELOPMENT OF THE ANTHER

Most anthers consist of four microsporangia arranged in pairs. The anther wall is made up of several layers, and the innermost, the **tapetum**, plays a key role in the development of the microspores and pollen. When the pollen matures and environmental conditions are appropriate, the anther opens to release the pollen. The opening, or dehiscence, of most angiosperm anthers is by a longitudinal slit on each side of the anther between the paired microsporangia (**longitudinal** or **slit dehiscence**). In a

few families, such as Ericaceae and Melastomataceae, pollen is shed through a small opening or pore at one end of the anther (**poricidal dehiscence**).

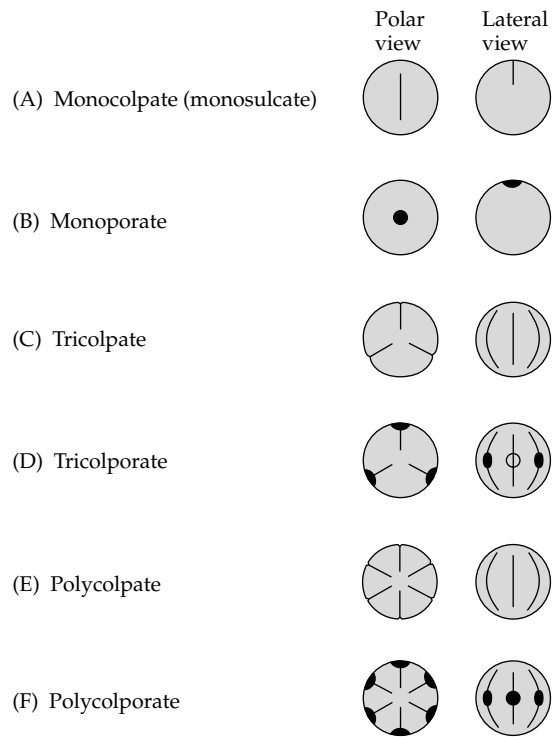### POLLEN STRUCTURE, VIABILITY, AND METHODS OF STUDY

Pollen grains may be released from the anthers singly or in clusters of two, four, or many. In many Apocynaceae (e.g., *Asclepias*) and Orchidaceae, pollen is aggregated into clusters called **pollinia** (singular **pollinium**). The smallest known pollen grains are about 10 μm in diameter, and the largest (in Annonacae) are 350 μm in diameter. Pollen shapes range from spherical to rod-shaped (19 × 520 μm in some Acanthaceae).

The two most important structural features of pollen grains are the apertures and the outer wall. **Apertures** are areas in the pollen wall through which pollen tubes emerge during germination. Pollen grains are often described according to the shape of their aperture(s): **colpate** (also referred to as **sulcate**), which have long and grooved apertures (Figure 4.46A,C,E; Figure 4.47A); **porate**, which have round and porelike openings (Figure 4.46B; Figure 4.47C,D,E,G,H); and **zonate**, which have ring-shaped or band-shaped apertures. **Colporate** apertures combine the groove of colpate and the pore of porate apertures (Figure 4.46D,F). Apertures may be located at the pole or equator of the pollen grain (Figure 4.47A,D), or more or less uniformly distributed over the grain surface (Figure 4.47E,G,H).

The nature and number of apertures is constant in many plant taxa. **Monosulcate** pollen grains (Figure 4.46A; Figure 4.47A) characterize many putatively basal, woody angiosperms of the Magnoliales. Monocots also are basically a monosulcate group. In contrast, members of one large clade of angiosperms—the eudicots—bear **tricolpate** or tricolpate-derived pollen types (Figure 4.47B,D).

The surface of the **pollen wall**, or **exine**, may be more or less smooth, as in many wind-pollinated species (Fig-
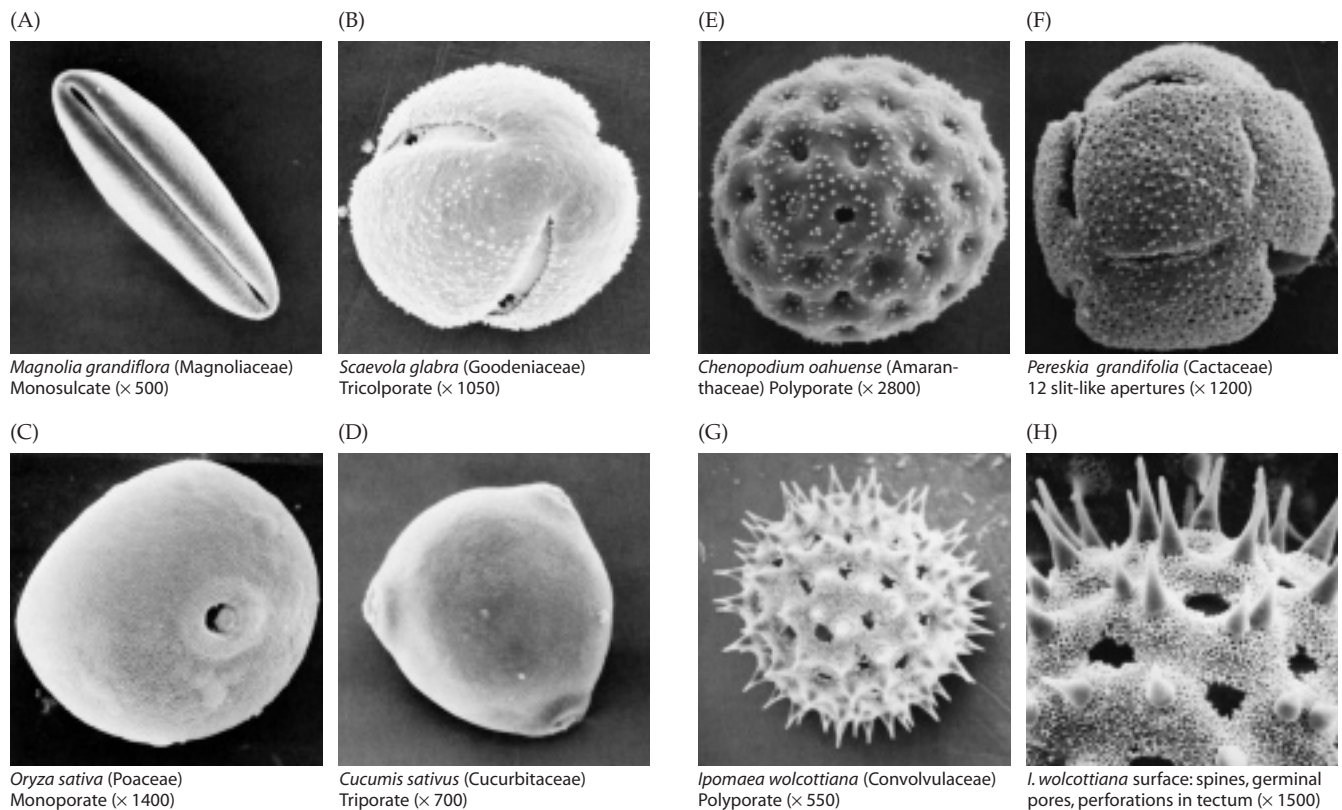
	Polar view	Lateral view
(A) Monocolpate (monosulcate)		
(B) Monoporate		
(C) Tricolpate		
(D) Tricolporate		
(E) Polycolpate		
(F) Polycolporate		

Figure 4.46   Some pollen aperture types. (After Gifford and Foster 1988 and Faegri and Iverson 1950.)

ure 4.47C,D), or variously sculptured by spines, striations, reticulating ridges, knobs, and other features (Figure 4.47E–H). These surface projections, which attach the pollen grain to animal pollinators, are a rich source of systematic characters. Systematists have also made use of internal exine features as characters at many taxonomic levels (Figure 4.48).

During the development of pollen, the microspore nucleus divides into a small generative cell and a much larger vegetative cell. The vegetative cell directs the growth of the pollen tube, while the generative cell usually divides into two sperm within the growing tube. In a minority of angiosperms, including both some tricolpates and some monocots, the generative cell divides into two sperm prior to anther dehiscence, and the pollen is shed in the three-celled stage.

Pollen varies greatly in its ability to function (**viability**) after being shed from the anther. Viability is strongly affected by temperature and humidity, but these effects depend upon taxonomic group. For example, grass pollen is short-lived, sometimes being viable for only minutes or hours, while the pollen of many other species remains viable for up to several years if properly stored. Viability can be evaluated by testing pollen for its capacity to germinate, for metabolic (enzymatic) activity, or for the presence of cytoplasm.

Features of the exterior pollen wall are obvious when it is viewed by scanning electron microscopy (see Figure

(A) *Magnolia grandiflora* (Magnoliaceae) Monosulcate (× 500)

(B) *Scaevola glabra* (Goodeniaceae) Tricolporate (× 1050)

(E) *Chenopodium oahuense* (Amaranthaceae) Polyporate (× 2800)

(F) *Pereskia grandifolia* (Cactaceae) 12 slit-like apertures (× 1200)

(C) *Oryza sativa* (Poaceae) Monoporate (× 1400)

(D) *Cucumis sativus* (Cucurbitaceae) Triporate (× 700)

(G) *Ipomaea wolcottiana* (Convolvulaceae) Polyporate (× 550)

(H) *I. wolcottiana* surface: spines, germinal pores, perforations in tectum (× 1500)

Figure 4.47   Scanning electron micrographs of representative angiosperm pollen grains, showing aperture types and surface features. (From Gifford and Foster 1988; original photos by J. Ward and D. Sunnell.)

Figure 4.48 Cross-section of a typical angiosperm pollen wall (exine, endexine, and intine). (After Gifford and Foster 1988.)
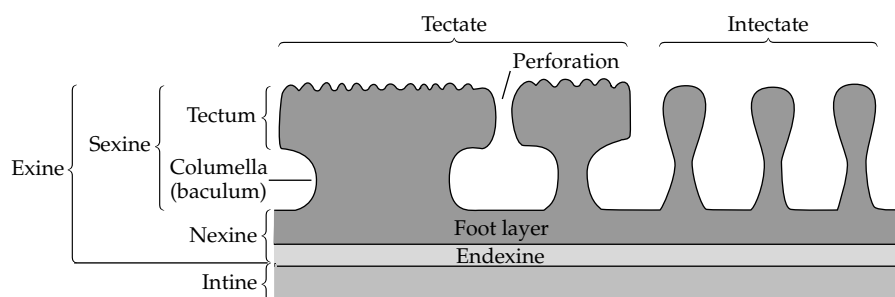
4.47). In this procedure the image is formed from electron beams. The internal structure of pollen, especially the nature of the exine, is commonly examined with transmission electron microscopy.

Secondary Plant Compounds

The biochemical characters of plants have been employed taxonomically for some 100 years, and indirectly through the use of odors, tastes, and medicinal characteristics for much longer. Chemical compounds have been used extensively in plant systematics, from analyses of infraspecific variation (see Adams 1977; Harborne and Turner 1984) to determination of phylogenetic relationships of families and other high-level taxonomic groups (see Dahlgren 1975, 1983; Gershenzon and Mabry 1983). Two major categories of systematically useful chemical compounds can be recognized: **secondary metabolites**, chemicals that perform nonessential functions in the plant; and the information-containing proteins, DNA, and RNA. Proteins are discussed at the end of this chapter, while the taxonomic use of DNA and RNA is covered in detail in Chapter 5.
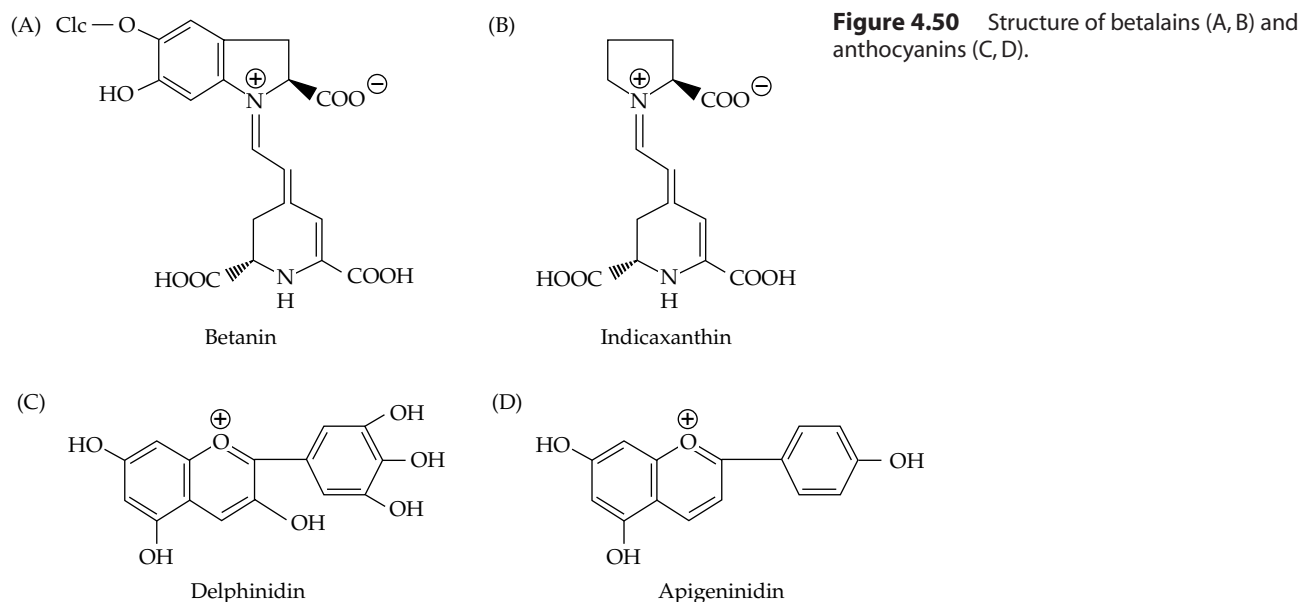
Most secondary compounds function in defense against predators and pathogens, as allelopathic agents, or as attractants in pollination or fruit dispersal (Levin 1976; Cronquist 1977; Swain 1973). The major categories of secondary compounds are briefly discussed below, and some aspects of their distribution among angiosperms are outlined. (For more information on the categories of secondary compounds and their taxonomic use see Gibbs 1974; Young and Seigler 1981; Gershenzon and Mabry 1983; Goodwin and Mercer 1983; Harborne 1984; Harborne and Turner 1984; Kubitzki 1984; Giannasi and Crawford 1986; and Stuessy 1990.)

ALKALOIDS

Alkaloids are structurally diverse (Robinson 1981) and are derived from different amino acids or from mevalonic acid by various biosynthetic pathways. They are physiologically active in animals, usually even at very low concentrations, and many are widely used in medicine (e.g., cocaine, morphine, atropine, colchicine, quinine, and strychnine). A few structural classes of alkaloids are shown in Figure 4.49 (see also Li and Willaman 1976).
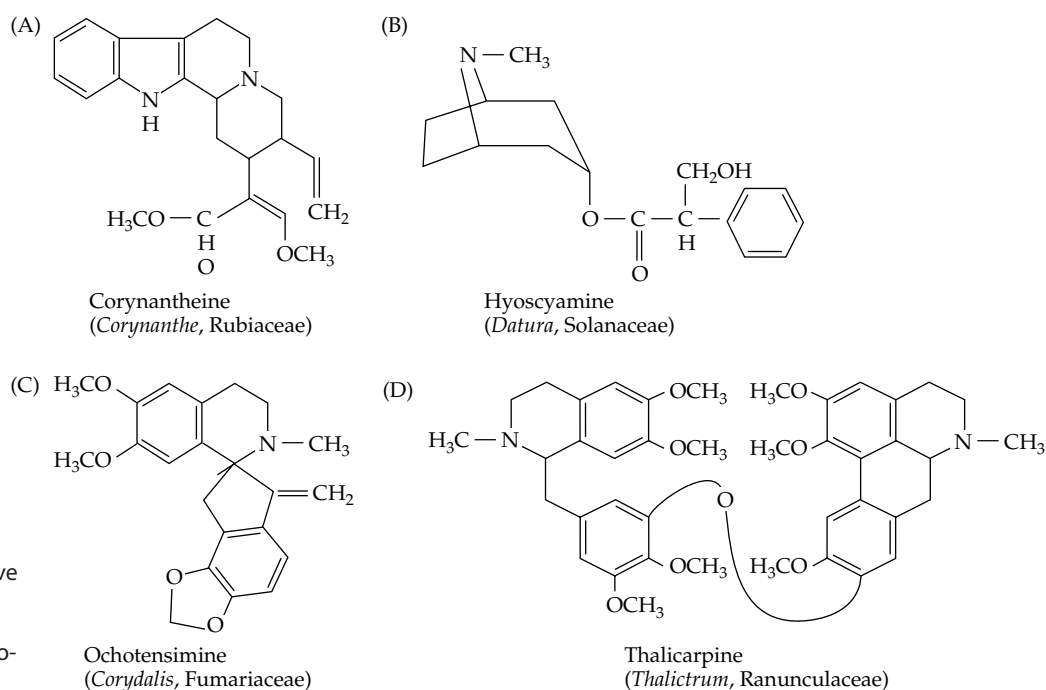
Figure 4.49 Representative alkaloids. (A) A secologanin-type alkaloid. (B) A tropane alkaloid. (C, D) Benzylisoquinoline alkaloids.

(A) Corynantheine (*Corynanthe*, Rubiaceae)

(B) Hyoscyamine (*Datura*, Solanaceae)

(C) Ochotensimine (*Corydalis*, Fumariaceae)

(D) Thalicarpine (*Thalictrum*, Ranunculaceae)

Figure 4.50 Structure of betalains (A, B) and anthocyanins (C, D).

(A) Betanin

(B) Indicaxanthin

(C) Delphinidin

(D) Apigeninidin

Secologanin-type indole alkaloids are limited to the Apocynaceae, "Loganiaceae," and Rubiaceae of the Gentianales. **Tropane alkaloids** occur in a wide array of families, but similar ones are characteristic of Solanaceae and Convolvulaceae (of the Solanales). **Benzylisoquinoline alkaloids** occur in many members of Magnoliales, Laurales, and Ranunculales, as well as the Nelumbonaceae. Other groups, such as **isoprenoid alkaloids** and **pyrrolizidine alkaloids**, show a more scattered distribution among angiosperms and therefore are of less systematic interest.

BETALAINS AND ANTHOCYANINS

Betalains are nitrogenous red and yellow pigments (Figure 4.50A,B) that are restricted to Caryophyllales except for the Caryophyllaceae and Molluginaceae (Clement et al. 1994). In contrast, the pigments of most other plants are **anthocyanins** (Figure 4.50C,D). Betalains and anthocyanins are mutually exclusive; they have never been found together in the same species. Such pigments, occurring in the perianth parts, are of course important in attracting pollinators, but they also occur in young
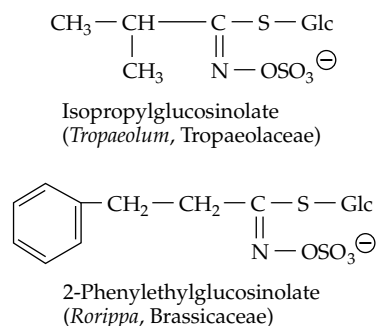
shoots, stems, leaves, and fruits, and probably have additional functions, such as UV absorption and deterrence of herbivory.
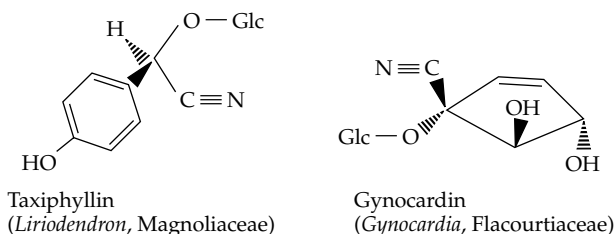
GLUCOSINOLATES

The **glucosinolates** (Figure 4.51), also called mustard oil glucosides, are hydrolyzed by enzymes known as myrosinases to yield pungent hot mustard oils (Rodman 1981). Glucosinolates are synapomorphic for the Brassicales. The glucosinolates of the four core families of the Brassicales (Brassicaceae, Resedaceae, Tovariaceae, and Moringaceae) are biosynthetically more complex than those of the other families of the order. Current evidence suggests that these compounds evolved only twice, in the common ancestor of Brassicales and in the common ancestor of the species of *Drypetes* (see Euphorbiaceae) (Rodman et al. 1996).
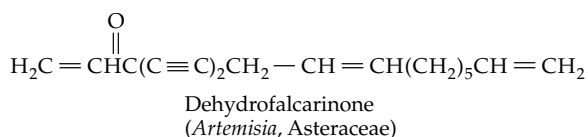
CYANOGENIC GLYCOSIDES

Cyanogenic glycosides (Figure 4.52) are defensive compounds that are hydrolyzed by various enzymes to release hydrogen cyanide (Hegnauer 1977). This process is called **cyanogenesis**. Cyanogenesis is widespread in angiosperms, and five different biosynthetic groups of cyanogenic glycosides are known. Some biosynthetic

Isopropylglucosinolate
(*Tropaeolum*, Tropaeolaceae)

2-Phenylethylglucosinolate
(*Rorippa*, Brassicaceae)

Figure 4.51 Representative glucosinolates.

Taxiphyllin
(*Liriodendron*, Magnoliaceae)

Gynocardin
(*Gynocardia*, Flacourtiaceae)

Figure 4.52 Representative cyanogenic glycosides.

$$H_2C = \overset{\overset{\displaystyle O}{\parallel}}{C}HC(C \equiv C)_2CH_2 - CH = CH(CH_2)_5CH = CH_2$$

Dehydrofalcarinone
(*Artemisia*, Asteraceae)

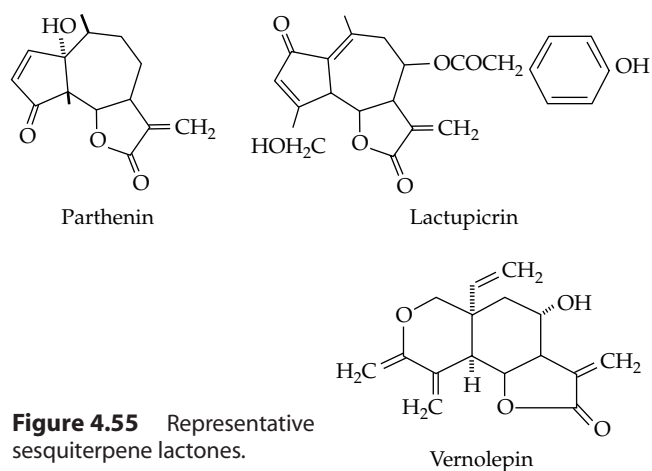**Figure 4.53**   A representative polyacetylene.

types probably have evolved numerous times, but others, such as the **cyclopentenoid cyanogenic glycosides**, are more restricted in distribution (in this case to "Flacourtiaceae," Passifloraceae, Turneraceae, and Malesherbiaceae). Cyanogenic glycosides synthesized from leucine are common in subfamilies Amygdaloideae and Maloideae of the Rosaceae. Similar cyanogenic compounds are found in Fabaceae and Sapindaceae. Cyanogenic glycosides derived from tyrosine are common in several families of Magnoliales and Laurales.

POLYACETYLENES

Polyacetylenes (Figure 4.53) are a large group of nonnitrogenous secondary metabolites formed from the linking of acetate units via fatty acids. These compounds characterize a related group of asterid families, including Asteraceae, Apiaceae, Pittosporaceae, Campanulaceae, Goodeniaceae, and Caprifoliaceae. **Falcarone polyacetylenes** are restricted to the Apiaceae (including Araliaceae) and Pittosporaceae. These two families are also similar in their essential oils, oleanene and ursene-type saponins, caffeic acid esters, furanocoumarins, and flavonoid profiles.

TERPENOIDS

Terpenoids are a large and structurally diverse group of secondary compounds that are important in numerous biotic interactions (Goodwin 1971). They are formed by the union of 5-carbon isopentenoid pyrophosphate units formed in the mevalonic acid pathway. Terpenoids are very widely distributed, and many have primary physiological functions, being a part of membrane-bound steroids, carotenoid pigments, the phytyl side chain of

Geraniol   Menthol   Limonene

Carvone   Camphor

Figure 4.54   Representative monoterpenoids.

Parthenin   Lactupicrin

Figure 4.55   Representative sesquiterpene lactones.

Vernolepin

chlorophyll, and the hormones gibberellic acid and abcisic acid. The distribution of a few terpenoid types, however, is of taxonomic interest. Volatile **monoterpenoids** and **sesquiterpenoids** (10-carbon and 15-carbon compounds; Figures 4.54 and 4.55) are the major components of **essential** (or **ethereal**) **oils**, which are characteristic of Magnoliales, Laurales, Illiciales, and Piperales, as well as in only distantly related clades such as Myrtaceae, Rutaceae, Apiales, Lamiaceae, Verbenaceae, and Asteraceae. These compounds occur not only in vegetative tissues (in spherical cells or various cavities or canals in parenchymatous tissues) but also in floral odor glands (where they are released and often function as floral attractants).

Sesquiterpene lactones (Figure 4.55), another terpenoid type, are primarily known from the Asteraceae (where they are diverse and taxonomically useful; Seaman 1982), but they also occur in a few other families, such as Apiaceae, Magnoliaceae, and Lauraceae.

Various **diterpenoids** (20-carbon), **triterpenes** (30-carbon), and **steroids** (triterpenes based on cyclopentane perhydro-phenanthrene ring system) are widely distributed and also have some systematic significance (Young and Seigler, 1981). The triterpenoid **betulin** occurs in the bark of the white birches (*Betula papyrifera* and relatives); it is waterproof, highly flammable, and virtually unknown outside this group. Betulin is taxonomically useful at the species level (O'Connell et al. 1988). **Triterpene saponins** occur in both Apiaceae and Pittosporaceae, and support the hypothesized close phylogenetic relationship of these two families. The triterpenoid derivatives **limonoids** and **quassinoids** (Figure 4.56), which are biosynthetically related, are limited to the Rutaceae, Meliaceae, and Simaroubaceae of the Sapindales; quassinoids constitute a distinctive synapomorphy of the Simaroubaceae. **Cardenolides** are highly poisonous glycosides of a type of 23-carbon steroid, which occur in Ranunculaceae, Euphorbiaceae, Apocynaceae, Liliaceae, and Plantaginaceae.

Iridoids are 9- or 10-carbon monoterpenoid derivatives that usually occur as O-linked glycosides (Figure
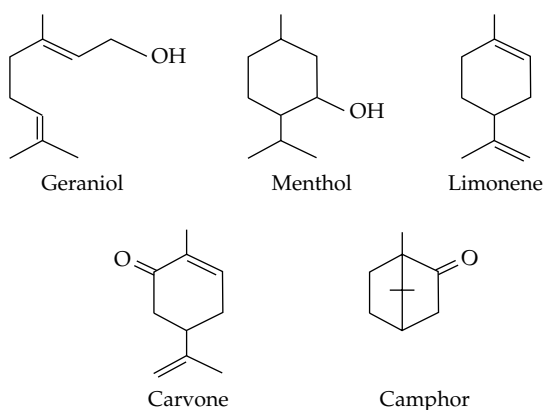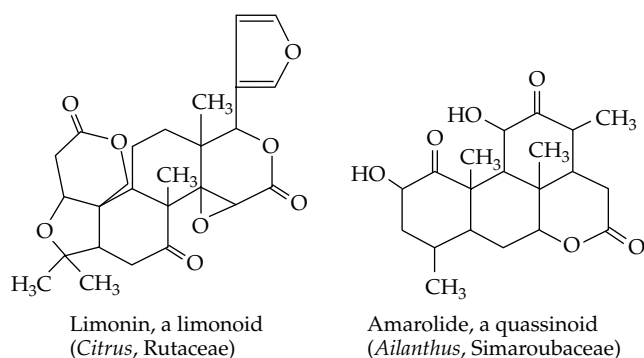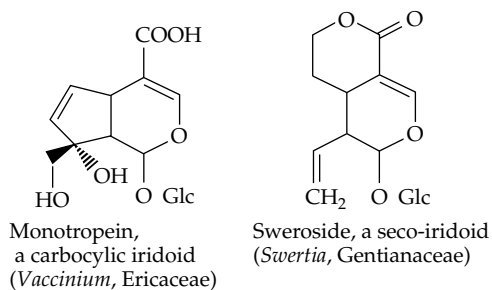
Figure 4.56   Representative triterpenoid derivatives.
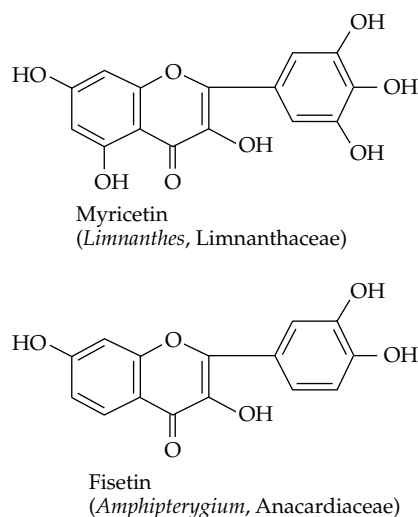

Figure 4.58   Representative flavonoids.

4.57). Iridoid compounds are found in many families of the asterid clade, and iridoid types have been used to support relationships within this group (Jensen et al. 1975; Jensen 1992). For example, **seco-iridoids**, a chemically derived type of iridoid compound that lacks a carbocyclic ring, occur in Gentianales, Dipsacales, and many families of Cornales and Asterales. In contrast, **carbocyclic iridoids**, which have two rings, one composed entirely of carbon, are characteristic of the Lamiales (except for the Oleaceae). The presence of iridoids in the Ericales and Cornales provides evidence that these taxa actually belong to the asterid clade, even though they frequently have been excluded from that group (see Cronquist 1981).

FLAVONOIDS

Flavonoids (Figure 4.58) are phenolic compounds that usually occur in a ring system derived through cyclization of an intermediate from a cinnamic acid derivative and three malonyl CoA molecules. They probably function in defense against herbivores and in regulation of auxin transport. Flavonoids are extensively employed in plant systematics, probably because they can be fairly easily extracted and identified. They are found throughout the embryophytes (and are also known from the charophyte algae), and have a diverse array of side groups attached to a common system of rings. Although primarily useful in assessing relationships among close-

ly related species (or in studies of infraspecific variation), flavonoids are occasionally useful in assessing phylogenetic relationships at higher levels (Bate-Smith 1968; Crawford 1978; Gornall et al. 1979; Harborne and Turner 1984). For example, the presence of certain 5-deoxyflavonoids in *Amphipterygium* (which has often been placed in its own family, the Julianiaceae; see Cronquist 1981) support its placement in Anacardiaceae. Flavonoid chemistry also has been used to support a hypothesized relationship between Fabaceae and Sapindales. Finally, flavonoid profiles have been shown to be quite useful in studies of interspecific hybridization (see Alston and Turner 1963; Smith and Levin 1963; Crawford and Giannasi 1982).

Proteins

Proteins are an extremely diverse class of molecules made up of amino acids linked into a chain by peptide bonds. This chain of amino acids—a **polypeptide chain**—is three-dimensionally folded, resulting in a diversity of molecular shapes. Proteins function as enzymes, storage molecules, transport molecules, pigments, and structural materials. Proteins have been used systematically in several different ways; the majors methods, such as amino acid sequencing, systematic serology, and electrophoresis, are discussed briefly here.

AMINO ACID SEQUENCING

Phylogenetic information is contained in the **amino acid sequence** (the **primary structure**) of proteins. These sequences can be used as taxonomic characters, just as the nucleotide sequences of DNA and RNA are used to reconstruct phylogenetic relationships. Proteins such as cytochrome *c*, plastocyanin, ferredoxin, and ribulose-1,5-bisphosphate carboxylase (small subunit) have been used in determining phylogenetic relationships among

Figure 4.57   Representative iridoids.

diverse groups of living organisms and within angiosperms (Boulter et al. 1978; Fairbrothers et al. 1975; Fairbrothers 1983; Martin et al. 1985). However, at the present time most taxonomic interest has shifted away from amino acid sequencing in favor of nucleotide sequencing, because of technological advances in the extraction, amplification and sequencing of DNA and RNA (see Chapter 5).

SYSTEMATIC SEROLOGY

Systematic serology first developed in the early 1900s, following the discovery of serological reactions and the discipline of immunology (Fairbrothers et al. 1975; Fairbrothers 1983). In this method, proteins—antigens—are extracted from a particular species and injected into rabbits to produce antibodies. The antibodies are then cross-reacted to antigens from a series of taxa related to the original species. The degree of precipitation observed is an indication of how similar the taxa are: a strong precipitation reaction indicates that the antigen proteins of a particular species are very similar to the proteins of the species that originally stimulated antibody production. A high level of protein similarity is taken as evidence that taxa are closely related, whereas a low level (as assessed by low antibody/antigen reactivity) indicates that the taxa are only distantly related.

Crude protein extracts from seeds or pollen grains are often used to produce antibodies; however, more elaborate methods have been developed, allowing single proteins from different taxa to be compared. Serological techniques have proven to be quite useful in assessing evolutionary relationships. For example, such studies have supported the placement of *Hydrastis* in the Ranunculaceae (and not the Berberidaceae), the placement of *Mahonia* within *Berberis* (Berberidaceae), the close relationship of *Typha* and *Sparganium* (Typhaceae), and the removal of *Nelumbo* (Nelumbonaceae) from the Nymphaeaceae (Fairbrothers et al. 1975; Fairbrothers 1983).

ELECTROPHORESIS

Electrophoresis is a technique for measuring the rate and direction of movement of organic molecules (in this case, proteins) in response to an electric field. The rate and direction of protein movement in a starch or an agar gel will depend on the protein's net surface charge, size, and shape. Proteins can then be stained, resulting in a series of bands in the gel. Those proteins that migrate to the same place in a slab of agar gel and yield similar banding patterns when stained are considered to represent homologous proteins. The banding patterns resulting after electrophoresis of seed or pollen proteins (or of specific types of enzymes) can be compared, and the presence or absence of particular bands used as taxonomic characters.

Electrophoresis is most useful at the level of populations within a species or among closely related species, and the resulting taxonomic characters (banding patterns) are usually analyzed phenetically (Crawford and Julian 1976; Crawford 1979, 1983). In recent years DNA (Chapter 5) has replaced proteins as a source of data about variation at and below the species level.

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