

Angiosperms



PLANTS WITH AN ENCLOSED SEED

THE MYSTERIOUS ORIGIN OF THE ANGIOSPERMS

Key Innovations of Angiosperms Include Both Vegetative and Reproductive Features

THE RISE OF ANGIOSPERMS TO DOMINANCE

*Angiosperm Fossils Show Climate Change during the Tertiary Period
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KEY CONCEPTS

1. Angiosperms, or flowering plants, are unique in having ovules borne inside carpels, rather than on naked scales or leaves, as in gymnosperms. The ovule is fertilized by a pollen grain that is transferred from a stamen to a carpel by wind, water, or animals and then germinates into a tube that grows through ovary tissue, ultimately reaching the ovule and its haploid egg cell. The tube bursts, releasing two sperm nuclei. After one nucleus fertilizes the egg, the egg becomes an embryo, the ovule becomes a seed, and the ovary becomes a fruit. The new features--ovary and fruit--increase the protection of the gametophyte generation and of the embryo; they also widen the dispersal of the seed over time and space.
2. Ovaries are part of a new structure called the carpel. Ovule-containing carpel(s) plus pollen-containing stamens and variously colored and shaped petals and sepals collectively comprise a new structure called a flower
3. Double fertilization is an innovation of the angiosperm life cycle. When a pollen grain becomes a mature microgametophyte, it produces a long pollen tube that contains two sperm nuclei. One nucleus unites with an egg to produce a zygote, whereas the other unites with two other nuclei in the gametophyte (the polar nuclei) to produce an endosperm nucleus. As the embryo develops from the zygote, the endosperm nucleus divides repeatedly and surrounds the embryo with stored food. Double fertilization conserves energy, because food for the embryo does not accumulate until after fertilization.
4. The first angiosperm fossils date to approximately 135 million years ago. However, the initial split of the lineage leading to angiosperms from other seed plants may have occurred during the time of the early seed plants, more than 250 million years ago. Currently, it is not possible to say which seed plants are the closest relatives, and it may be that no living group of seed plants is closely related to the angiosperms. During the Cretaceous period, angiosperms speciated rapidly, and by the early Cenozoic era, they had become the dominant terrestrial plant groups.
5. Angiosperms form a monophyletic group. A basal grade of lineages includes *Amborella*, water lilies, and star anise and its relatives. The remaining taxa--that is, the core angiosperms--comprise three major clades: magnoliids, monocots, and eudicots. All together, angiosperms number 257,000 species in 14,000 genera.
6. Magnoliids vary from woody to herbaceous. Magnoliid flowers vary from large and showy, with numerous spirally arranged parts, to small and inconspicuous, with parts in threes. Many important foods, timber, spices, and medicinal and ornamental plants, such as cinnamon, camphor, avocado, bay, saffron, magnolia, and tulip tree, are magnoliids.

7. Monocots typically have parallel-veined leaves, flower parts in threes, embryos with a single cotyledon, sieve-tube members having plastids with protein crystals lacking starch grains, scattered vascular bundles, and prominent adventitious roots. Monocots consist of such economically and ecologically important plants as agaves, bananas, grasses, irises, lilies, onions, orchids, palms, rushes, sedges, yams, and yuccas.

8. Eudicots typically have net-veined leaves, flower parts in fours or fives, embryos with two cotyledons, sieve-tube members having plastids with starch grains, stem vascular bundles in a ring, stamens with slender filaments, and three-apertured (tricolpate) pollen. Basal eudicots include Ranunculales and Proteales, whereas the main group contains three major lineages: caryophyllids, rosids, and asterids. Eudicots include such economically and ecologically important plants as blueberries, buckwheat, cacti, carrots, coffee, grape vines, hemp, legumes, melons, poppies, potatoes, roses, sandalwood, stone fruits, strawberries, sunflowers, tea, teak, tomatoes, and walnuts.

9. Plant geography is the study of plant distribution throughout the world. Some clades are widely distributed, whereas others are narrowly restricted to one part of the world and one type of environment. In the last thousand years, human populations have purposely and accidentally carried plants into regions those plants had not yet reached on their own, creating a more homogenous global landscape. Angiosperms are of exceptional importance to people for food, fiber, pharmaceuticals, building materials, ornaments, and beverages.

25.1 PLANTS WITH AN ENCLOSED SEED

Flowering plants dominate the earth's vegetation (Fig. 25.1). Hardwood forests and woodlands, shrublands, grasslands, wetlands, deserts, cold high-elevation tundras, and warm low-elevation rain forests have a biomass (weight of organic matter) composed chiefly of flowering plants. Nearly all of the earth's crop plants, orchard trees, garden plants, and ornamentals are flower plants. Coffee, tea, and cocoa beverages are made from flowering plants; cotton and linen are fabrics made from flowering plants. Many pharmaceuticals--from aspirin to morphine--come from metabolic chemicals in flowering plants or are patterned after these chemicals.

Angiosperm is a synonym for flowering plant. It means "seed within a vessel" or "enclosed seed." The defining angiosperm feature is the enclosure of the ovules within surrounding tissue called an **ovary**. The ovary is part of a flower, a structure that occurs only in angiosperms. The ovary, and sometimes associated tissues, eventually forms a fruit, another unique angiosperm structure.

This chapter brings us full circle within this textbook. The initial chapters focused on the development, structure, physiology, and genetics of flowering plants. Then the key features of fungi, protists, algae, bryophytes, seedless vascular plants, and gymnosperms were examined in a sequence that roughly parallels the evolutionary appearance of these groups in the fossil record. Within the green plant lineage, this sequence shows three trends: (1) increasing prominence and

complexity of the diploid sporophyte generation; (2) decreasing prominence and complexity of the haploid gametophyte generation; and (3) ever more elaborate adaptations to life on land. The survey, the sequence, and the trends all peak with the angiosperms, one of the most successful groups of terrestrial organisms. When did this group evolve, and how did it come to dominate the land?



Figure 25.1. Vernal pool vegetation in full flower, springtime, Sacramento Valley, CA. (a) Aspect, the dominant color coming from gold fields (*Lasthenia* sp.). (b) Close-up of *Downingia*, a smaller vernal pool plant.

25.2 THE MYSTERIOUS ORIGIN OF THE ANGIOSPERMS

Charles Darwin called the origin of flowering plants "an abominable mystery," because they appear suddenly in the geologic record without a clear fossil history showing a transition from some other plant group (Fig. 25.2). The first angiosperm fossils—from the early Cretaceous period, about 135 million years ago—are limited to microfossils such as pollen grains and bits of stem or leaf cuticle. By the mid-Cretaceous period, macrofossils are numerous, diverse, and complex. Fossil leaves, stems, flowers, fruits, and seeds are common.

How can we explain the sudden appearance of flowering plants? Some paleobotanists suggest that the initial line leading to angiosperms diverged from other seed plants very early.

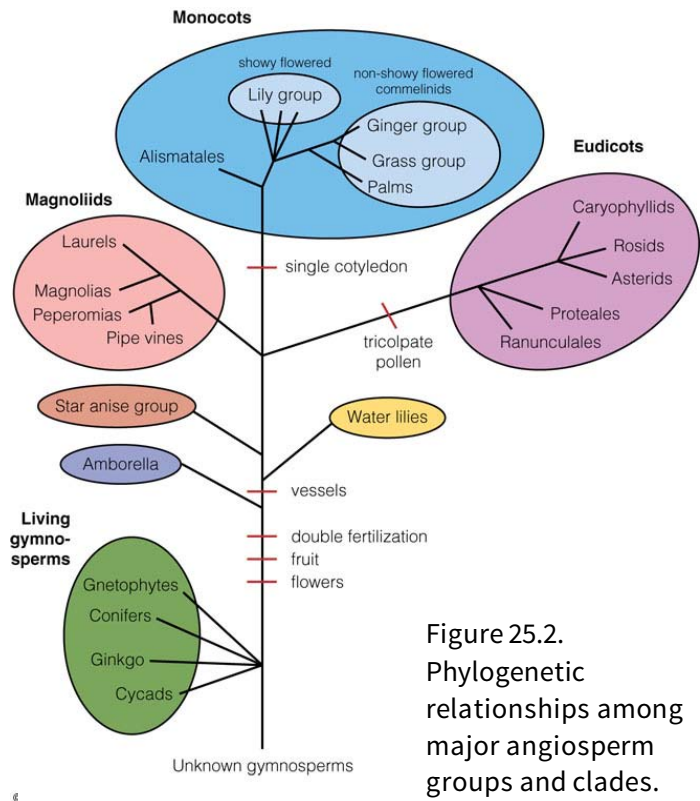


Figure 25.2. Phylogenetic relationships among major angiosperm groups and clades.

These early ancestors of angiosperms would have lacked many of the traits typical of angiosperms today, and they might be difficult to identify in the fossil record. Over millions of years, the full set of characteristics that make angiosperms so distinctive and successful evolved one by one.

The question of when angiosperms originated is connected to the equally difficult problem of identifying their closest relatives. Only a few years ago, many evolutionists hypothesized that the angiosperms were most closely related to gnetophytes, because they share such striking morphological traits as insect pollination, flowerlike structures, vessels, reduced gametophytes, and double fertilization (both sperm fuse with a cell in the megagametophyte). However, when botanists began constructing cladograms using molecular data from the relatively unexplored mitochondrion, and then combined these data with sequences from the chloroplast and nucleus, a different picture emerged (Fig. 25.3). As these ongoing studies have expanded in scope and scale, they have increasingly supported the idea that angiosperms diverged early in the history of seed plants, not more recently, as most botanists had assumed.

An early divergence, if true, could mean that the closest relatives of angiosperms are now extinct. According to **paleobotanists** Michael Donoghue and James Doyle, it may well be that there are no *living* seed plants closely related to angiosperms. In other words, Darwin's famous statement about the angiosperms' origin being an abominable mystery is still appropriate today.

Well-preserved, early angiosperm macrofossils have been found in China and have been given the name *Archaeofructus*. These small, herbaceous plants had no petals or sepals, but they did bear prominent ovaries with enclosed seeds and paired stamens. They flourished in aquatic habitats 125 million years ago to perhaps as early as 140 million years ago, although an origin preceding the Cretaceous period is possible. They do not resemble any known modern group and may actually be submerged aquatic plants that are reduced and highly specialized; they may not preserve many primitive features of the earliest angiosperms.

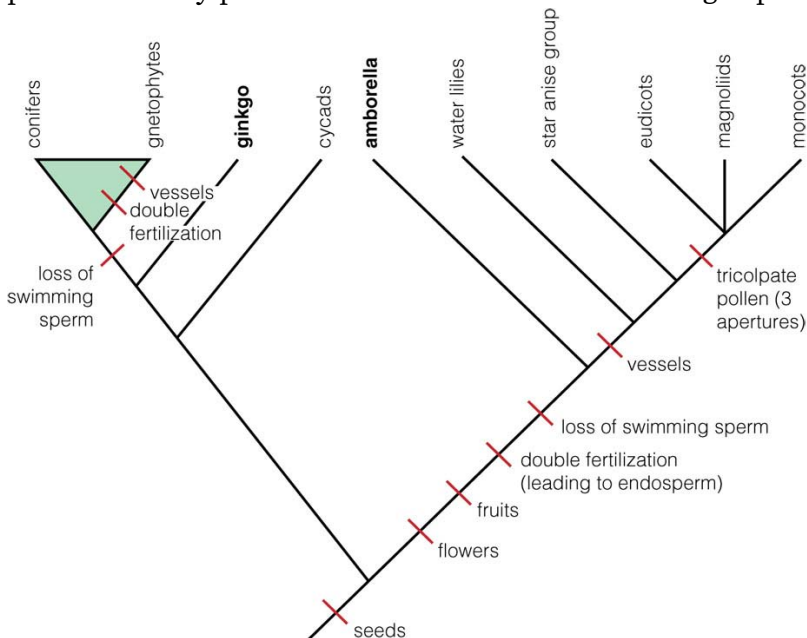


Figure 25.3. A phylogeny for the seed plants, showing the relationships between angiosperms (right) and gymnosperms (left)

Key Innovations of Angiosperms Include Both Vegetative and Reproductive Features

Why were flowering plants able to supplant gymnosperms, as well as many fern groups? Probably because they had new vegetative and reproductive features that promoted survival and gave them a competitive advantage. One such feature is an improved vascular system. Angiosperm xylem typically contains large, relatively thin-walled **vessels** in addition to the tracheids. The movement of water is much more efficient through these vessels. Angiosperm phloem contains **sieve-tube members** in association with companion cells, in contrast to the sieve cells of gymnosperms. Sieve-tube members have a larger diameter and larger sieve pores, increasing the efficiency of sugar transport.

Another novel feature is the **fruit**, the ripened ovary with enclosed seeds. Fruits aid in the dispersal of seeds by catching the wind, adding buoyancy in water, or being moved by animals. Some gymnosperms have fleshy arils or scales that accomplish the same end, but not to the same degree of elaboration as in angiosperms.

William Bond (Cape Town University, South Africa) combined these features and others to formulate a **seedling hypothesis** as an explanation of angiosperm dominance. His hypothesis compares gymnosperms to a tortoise and angiosperms to a hare. Gymnosperms are woody and slow-growing and have lengthy reproductive cycles. The juvenile stage is long. Cotyledons and young leaves are thick and evergreen, energetically expensive to manufacture and not changeable in shape. Gymnosperm tracheids and sieve cells are relative inefficient. All this leads to a slow seedling growth rate.

In contrast, many angiosperms are herbaceous and fast-growing and have short reproductive cycles. The juvenile stage can be short. Cotyledons and young leaves often are thin, deciduous, energetically cheap to make, and variable in shape. Vessels and sieve-type members are highly efficient pipelines. All this leads to a rapid seedling growth rate. Bond's theory predicts that gymnosperms will be outcompeted everywhere except where angiosperm seedling competition is reduced, as in cold-temperate regions with nutrient-poor soils.

Angiosperms produce a novel structure: the **flower**. The ovary, with its enclosed seeds, is part of this new structure, which serves to aid pollination, protect the developing seeds, and disperse the mature seeds. How could the flower have developed from preexisting organs, such as stems and leaves? The flower is thought to be a modified branch whose leaves have become sepals, petals, stamens, and carpels. Several types of indirect evidence support this hypothesis. The early developmental phases resemble those of leaves, and they are found in the same place that a leaf would be found. The stamens or carpels of some plants, such as *Firmiana simplex*, bear a striking resemblance to leaves. When the ovary of this tree matures, it splits open to show five leaf-like carpels that bear seeds along their margins (Fig. 25.4).

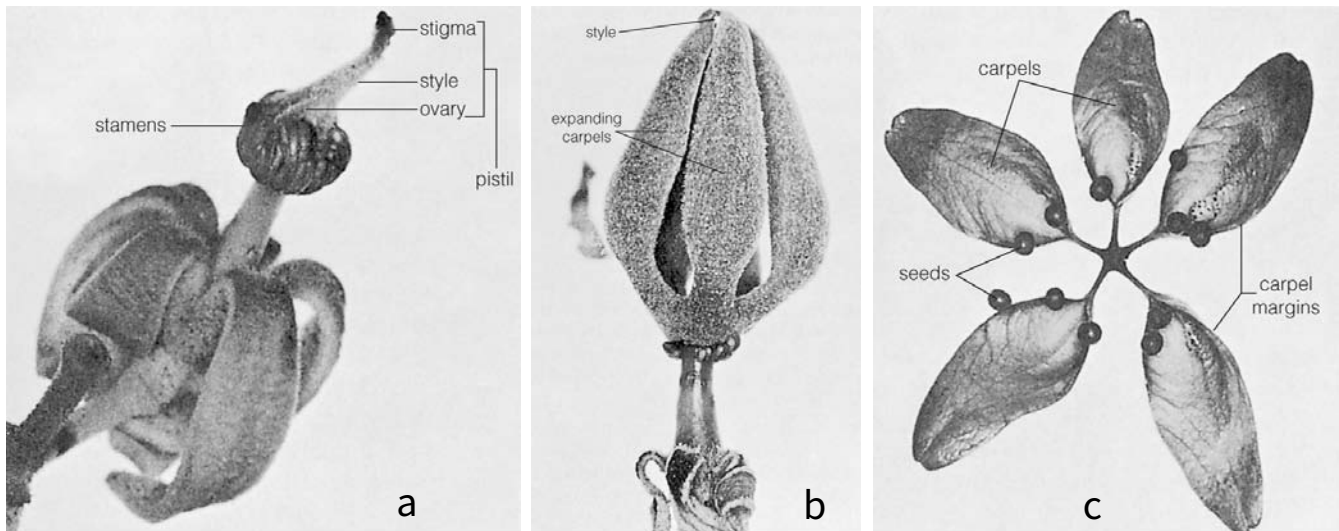


Figure 25.4. *Firmiana plantanifolia*. Note that the pistils (carpels) resemble leaves. (a) A single pistil of the flower. (b) After pollination, the pistils separate, except along the style and stigma. (c) At maturity, each ovary splits open, exposing seeds attached to a leaflike surface.

25.3 THE RISE OF ANGIOSPERMS TO DOMINANCE

Angiosperms diversified and became so abundant in the fossil record of the late Cretaceous period that we can conclude they were the dominant plant life on land. As the Mesozoic era ended, so did dominance by gymnosperms and dinosaurs. As far as can be inferred from fossils, approximately 75% of all species on Earth at the time went extinct. There also was a rather sudden cooling of the climate at the boundary of the Mesozoic and Cenozoic eras--so sudden that some paleobotanists turn to theories of catastrophic events to explain the massive environmental change and extinctions that occurred in such a brief time. There is evidence that a relatively large meteorite slammed into what has become the Gulf of Mexico, along the Yucatan Peninsula, creating disastrous fires and throwing debris into the atmosphere. During the months or years the debris took to settle back to Earth, it reflected solar radiation back to space; consequently, temperatures on Earth plummeted, extinguishing entire groups of organisms. One extension of this theory is that such disturbances of extraterrestrial origin have occurred many times--not just at the end of the Mesozoic era--and will occur again in the future.

It is unknown whether such an event alone ushered in the Cenozoic era or whether some other factor contributed, such as the extensive volcanic activity of this period. It is known, however, that the following 65-million-year span of the Cenozoic era has been one of continuous climatic change (Fig.25.5), and that through it all, angiosperms have held dominance.

Angiosperm Fossils Show Climatic Change during the Tertiary Period

The Cenozoic era is traditionally divided into two periods, the Tertiary and the Quaternary. The Tertiary period extended from approximately 65 million to 2 million years ago. During this time, continents continued to break apart, increasing the

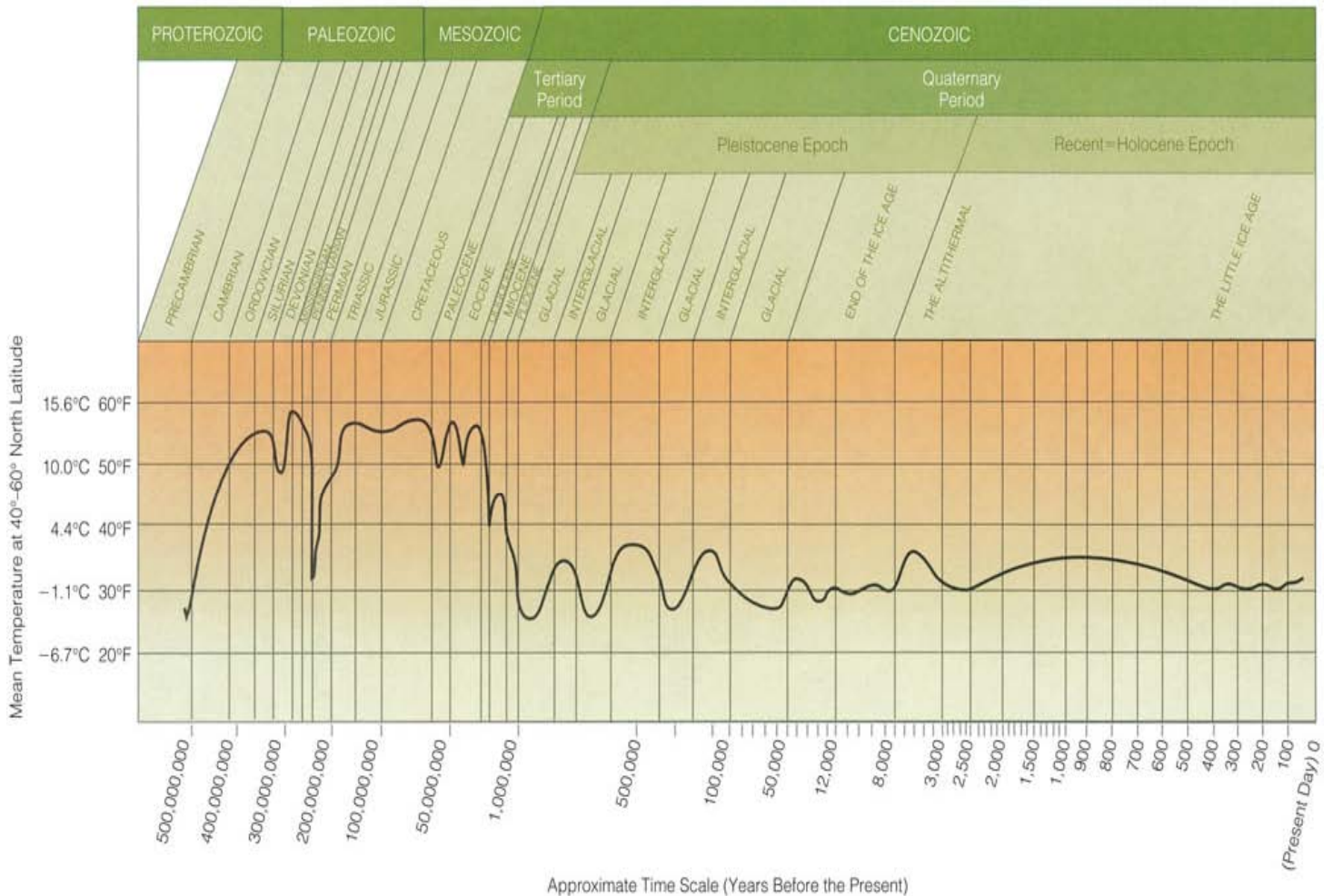


Figure 25.5. Average temperatures over geologic time for the earth at 40 to 90 degrees north latitude. The time scale is distorted to show more detail for the last 1 million years. The current mean temperature (extreme right) is approximately 0°C. In the Cretaceous period, when angiosperms first appeared in the fossil record, the mean temperature was about 13°C warmer than the current temperature.

diversity of climate and vegetation types (Fig. 25.6). An excellent case study example of climate and vegetation change during that time comes from the fossil record of the John Day Basin in northeastern Oregon (see "PLANTS, PEOPLE, AND THE ENVIRONMENT: *We Live on a Changing Surface*" endnote).

The Ice Age Affected the Diversity of Plants in Temperate Zones

The Quaternary period began about 2 million years ago, when the earth's climate cooled by a few degrees--just enough to alter hydrologic balances near the poles and at high elevations. Summer melting no longer kept up with winter snowfall, resulting in snow accumulation year after year. Its layers compressed into ice, and

great ice sheets called *glaciers* coalesced, moved, and came to cover much of the cool-temperate zone. The balance of water shifted from the oceans toward bodies of freshwater and ice; sea level fell. This **Ice Age**, which has occupied most of the Quaternary period, is known as the Pleistocene epoch (Fig. 25.5).

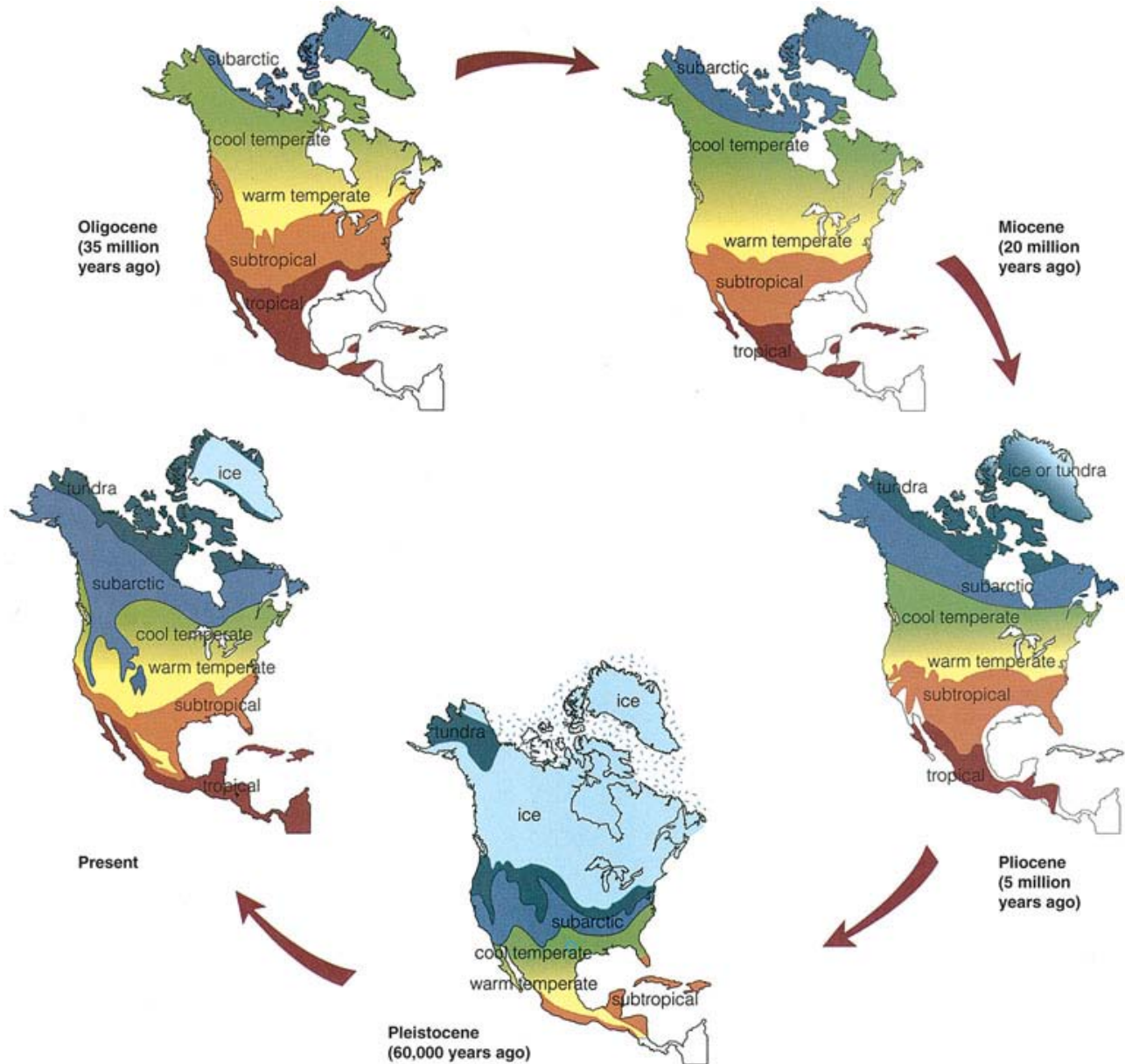


Figure 25.6. Climate zones of North America during the last 35 million years.

Periodically during the Pleistocene, the climate warmed and glaciers retreated; then the climate cooled and glaciers readvanced. Glacial-interglacial cycles occurred approximately every 41,000 years until about 800,000 years ago. Since then, the cycle has been on the order of 100,000 years. During glacial advance, almost all of Canada, the northern third of the United States, most of Europe, all of Scandinavia, and large parts of Siberia were covered by ice. Mountain chains that

extended well into the tropics were all capped by glaciers that extended downslope, filling wide canyons and mountain valleys. Ice covered 30% of the earth's land surface. Sea level was 100 m (325 feet) lower than current levels because so much water was locked in glacial ice.

When glaciers advanced, vegetation zones were pushed lower in elevation or lower in latitude. For example, at full glacial advance 18,000 years ago (Fig. 25.7), a spruce-pine boreal forest covered the eastern United States as far south as North Carolina. Treeless tundra covered the Appalachian Mountains. A thin strip of mixed conifer-hardwood forest formed a northern cap to oak-hickory deciduous forest, and Florida (much wider then) was covered by sand dune scrub. Only 800 km of north-to-south distance separated the front of an ice sheet from deciduous forest, indicating a steep gradient in climate.

When glaciers retreated, vegetation zones rebounded, the climatic gradient softened, and landscape diversity increased (Fig. 25.7). Each cycle of advance and retreat caused some extinctions, however, so that the biota of the temperate zone became simpler during the Pleistocene epoch.

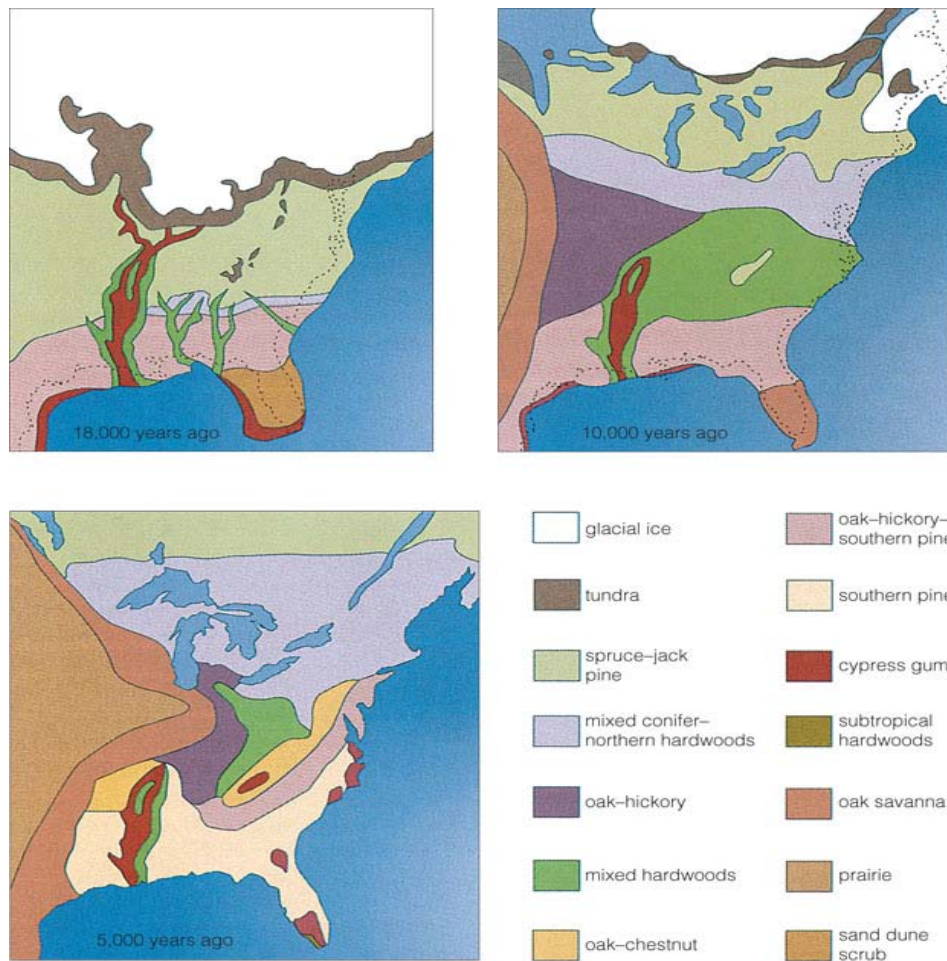


Figure 25.7. Reconstruction of major vegetation zones in eastern North America since the last glacial maximum.

Angiosperm Evolution Was Affected by Humans in the Quaternary Period

Humans also played a role in plant distribution and evolution during the Quaternary period. Initially, humans in hunter-gatherer cultures might merely have harvested wild plants as they found them. However, they gradually began to cultivate and select some of those species for convenience and greater yield. They did not sow seeds in geometric patterns and till the land, but they did use fire, pruning, selective harvesting, and sowing of rhizomes, bulbs, or seeds *without* cultivation to favor the abundance of certain food plants. Anthropologists call this stage **protoagriculture**. Protoagriculture might have gone on for thousands of years before agriculture and the domestication of crops were fully established.

The "root" crops cassava (*Manihot esculenta*) and taro (*Colocasia esculenta*) were cultivated in southeastern Asia as early as 15,000 years ago. Human-induced selection in these species has gone on for so long that some varieties have lost, or nearly lost, their capacity for sexual reproduction. It is doubtful that they could survive in nature. The earliest archaeological evidence for seed agriculture (cultivation of annuals such as rice, wheat, beans, or squash) goes back 11,000 years. Wild annuals that demonstrated exceptional productivity were valued and propagated. Over time, such artificial selection pressure on the genetic makeup of plants resulted in so much change from their wild relatives that it is now difficult to determine where, and from what wild stock, they were first domesticated.

Humans have also accidentally domesticated and favored the evolution of weeds. Weeds are plants that grow well in disturbed or trampled soil, in waste areas rich in nitrogen, or interspersed with crop plants. Some weeds have evolved seeds that are the same size as crop seeds; therefore, they are not easily separated during threshing or sieving. Thus, when the next season's crop is sown, the weeds are sown inadvertently along with it.

As humans explored new lands, they brought along not only their culture but also their domesticated plants and companion weeds. Sometimes ornamental plants were brought into new regions. The weeds and ornamentals often turned out to be aggressive competitors in their new homes, able to displace native species from the landscape. As much as one third of the flora of some parts of the United States is composed of weeds imported from various parts of the world, including Europe, Australia, Asia, and Africa. Introduced plants have become common in forests, grasslands, woodlands, wetlands, coastal strands, and deserts. Only the most stressful habitats, such as alpine tundra, salt marshes, and rocky outcrops, seem free, or almost free, of introduced species. The accelerated pace of land disturbance, single-species cultivation, and travel are making the flora of the world increasingly homogeneous and lower in biological diversity.

25.4 NOVEL FEATURES OF THE ANGIOSPERM LIFE CYCLE

Angiosperms share with gymnosperms the characteristic of producing a seed, but the life cycles of the two groups are different in several important features. In flowering plants, the size and complexity of the gametophyte generation become reduced, the location of the ovule becomes hidden, there are two fertilization events,

and the dispersal of the seed is improved by its enclosure within a fruit. These novel life cycle features help flowering plants adapt to life on land and conserve their food reserves.

Our survey of plants has revealed a trend of decreasing gametophyte size and increasing dependence on the sporophyte. Angiosperms carry the reduction further than gymnosperms for both male and female gametophytes. In angiosperms, the male gametophyte (in the form of a pollen grain) has only two or three nuclei. The female gametophyte has been reduced to seven cells and eight nuclei, and an archegonium is no longer recognizable. This reduction probably leads to more efficient reproduction. When an egg is not fertilized or when a pollen grain does not land in a suitable flower, less energy is wasted.

Additional savings in energy result when animal vectors transfer pollen grains to the stigmas of other flowers (Fig. 25.8). Many of these living pollen carriers move selectively, not randomly, visiting sequential flowers of the same species. Thus fewer pollen grains are needed to make seeds.

The enclosure of an ovule within an ovary shelters the ovule against drying and attack by herbivores or pathogens. Enclosure also allows selectivity for appropriate pollen because the pollen has to germinate on a receptive stigma and then grow through an accepting style. Finally, the ovary wall later matures into the fruit. Fruits protect the seeds, enhance seed dispersal, and can control seed germination. The consequences are that seedlings will emerge when and where conditions are most favorable.

Double fertilization (Fig. 25.8) also conserves energy because food storage tissue does not accumulate until after fertilization. Energy-rich **endosperm** tissue is not part of a preexisting female gametophyte; it is a new tissue that is created only by the act of fertilization. If unfertilized ovules contained as much energy-rich tissue

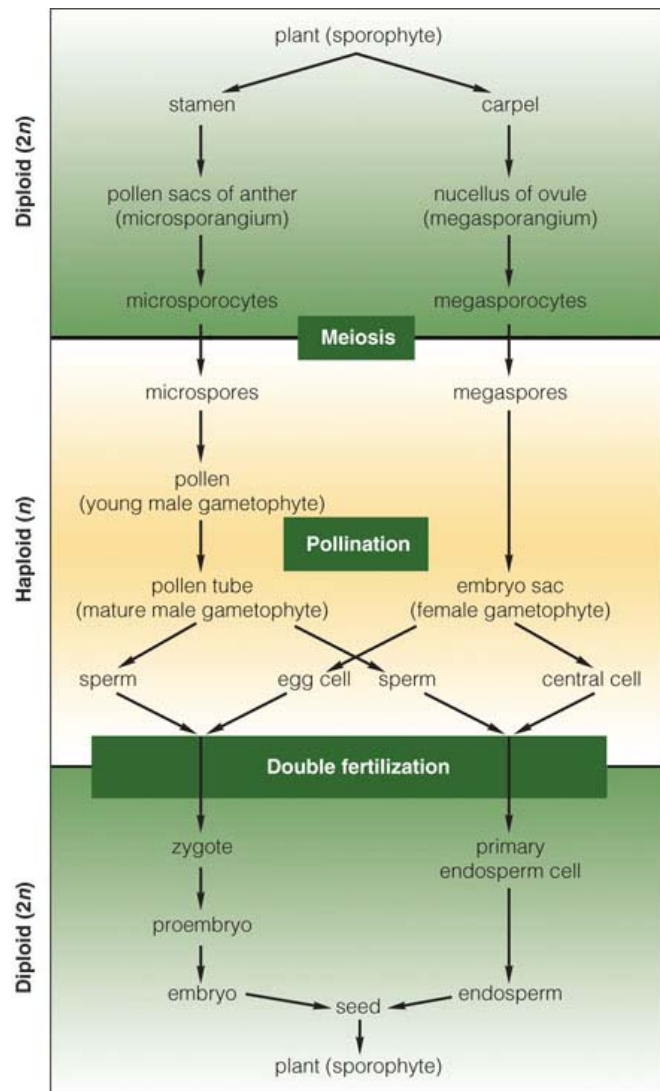


Figure 25.8. Generalized life history of an angiosperm.

around them as fertilized ovules, a significant amount of food reserves would be wasted.

About 257,000 species of flowering plants have been described, and taxonomists estimate that many more thousands of unknown species exist in poorly explored regions. Certainly the number of described species increases each year. When Linnaeus published *Species Plantarum*, his compendium of the plant world in the mid-eighteenth century, he listed fewer than 8,000 species. The novel life cycle traits described above are possibly a major reason for the diversity, success, and dominance of this group.

25.5 ANGIOSPERM DIVERSITY

Our understanding of angiosperm relationships has undergone a revolution in the last several years. The advent of cladistic techniques, bolstered by the development of powerful computers, software, and a rapidly growing wealth of molecular characters, has been the driving force behind this revolution.

Early taxonomists created arbitrary (non-phylogenetic) classifications that were based on ease of use or similarity of form. In the twentieth and twenty-first centuries, the trend has been to classify plants on the basis of evolutionary relationships--phylogeny. A great variety of phylogenetic classification systems have been proposed. The system of Arthur Cronquist has been particularly influential and remains standard in many places. However, Cronquist's system is based on his great experience and intuition. It has been contradicted by recent cladistic studies. Some researchers have proposed that a completely new classification system, based on naming nodes on a cladogram rather than on assigning each taxon a rank with a standard suffix in the manner of Linnaeus and Cronquist, is desirable. Many articles are currently being published that name groups on the basis of phylogeny rather than on hierarchical rank.

Currently, we have a clear picture of the basic phylogenetic structure within the angiosperms. A variety of molecular studies have pointed to a series of well-supported clades and subclades. Several distinctive lineages of angiosperms form a basal grade. These include: the shrub *Amborella*; the shrubs, vines, or trees of star anise and its relatives; and the aquatic, herbaceous water lilies. These three lineages comprise the basal-most groups in the angiosperms, and therefore are sister taxa to all other flowering plants (see Fig. 25.2 and 25.3).

The remaining angiosperms comprise three large, diverse groups: magnoliids, monocots, and eudicots.

Basal Angiosperm Groups Include the Water Lilies

The currently identified **basal angiosperms** consist of about 170 species of herbs, shrubs, and trees widely distributed throughout tropical and temperate zones. Shared traits include elongate vessels with slanted perforation plates (or else no vessels); radially symmetrical flowers with several to many free carpels and stamens; stamens with broad, short, petal-like, or poorly differentiated filaments; carpels with short or missing styles but with an elongated stigmatic region; pollen

with a single aperture; and seeds with small embryos but with a significant amount of endosperm.

The living lineage that may have been the first to diverge is represented today by a single species, a shrub called *Amborella trichopoda*, which is found only on New Caledonia. *Amborella* lacks vessels in its wood, and although the plants are dioecious, the flowers have vestigial structures that suggest they evolved from plants that produced both pollen and ovules in the same flower.

The water lilies are another group of basal angiosperms. They consist of 70 aquatic, rhizomatous wetland herb species. Their leaves and flowers float, because oxygen is carried from the leaves down through the petioles to rhizomes and roots through conspicuous air canals. Flowers are large, with numerous tepals (colored flower parts not differentiated into petals and sepals), stamens, and carpels (Fig. 25.9). Many wild species occur in North American ponds and lakes, but they also are common ornamentals in garden pools.

The star anise group contains 100 species of plants, some with medicinal value. Star anise (*Illicium verum*) is the most economically important, as it is a source for spice and anise oil. These plants are vines, shrubs, or trees mostly of warmer climates. Few morphological features identify these plants as a clade, but DNA has strongly supported the group as monophyletic and as a basal angiosperm lineage.

Core Angiosperm Groups Include Most of the Flowering Plants

Most angiosperm species are classified in a clade called **core angiosperms**. Phylogenetic data support dividing the core angiosperms into three subclades: **magnoliids**, **monocots**, and **eudicots**.

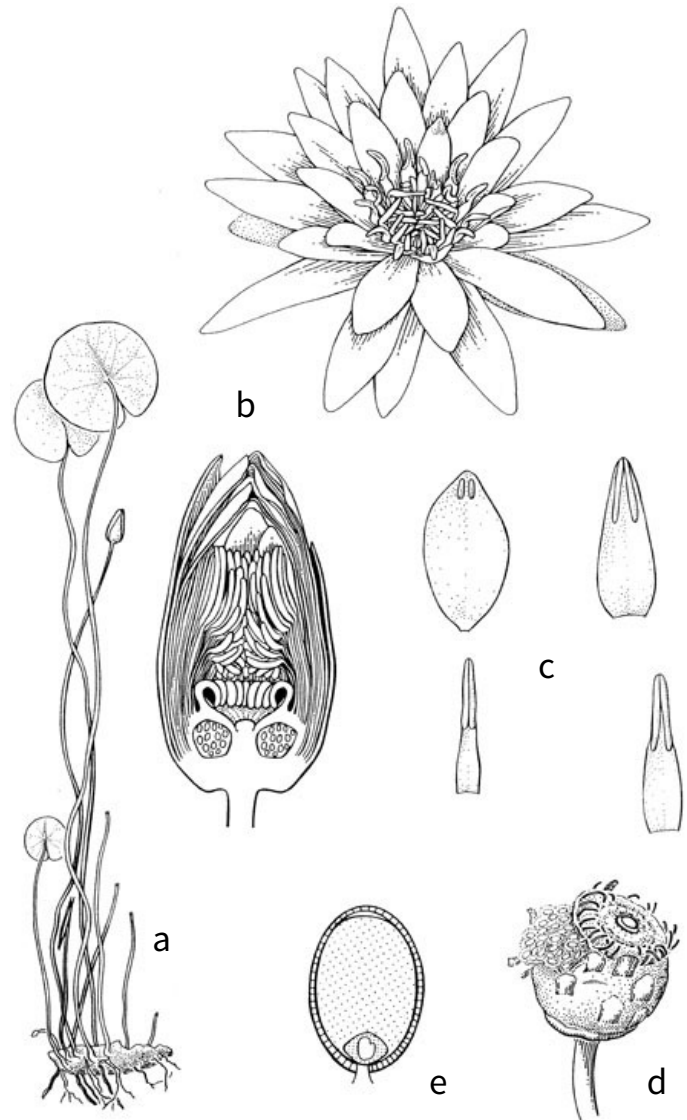


Figure 25.9. The water lily *Nymphaea odorata*. (a) Leaves on long petioles, growing upward through water from a rhizome anchored to the pond's bottom sediments. (b) A flower with numerous parts. (c) Petal-like stamens. (d) An opening fruit and many small seeds. (e) A longitudinal section of a seed, showing a small embryo and abundant endosperm.

Although each of these contains a great variety of forms and characteristics, two of them can be distinguished by single characters: monocots by a single cotyledon and eudicots by three-apertured pollen (or evolutionary derivatives of three-apertured pollen). The exact relationships among the core angiosperm groups currently are unknown, but we believe each of the groups is monophyletic.

MAGNOLIIDS Before the advent of molecular cladistic evidence, the magnoliid group often was considered typical of the earliest angiosperms. However, because the group ranges from herbs to trees and has extensive morphological, anatomical, biochemical, and cellular variety, reconstructing the features of the earliest angiosperms was a complex task. Now that it is known that the magnoliid group does not represent a basal angiosperm lineage, the characteristics can be assessed more appropriately. For example, some of the angiosperms that lack vessels are nested within the magnoliids, suggesting that vessels have been lost several times.

Magnoliids typically are tropical and warm-temperate, although some occur in temperate zones. Many are woody plants with simple leaves and pinnate venation. Some have large flowers with many spirally arranged tepals, stamens, and carpels, such as *Magnolia* (Fig. 25.10). Others have small flowers with parts in threes, such as cinnamon and camphor (*Cinnamomum*). Magnoliids include important spices and fruits, such as nutmeg (*Myristica fragrans*), sassafras (*Sassafras*), avocado (*Persea americana*), bay laurel (*Laurus nobilis*), black pepper (*Piper nigrum*), and pawpaw (*Asimina triloba*). Some magnoliids are medicinal and ornamental as well, such as peperomia (*Peperomia*), betel pepper (*Piper betle*), wild ginger (*Asarum*), and pipe vine (*Aristolochia*).

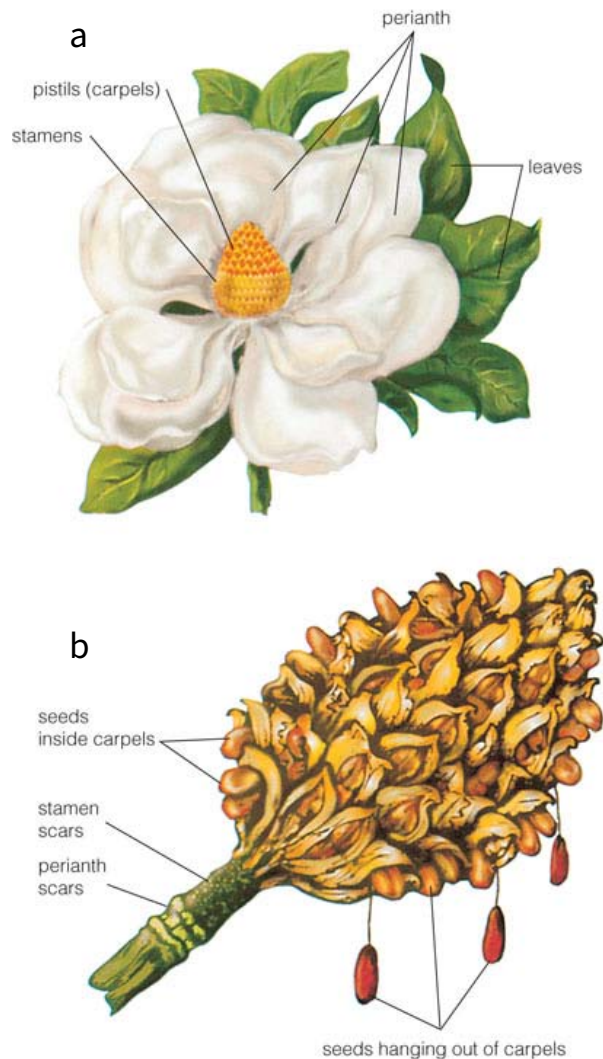


Figure 25.10. the southern magnolia (*Magnolia grandiflora*), a member of the magnoliid group. (a) Flower. (b) The fruit and scars showing where the stamens and petals had once been attached.

MONOCOTS In addition to the single cotyledon, monocots typically have parallel-veined leaves, flower parts in threes, sieve-tube members with plastids containing protein crystals, stems with scattered vascular bundles, an absence of secondary growth, and primary roots that abort early and are replaced by an adventitious root system.

Monocots number about 65,000 species and include such economically and ecologically important plants as the grains, known as the "staff of life" because so many humans depend on them as a food staple--for example, barley, corn, millet, oats, rice, rye, and wheat. Domestic animals also depend on grain and other grasses for forage. Other important monocots are the agaves, bananas, irises, lilies, onions, orchids, palms, rushes, sedges, yams, and yuccas.

Relationships within monocots are poorly known. A variety of analyses suggest that a clade called **Alismatales** forms the basal lineage (Fig. 25.11). This basal group of some 3,000 species includes a number of important plants such as the aroids, many of which are well-known plants with distinctive flowers. Members include *Philodendron*, the calla lily (*Zantedeschia*), *Anthurium*, and taro (*Colocasia*). Other alismatales include a widespread assemblage of aquatic plants, such as the pernicious aquatic weeds *Hydrilla* and *Elodia*, and the ecologically important pondweeds. Arrowhead species, such as *Sagittaria* (Fig. 25.12), have been cultivated for their edible tubers in Hawaii, Malaya, Kashmir, and by natives of North America. Arrowhead is a perennial herb commonly found in freshwater marshes, ponds, swamps, and lakes. It has a rhizomatous stem rooted in bottom sediments and arrowhead-shaped leaves on long petioles, which may float on the surface or be submerged. Sepals and petals are distinct with three in each whorl; stamens and carpels can be numerous; nectaries are present, and pollinators include bees and flies. Seeds disperse by floating on water, or they are eaten and spread by birds.

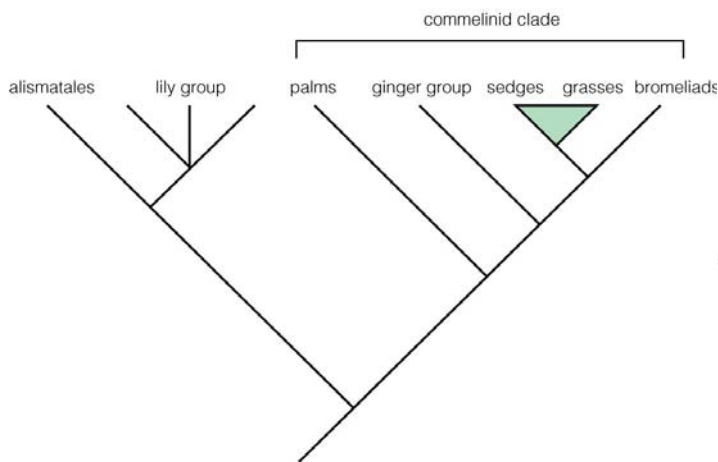


Figure 25.11. Simplified cladogram of monocot orders, on the basis of DNA analysis. The lily group is shown as a polytomy, but it could be a grade of lineages leading to the commelinid clade.

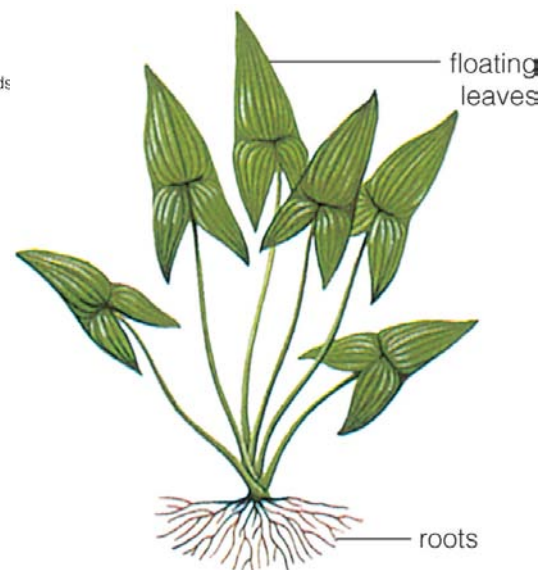


Figure 25.12. Arrowhead (*Sagittaria*), a basal monocot in the order Alismatales.

The remaining monocots include two large groups: one with typically showy flowers and another primarily composed of plants lacking showy flowers. There is strong evidence that the nonshowy group, the **commelinids**, forms a clade. The showy flowered (or lily) group may or may not be a clade. More research is needed.

Among the showy-flowered group are yams (*Dioscorea*) and a large clade of lilies and their relatives, including irises (Fig. 25.13), amaryllis, hyacinth, daffodil, tulip, agave, asparagus, onion, and one of the largest of all plant groups, the orchids, with 17,500 species.

The palms, with 2,700 species distributed throughout the tropics, comprise the basal lineage in the nonshowy-flowered commelinid clade. A few species enter the warm-temperate zone, such as California fan palm and saw palmetto (Fig. 25.14). Palms have a distinctive growth form of a typically unbranched trunk, a terminal tuft of compound or dissected leaves, and fruits called drupes, which have a berry-like, fleshy outer layer, but contain one to several hard pits. The coconut is a large drupe. Most palms are sensitive to frost, and if their single apical meristem is killed, the entire plant dies. One advantage of an unbranched morphology is that it bends less in damaging winds of hurricanes or typhoons. Palms are among the most important tropical groups. Coconut palm (*Cocos nucifera*) yields edible endosperm from its huge seeds, oil pressed from dried coconut meal (copra), and cordage (coir) from its stringy outer husk. Dates are produced by *Phoenix dactylifera*, carnauba wax is extracted from *Copernicia*, cooking oil comes from *Elaeis*, betel nuts from *Areca*, and basketry material from *Raffia*. Many species are popular ornamentals in warm climates.

Other commelinids include a subclade of largely wind-pollinated plants such as bamboo and other grasses, cattails, rushes, sedges, and

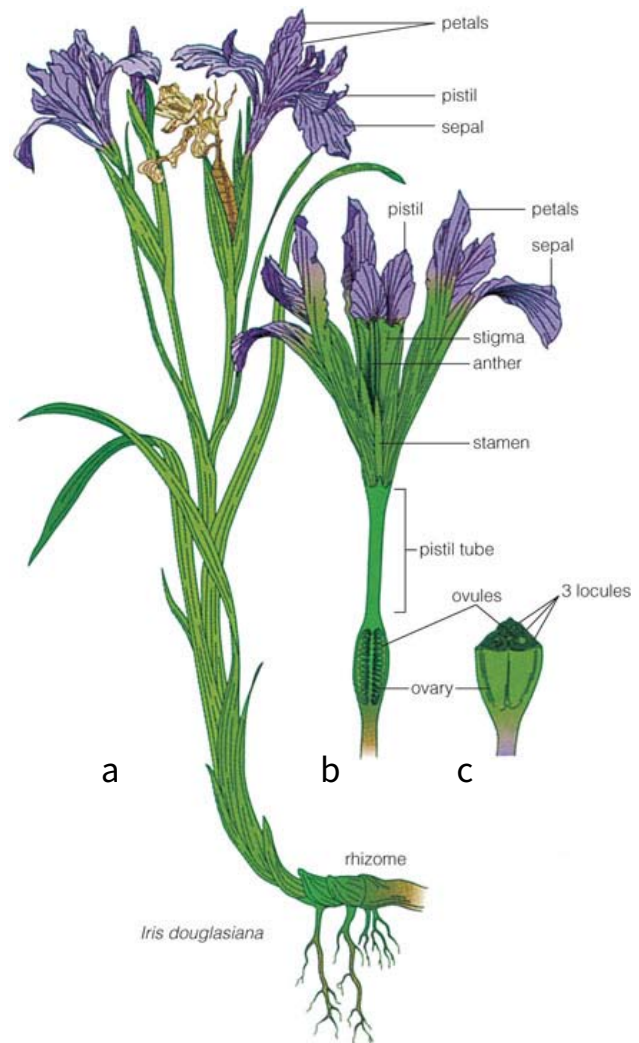


Figure 25.13. The monocot Douglas iris (*Iris douglasiana*). (a) A whole plant. (b) One flower with the ovary sectioned lengthwise to show many ovules. (c) Cross section of the ovary, showing three locules that represent three fused carpels.

tules. This subclade also includes, as one of its basal lineages, the bromeliads, of which pineapple (*Ananas*) is a member. This group is one of the most species-rich among the monocots, the grasses alone comprising more than 8,000 species and the sedges comprising 3,600 species. Another subclade of commelinids, the ginger group, is not typical because it has showy, insect-pollinated flowers, some of economic importance. Members include ginger (*Zingiber*), cardamom (*Elettaria*), turmeric (*Curcuma*), banana (*Musa*), canna (*Canna*), maranta (*Maranta*), bird-of-paradise (*Strelitzia*), and the large tropical genus *Heliconia*.



Figure 25.14. Palms that grow in warm-temperate latitudes. (left) A California fan palm (*Washingtonia filifera*) in a southern California desert oasis. (right) A saw palmetto (*Seroenoa repens*) in the understory beneath pine trees in north-central Florida.

EUDICOTS The third major lineage of core angiosperms, eudicots, is defined by a single feature: pollen with three apertures (Fig. 25.15). The simplest type of three-apertured pollen is called tricolpate. These pollen grains have three slits (*colpi*) that divide the grain into three longitudinal wedges. Some members of this group have modified their tricolpate pollen to other forms. Some, for example, may have pores located in the slits (tricolporate; Fig. 25.15), and others have only pores (triporate). Some types of pollen may have more than three apertures, but all of the variations are clearly derived from a tricolpate ancestor.

Eudicots typically have net-veined leaves, flower parts in fours or fives, embryos with two cotyledons,



Figure 25.15. Pollen with three apertures, characteristic of eudicots. Two of three longitudinal slits are visible.

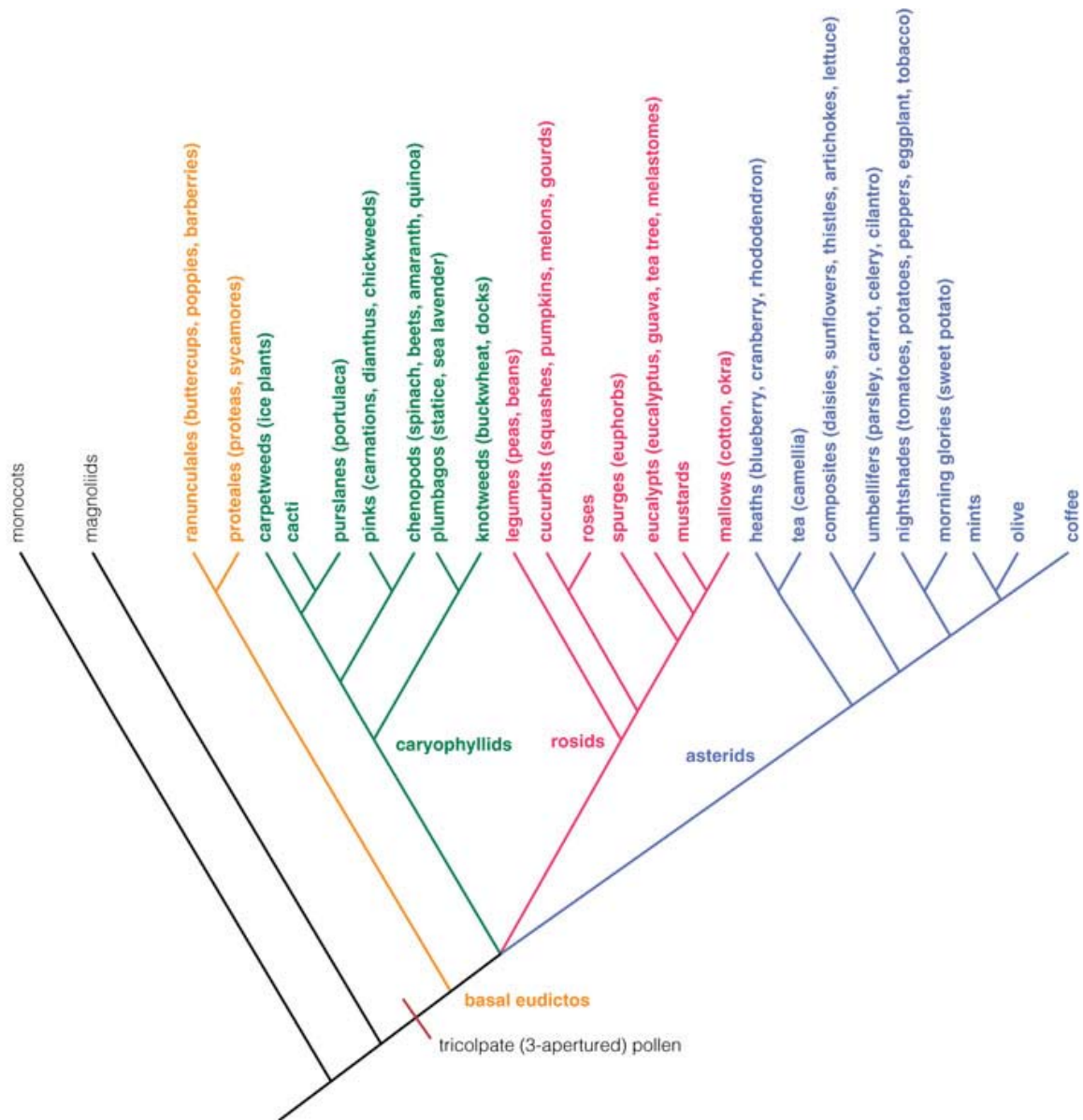


Figure 25.16. Simplified cladogram of eudicots. Based on several data sets: nuclear ribosomal genes, chloroplast photosynthetic genes, morphology, and others.

sieve-tube members usually having plastids with starch grains, stem vascular bundles arranged in a ring, and stamens with slender filaments. This group includes many economically and ecologically important plants such as blueberries, buckwheat, cacti, carrots, coffee, grapes, hemp, legumes, melons, poppies, potatoes, roses, sandalwood, stone fruits, strawberries, sunflowers, tea, teak, tomatoes, and walnuts.

A cladogram of eudicots based on Rubisco genes and ribosomal genes from the nucleus shows several basal lineages and three major clades: the rosids, the asterids, and the caryophyllids (Fig. 25.16). The basal lineages include Ranunculales and Proteales. Ranunculales consists of about 3,500 species. They are mainly herbs in temperate latitudes with lobed leaves, numerous flower parts, superior ovary

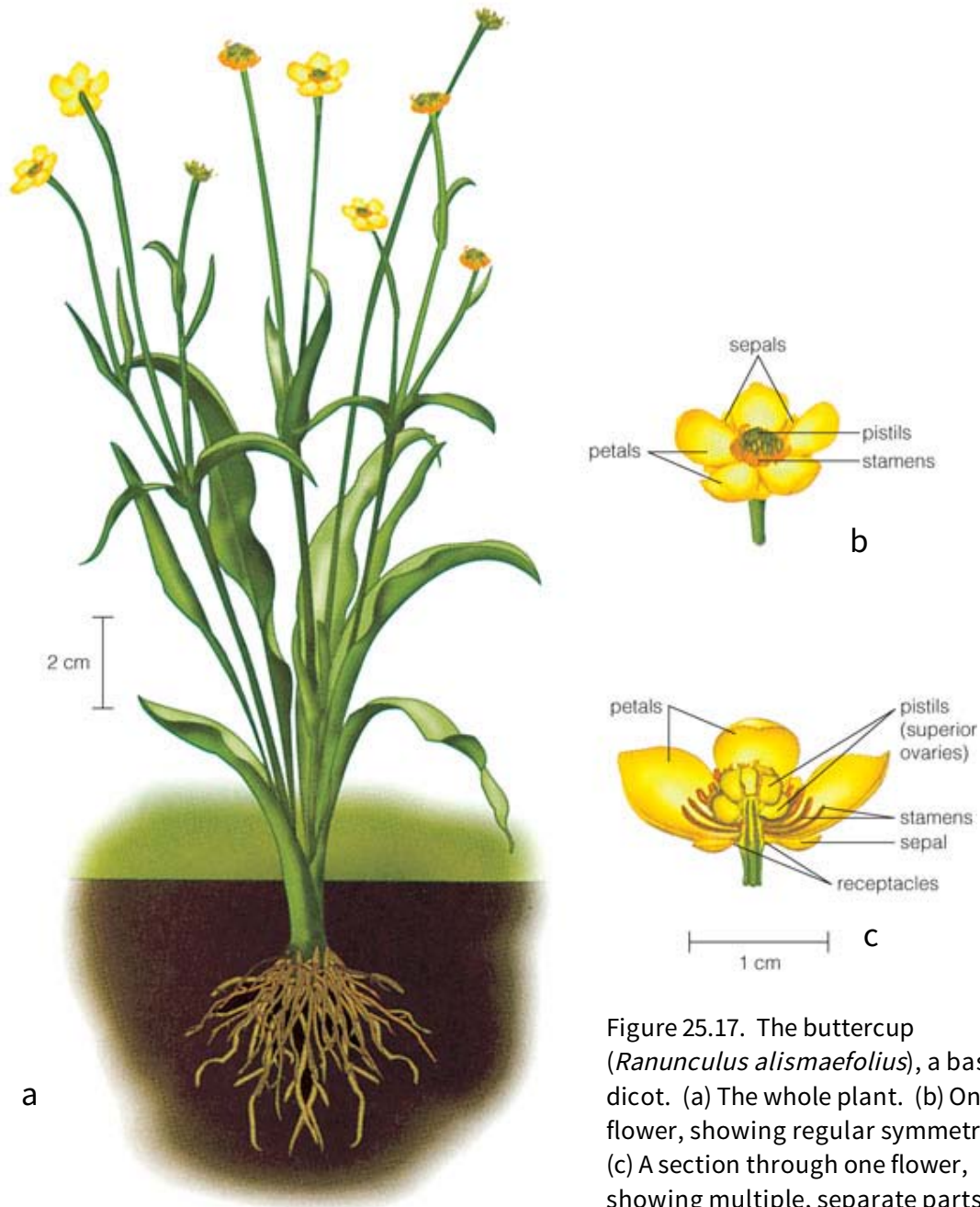


Figure 25.17. The buttercup (*Ranunculus alismaefolius*), a basal dicot. (a) The whole plant. (b) One flower, showing regular symmetry. (c) A section through one flower, showing multiple, separate parts and superior ovary position.

position, and seeds with small embryos. Buttercups (*Ranunculus*; Fig. 25.17) are a good example, but other genera in this lineage are *Anemone*, *Aquilegia* (comlumbine), *Delphinium* (larkspur), *Berberis* (barberry), and *Papaver somniferum* (opium poppy). Edible species are uncommon because most contain poisonous alkaloids.

Proteales are especially abundant in Africa and Australia, but the widespread Northern Hemisphere sycamors (*Platanus*) also are members, Proteales typically are

trees or shrubs with highly reduced, wind-pollinated flowers. They frequently are grown as ornamental shrubs (for example, the genera *Banksia*, *Grevillea*, *Hakea*) or street trees (sycamore).

The **caryophyllid clade** contains ice plants, carpetweeds, cacti (Fig. 25.18), pinks, and amaranths. Plants important to humans include sugar beet (*Beta*), spinach (*Spinacea*), purslane (*Portulaca*), rhubarb (*Rheum*), buckwheat (*Fagopyrum*), amaranth (*Amaranthus*) that produces a kind of grain, and the South American quinoa plant (*Chenopodium quinoa*). Landscape ornamentals include tropical *Bougainvillea*, temperate carnations (*Dianthus*), sea lavenders (*Limonium*), and many succulents.



Figure 25.18. A cactus flower with multiple parts.

The **rosid clade** is a diverse group, the largest and most familiar members of which are the legumes (16,400 species), spurge (7,800), tropical melastomes (4,800 species), Australasian eucalypti (3,900 species), roses (3,000 species), and mustards (3,000 species). Economically important products from rosids include fruits, nuts, vegetables, ornamentals, timber trees, spices and flavorings, fibers, dyes, and drugs. Botanical oddities range from the small insectivorous Venus flytrap, to parasitic mistletoes, to giant ground-hugging *Rafflesia* flowers 1 m across.

The flowers of a typical rosid, boysenberry, are illustrated in Figure 25.19. Sepals and petals often are fused into a ring, which can either be fused to the ovary or free from it. Sepals and petals typically occur in fives, and the two whorls are distinctly different in texture and color. Stamens are numerous, and sometimes so are the carpels. Flowers are moderately large, usually radially symmetrical, and present such rewards as nectar or pollen to bee pollinators. Two other representatives of the rosid group are gourds (Fig. 25.20) and cotton plants (Fig. 25.21). Gourds usually are monoecious (separate pollen and seed-producing flowers, both of which are found on the same plant), petals are fused into an elongate funnel shape; flower parts are reduced in number; the ovary is inferior; and plants are herbaceous vines. Cotton flowers have separate petals, but the numerous stamens are characteristically fused together in a tube that surrounds the elongated style. When the seeds are mature, the dry-papery capsule splits open, revealing seeds whose coats have long white hairs; these are the hairs that are mechanically harvested and separated from the seed to become cotton fabric.

The **asterid clade** contains some of the most highly specialized core angiosperms. Fused petals predominate. The heaths (2,700 species); tomatoes (Fig. 25.22); potatoes; peppers and relatives (2,900 species); mints (7,000 species; Fig. 25.23); carrot (Fig. 25.24); parsley and relatives (3,100 species); and sunflowers, daisies, and related genera (21,000 species) are included in this group. Flower parts typically are

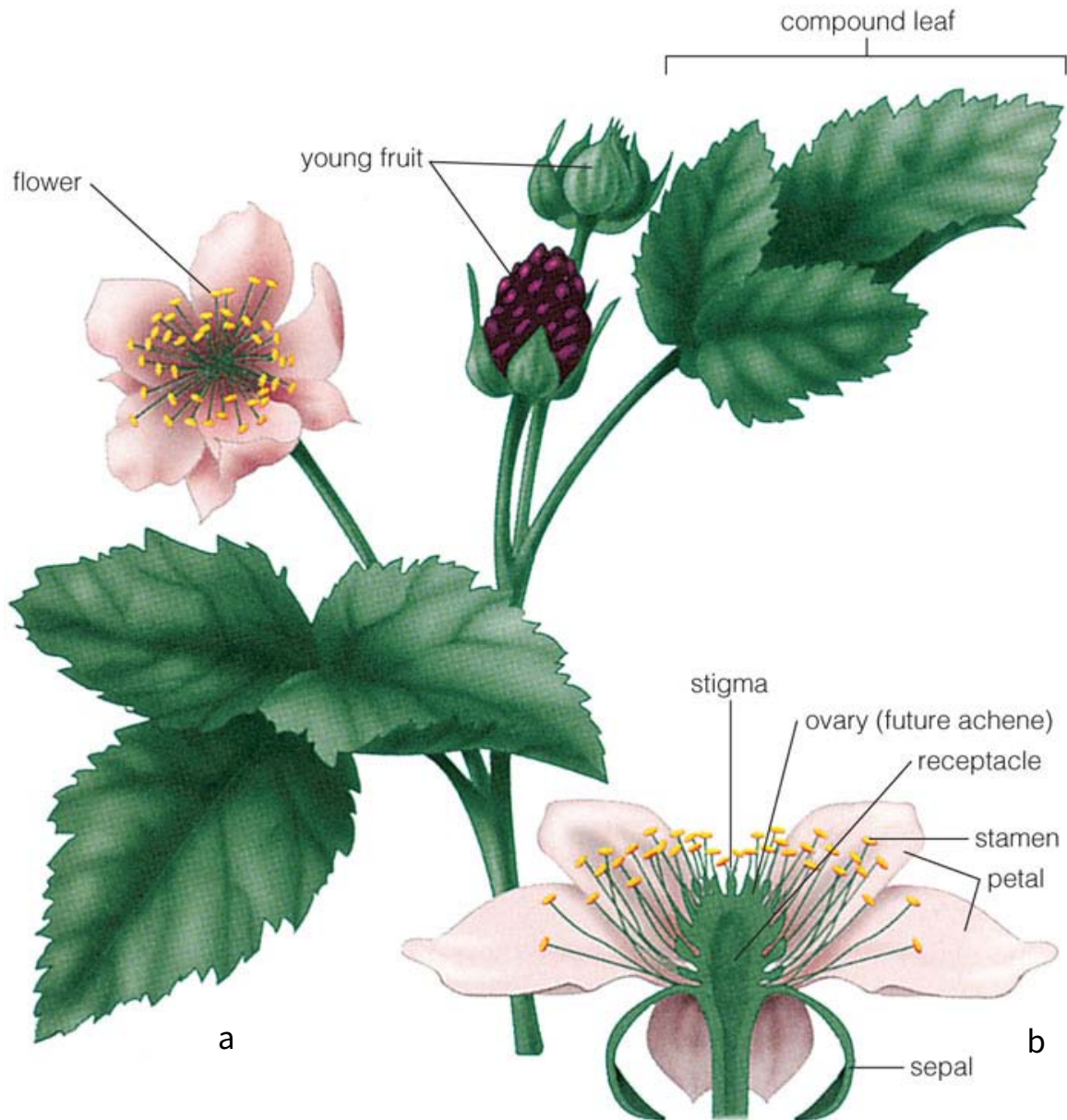


Figure 25.19. The rosoid group includes many species in the family Rosaceae with edible fruits, such as boysenberry (*Rubus ursinus* var. *loganbaccus*). (a) A portion of a stem, showing compound leaves, a mature flower, and young fruits. (b) A section of one flower. Primitive traits include regular symmetry and many flower parts; derived traits include compound, toothed leaves and some degree of fusion of petals and sepals at their bases.

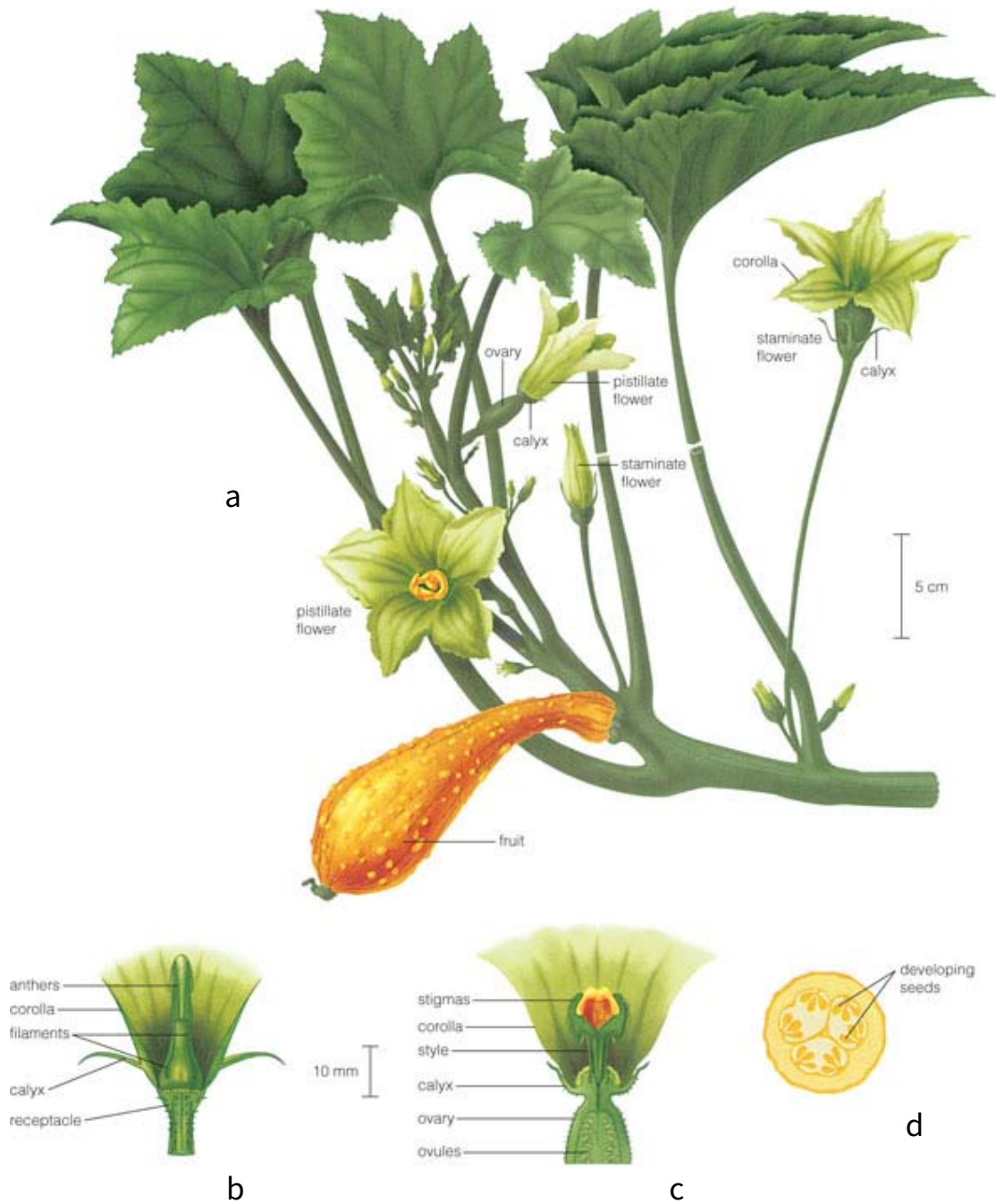


Figure 25.20. The gourd family, Cucurbitaceae, another member of the rosoid group. (a) A *Cucurbita pepo* plant, showing creeping stem, leaves, dioecious flower, and a fruit. (b) A staminate flower. (c) A pistillate flower with the ovary sectioned to show ovules. (d) A young fruit in cross section, showing that the pistil is made from several fused carpels. Derived traits include fusion of flower parts, inferior ovary position, reduction in number of flower parts, unisexual flowers, and lobed, toothed leaves.

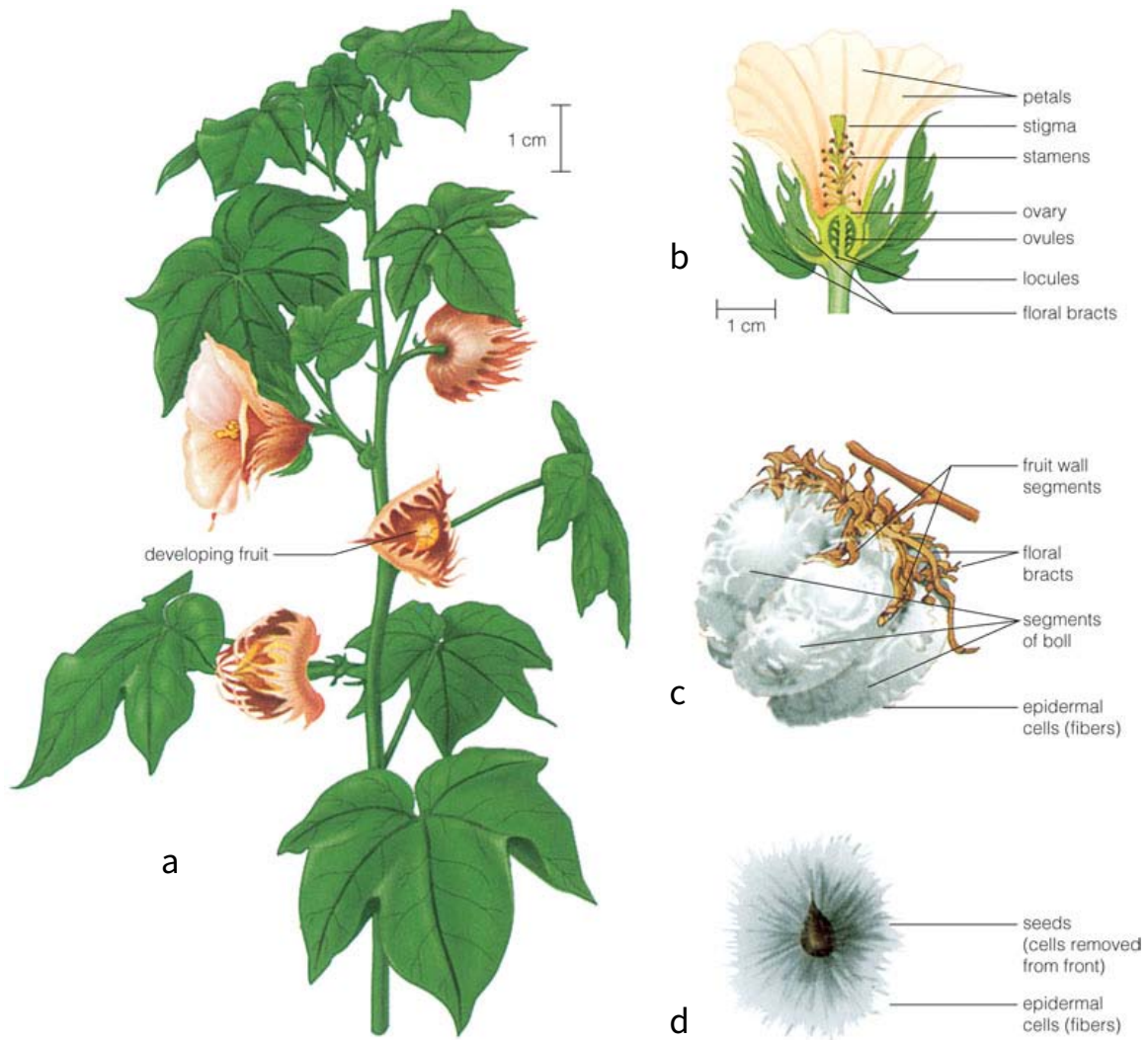


Figure 25.21. Cotton (*Gossypium hirsutum*), an economically important member of the rosid group. (a) Upper portion of one plant, showing leaves, a mature flower, and developing fruit. (b) A longitudinal section of one flower. (c,d) A mature five-section fruit, within which are many seeds densely covered with epidermal fibers.

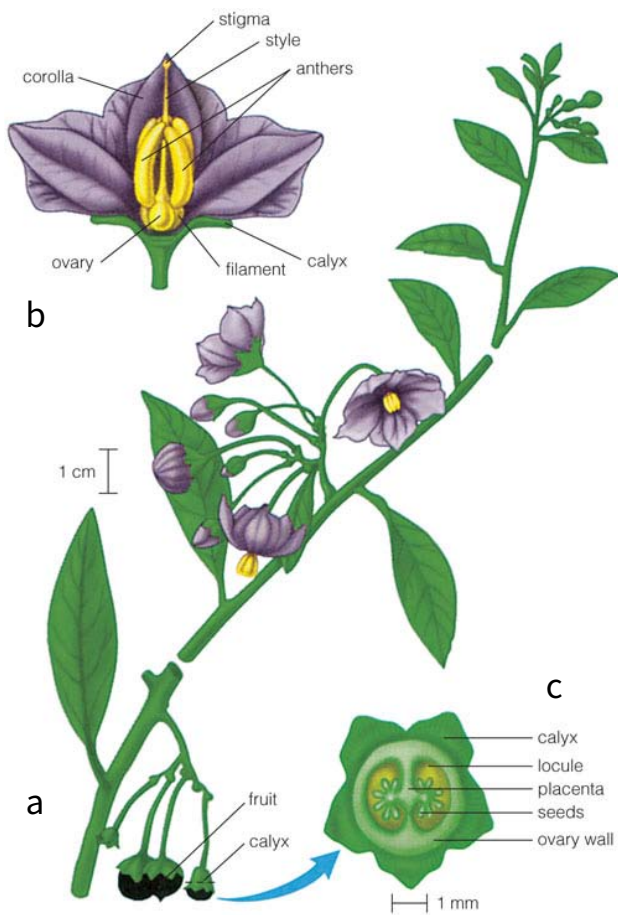


Figure 25.22. Nightshade (*Solanum parishii*), of the Solanaceae or tomato family, in the asterid group. (a) Upper portion of one plant showing flower buds, mature flowers, and developing fruit. (b) One flower with some stamens removed to show the superior ovary position. (c) Cross section of a young berry fruit showing two locules and developing seeds. Derived traits include small flower size and fused petals, sepals, and stamens.

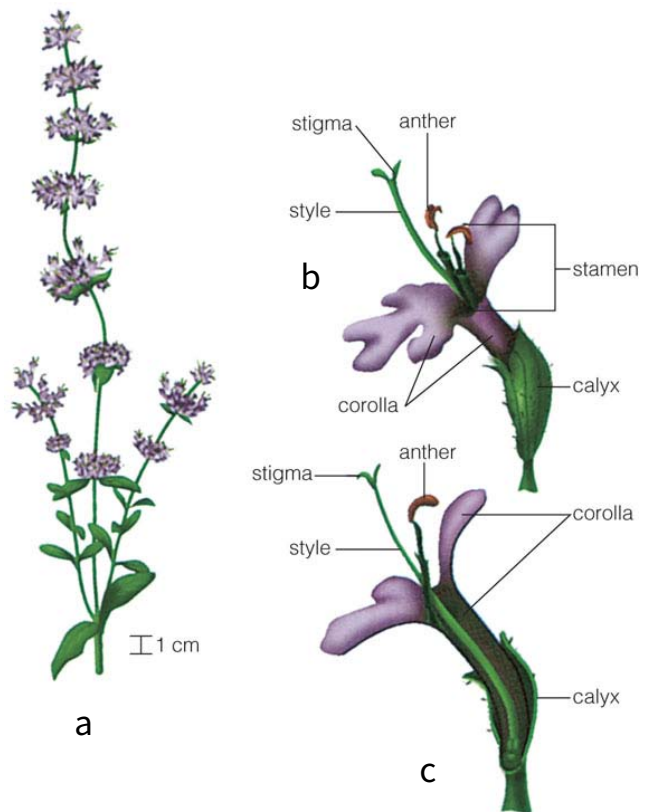


Figure 25.23. Sage (*Salvia mellifera*), of the Lamiaceae or mint family, in the asterid group. (a) Upper part of one plant showing opposite leaves, square stems, and lateral clusters of irregular flowers. (b) One flower, showing fused petals and sepals. (c) A longitudinal section of a flower, showing stamens fused to the petals. In this species, some stamens do not fully develop and are small pegs attached to the corolla near the throat. Derived traits include irregular symmetry, small flower size, fusion of parts within and between whorls, and a non-terminal inflorescence.

fewer, ovary position often is inferior, and the majority of species have irregular symmetry. Asterids typically are herbaceous.

No major global food plants are found in the asterid clade. However, components and flavors of regional diets are provided by artichoke (*Cynara*); basil (*Ocimum*); coffee (*Coffea*); tea (*Camellia*); elderberry (*Sambucus*); endive and chicory (*Cichorium*); lettuce (*Lactuca*); mint (*Mentha*); olive (*Olea*); oregano (*Oreganum*); peppers, paprika, and chilis (*Capsicum*); potato (*Solanum*); safflower (*Carthamus*);

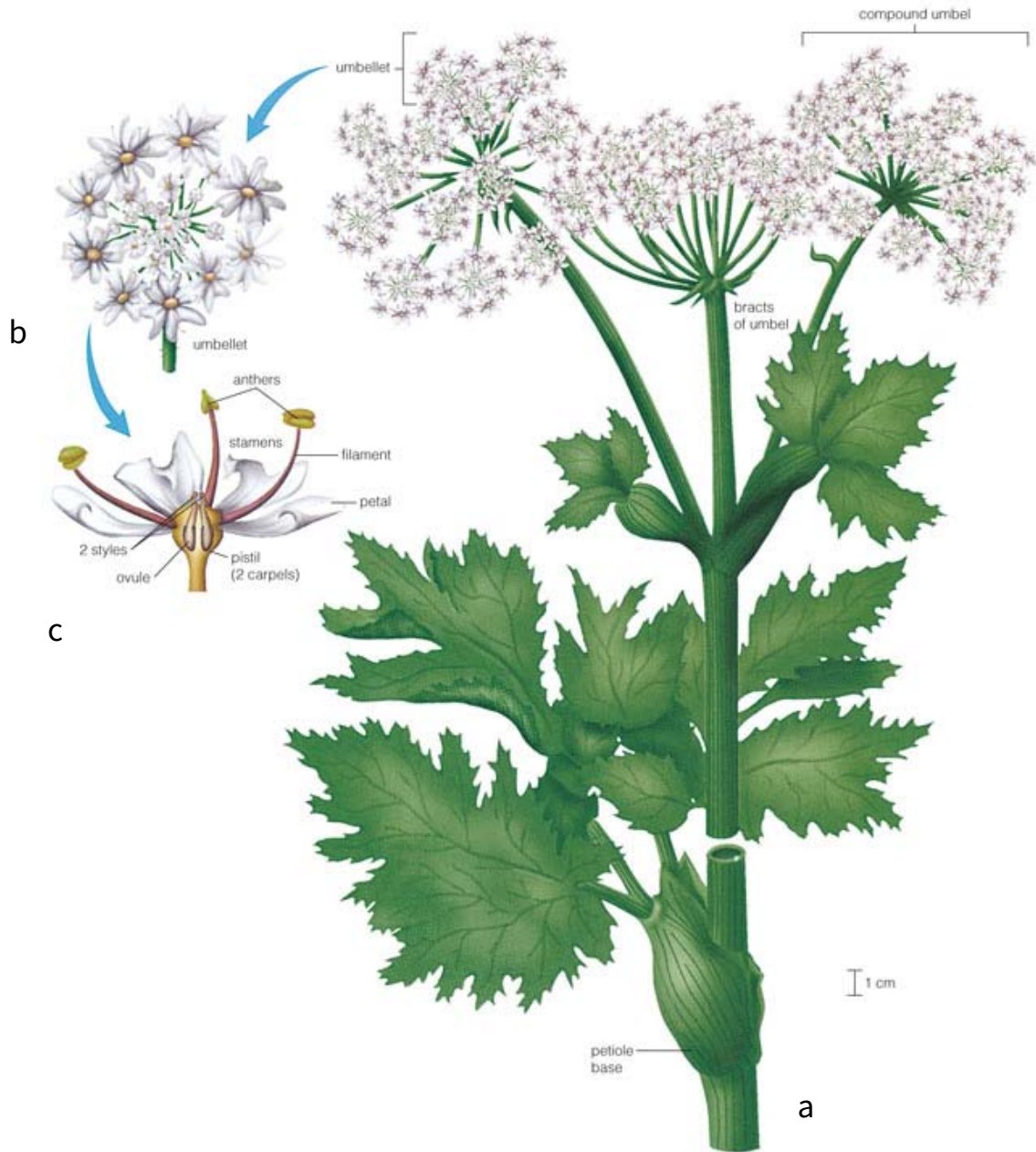


Figure 25.24. The carrot family (Apiaceae), in the asterid group, represented here by the large herb cow parsnip (*Heracleum lanatum*). (a) Upper portion of a large plant, about 1 m in height, showing deeply lobed leaves and several inflorescences called umbels or compound umbels. (b) One portion of a compound umbel (an umbellet) made up of two dozen flowers. (c) One flower, sectioned to show the inferior ovary position. Advanced traits include reduced flower size, reduced number of flower parts, inferior ovary, fusion of two carpels, and deeply lobed and toothed leaves.

sage (*Salvia*); sesame (*Sesamum*); sunflower oil (*Helianthus*); sweet potato (*Ipomoea*); thyme (*Thymus*); tomato (*Solanum lycopersicum*); tomatillo (*Physalis*); and tobacco (*Nicotiana*).

25.6 PLANT GEOGRAPHY

Plant geography is the branch of plant biology that describes the distribution of plants over the surface of the earth. It also studies possible explanations for how, why, or when these patterns of distribution occurred. Generally, seed plants--and particularly flowering plants--are the focus. Rather than relying on classification theories or technological breakthroughs, studies of plant distribution require only field trips conducted by energetic botanists with keen observational skills.

Plant geography was stimulated by voyages of exploration in the seventeenth, eighteenth, and nineteenth centuries. Plants new to science were brought back to botanical gardens in Europe alive and whole, as seeds, or as pressed herbarium specimens (see "ECONOMIC BOTANY: Botanical Gardens, Smuggling, and Colonialism" endnote). Important botanists who tried to make sense of this cascading mountain of information included Carl von Willdenow, Alexander von Humboldt, Johannes Schouw, August Griesebach, Alphonse de Condolle, Oscar Drude, Adolf Engler, George Marsh, Asa Gray, and Charles Darwin.

Humboldt, for example, led an expedition to Central and South America at the start of the nineteenth century. For 5 years he traveled in Cuba, Venezuela, Peru, Mexico, and the Orinoco and Amazon River basins. He walked through steamy lowland rain forest, semiarid thorn scrub, dry deserts, and cold alpine elevations as high as 6,000 m atop Mt. Chimborazo. His expedition took along the best equipment at that time for measuring elevation, location, and weather. More than 60,000 plant specimens were collected. On his return to Europe, Humboldt wrote a monumental 30-volume work summarizing the expedition; the first 14 volumes were devoted to botany. He is generally credited with being the founder of the science of plant geography. In addition, his keen observations, records, and interpretations became important contributions to the discipline of ecology.

It has become clear that the world's flora is not uniform. Although a dozen or so large families of flowering plants are cosmopolitan (Table 25.1), that is, commonly found on every continent except Antarctica, most families have a regional flavor or habitat bias in their distribution. Entire clades or subclades are restricted to certain continents or regions. As a result, plant geographers have divided the world into floristically homogeneous units. Ronald Good's scheme recognizes more than 30 global units (Fig. 25.25). Each unit is characterized by its own endemic plants, in addition to unique mixes of the more cosmopolitan lineages.

Studies by plant geographers also have shown that the vegetation of one particular kind of climate sometimes looks similar wherever that climate is found around the world, even though plants at each location may belong to taxa that are not closely related. For example, desert vegetation, with cactus-like growth forms, exists in the New and Old Worlds. The New World species, however, are in the cactus family (*Cactaceae*), whereas the Old World species are in the *Euphorbiaceae*. Similar shrubby vegetation with a dense, stiff, small-leaved canopy occurs in five

Table 25.1 The Twenty Largest Families of Flowering Plants

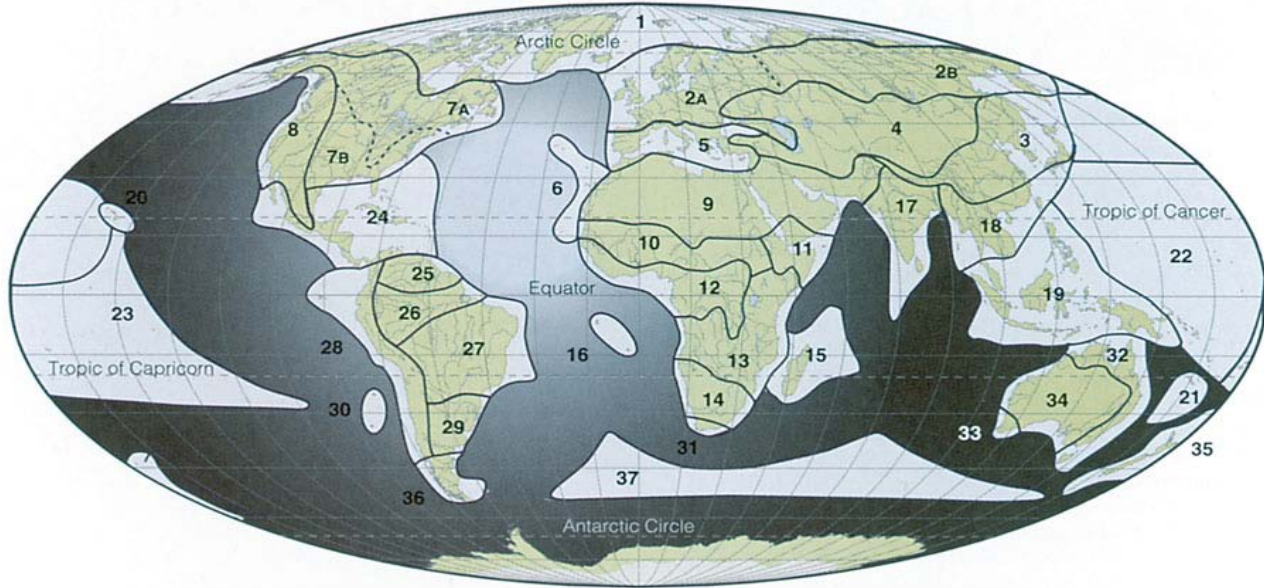
Rank	Family	Common Name	No. Species	Distribution
1	Asteraceae	Sunflower family	21,000	Cosmopolitan
2	Orchidaceae	Orchid	17,500	Cosmopolitan
3	Fabaceae	Bean	16,400	Cosmopolitan
4	Rubiaceae	Madder	10,700	Cosmopolitan
5	Poaceae	Grass	7,950	Cosmopolitan
6	Euphorbiaceae	Spurge	7,750	Cosmopolitan
7	Lamiaceae	Mint	5,600	Cosmopolitan
8	Melastomataceae	Melastoma	4,750	Tropical, especially South America
9	Liliaceae	Lily	4,550	Cosmopolitan
10	Scrophulariaceae	Snapdragon	4,500	Cosmopolitan
11	Acanthaceae	Acanthus	4,350	Tropical
12	Myrtaceae	Eucalyptus	3,850	Tropical, especially Australia
13	Cyperaceae	Sedge	3,600	Cosmopolitan
14	Ericaceae	Heath	3,350	Cosmopolitan
15	Apiaceae	Carrot	3,100	Temperate
16	Rosaceae	Rose	3,050	Temperate, especially Northern hemisphere
17	Brassicaceae	Mustard	3,000	Cosmopolitan
18	Moraceae	Mulberry	2,975	Cosmopolitan
19	Araceae	Arum	2,950	Tropical and subtropical
20	Asclepiadaceae	Milkweed	2,900	Tropical, especially Africa

different places with a Mediterranean-type climate, yet the plants are not closely related. Tropical rain forests of Africa, Australasia, and South America share a similar climate, a similar array of plant growth forms, and a similar forest architecture, but on each continent the assemblage of important plants is different.

Sometimes, however, the environmental conditions, the isolation of a place, and the genetic potential of plants growing there combine to create unique and bizarre vegetation found nowhere else in the world. An excellent example is the flora and vegetation of alpine zones on tropical African mountains such as Mt. Kilimanjaro in Kenya. Tree-sized plants in the normally herbaceous genera *Senecio* and *Lobelia* dominate the landscape (Fig. 25.26). The plants have clustered leaves at the ends of irregularly formed branches, and they may live for a century.

The desert of Baja California is another place where unique taxa and growth forms exist. The boojum tree (*Fouquieria columnaris*), giant cacti, arborescent yuccas, and trees with succulent stems (*Bursera*, *Pachycormus*) give the horizon an otherworldly aspect (Fig. 25.27).

The process of evolution has not been equal for all taxa of flowering plants. Some groups have many species throughout the world, but nevertheless have a limited range of growth forms. Other groups have fewer species that are less widespread, yet they exhibit a wide range of growth forms. Still others are narrowly restricted and have few species. Apparently, some groups have the genetic potential to be numerous, aquatic, succulent, woody, frost tolerant, or salt tolerant; to evolve flowers pollinated by bats or fruits dispersed by birds; or to accumulate herbivore-



- | | | |
|----------------------------|------------------------------|------------------------------|
| 1. Arctic and Sub-arctic | 11. N.E. African Highland | 25. Venezuela and Guiana |
| 2. Euro-Siberian | 12. W. African Rain Forest | 26. Amazon |
| A. Europe | 13. E. African Steppe | 27. South Brazilian |
| B. Asia | 14. South African | 28. Andean |
| 3. Sino-Japanese | 15. Madagascar | 29. Pampas |
| 4. W. and C. Asiatic | 16. Ascension and St. Helena | 30. Juan Fernandez |
| 5. Mediterranean | 17. Indian | 31. Cape |
| 6. Macaronesian | 18. Continental S.E. Asiatic | 32. N. and E. Australian |
| 7. Atlantic North American | 19. Malaysian | 33. S.W. Australian |
| A. Northern | 20. Hawaiian | 34. C. Australian |
| B. Southern | 21. New Caledonia | 35. New Zealand |
| 8. Pacific North American | 22. Melanesia and Micronesia | 36. Patagonian |
| 9. African-Indian Desert | 23. Polynesia | 37. S. Temp. Oceanic Islands |
| 10. Sudanese Park Steppe | 24. Caribbean | |

Figure 25.25. Floristic regions of the world according to Good, *The Geography of the Flowering Plants*, 1961.

inhibiting chemicals. Others are not so genetically equipped. No group of plants has the potential to fill every terrestrial niche, but some groups can fill more niches than others. We also see the environmental stresses or problems are solved by different plants in different ways.

Plant biogeographers, like systematists, have benefited greatly from phylogenetic analyses. Cladograms can be used to infer centers of origin, to identify long-distance dispersal events, and to investigate the process of domestication in many groups. In addition, the ecological value of various characteristics can be studied by reference to a cladogram.

Perhaps future plant biologists will be able to explain why evolution has proceeded along the exact route it has taken among the flowering plants. For now, we can only marvel at the diverse results, treasure this biotic heritage of the past, and protect it for the future.



Figure 25.26. Alpine vegetation in African mountains. (a) A giant senecio, *Dendrosenecio kilimanjari*. (b) A giant lobelia.



Figure 25.27. Desert vegetation in Baja California, showing boojum trees, century plants, and cordon cactus. No other desert in the world has a similar collection of growth forms.

KEY TERMS

Alismatales
 angiosperm
 asterid clade
 basal angiosperms
 caryophyllid clade
 commelinids
 core angiosperms
 double fertilization
 endosperm
 eudicots
 flower
 flowering plants

fruit
 Ice Age
 magnoliids
 monocots
 ovary
 paleobotany
 plant geography
 protoagriculture
 rosid clade
 seedling hypothesis
 sieve-tube members
 vessels

SUMMARY

1. Angiosperms are seed plants. The ovule and the seed that develops from the ovule are enclosed within an ovary. The ovary is part of a new organ called a carpel, and the carpel is part of a new complex structure called the flower. The flower is thought to represent a modified leafy shoot.

2. The fossil record of angiosperms extends back to the early Cretaceous period, about 140 million years ago. Paleobotanists theorize that the first appearance of angiosperms on Earth may have been as early as 190 million years ago and that the initial split of the line that became angiosperms diverged from that of gymnosperms more than 300 million years ago during the Carboniferous period. It is not clear which non-angiosperm plants are the closest living relatives to angiosperms.
3. Flowering plants have dominated Earth's vegetation throughout the Cenozoic era, despite major geographic, climatic, and vegetational changes. The temperate zone of North America shows a trend toward a progressively cooler and drier climate.
4. Humans have affected plant evolution during the Pleistocene and Holocene epochs by selecting plants for food, managing the landscape with fire, and introducing exotic species to new locations.
5. Novel aspects of the angiosperm life cycle include reduction in the size and complexity of the gametophyte generation (compared to gymnosperms); location of the ovule within an ovary; double fertilization forming zygote and endosperm; and dispersal of seed within a fruit. Vegetative innovations include an improved vascular system with vessels, sieve-tube members, and companion cells.
6. About 257,000 named species of flowering plants exist on Earth today. Phylogenetic classification of these plants has recently become less subjective because of research using DNA and cladistic methods. Angiosperms consist of a basal group with three lineages: magnoliids, monocots, and eudicots.
7. Basal angiosperms include 170 species in three lineages, *Amborella*, water lilies, and star anise and relatives. Core angiosperms include magnoliids, monocots, and eudicots.
8. The magnoliids are mostly tropical and warm-temperate trees, shrubs, vines, and herbs with simple leaves, pinnate venation, large flowers with many stamens and pistils, and relatively simple wood anatomy. Monocots typically have parallel-veined leaves, flower parts in threes, embryos with a single cotyledon, sieve-tube members with plastids containing protein crystals, and stems with scattered vascular bundles. Eudicots typically have net-veined leaves, flower parts in fours or fives, embryos with two cotyledons, sieve-tube members having plastids with starch grains, vascular bundles in a circle, stamens with slender filaments, and tricolpate pollen (or a tricolpate derivative).
9. Plant geography is the study of distribution patterns of plants over the earth's surface and the processes that cause those patterns. Flowering plants usually are the focus. Some plant groups are cosmopolitan, but others are more narrowly distributed and characterize floristic regions. Each plant group has its own genetic limitations and cannot evolve to fit into all available niches. The same environmental stresses are solved by different plant groups in different ways.

Questions

1. Diagram the evolutionary steps necessary to create an ovary of a flowering plant. According to the fossil record as currently understood, when did the first flowering plant appear?
2. Compare the size, anatomical complexity, and degree of independence of a fern gametophyte, a pine female gametophyte, and a magnolia female gametophyte. Which one is the most insulated and protected from the environment?
3. The megagametophyte of angiosperms is greatly reduced, but may contain vestiges of the structures present in larger gametophytes of seed plants. Speculate about what the synergids and antipodals represent in an angiosperm megagametophyte.
4. How can a fossil assemblage of flowering plants in a given location be used to estimate the climate at that location at that time? What assumptions are made to reconstruct the previous climate?
5. In your opinion, which group or family of angiosperms is most important to the most people? Give some examples of which plants within that group you consider to be important. Are they rich in species or widely distributed?
6. How can far-apart places in the world have vegetation that is similar in appearance when the taxa of flowering plants that make up the vegetation are completely different?

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Molecular Clocks and the Age of the Angiosperms*

Scientists have been developing a method of dating the origin of angiosperms (and other groups) that does not depend on fossils. This technique uses the idea of a molecular clock, first proposed by Linus Pauling and Emile Zuckerkandl in the early 1960s and much improved with the advent of recent phylogenetic techniques. Pauling and Zuckerkandl had determined the sequences of amino acids that make up the protein hemoglobin for several species, including human, mouse, horse, bird, frog, and shark. The number of amino acid differences among the various species appeared to be proportional to how closely related the species were to each other. Human and mouse hemoglobins had 16 amino acid differences, whereas human and horse hemoglobin had about 18. Bird, frog, and shark hemoglobins differed from human by 32, 65, and 79 amino acids, respectively.

Pauling and Zuckerkandl's great insight was to compare these calculated differences in hemoglobin structure with paleontological data concerning the age of divergence of the various lineages to which these species belong. The fossil record provides a rough idea of when each of the groups represented by these species originated. When they compared the relative age of the lineages with the differences in their hemoglobin structures, they found a strong correspondence. Hemoglobin seemed to be evolving at a regular, steady rate. This was a surprising result, because few people expected that molecules would change at a steady rate over hundreds of millions of years.

If certain protein or DNA molecules could be shown to evolve in this constant fashion, lineages could be dated by simply assessing the number of differences among them, then figuring out what the rate of change was for that molecule. The time since any two species last shared a common ancestor could, in theory, be determined simply by calculating how much time was necessary for the accumulation of the differences in their amino acid or nucleotide sequences. Unfortunately, it is now known that many molecules do not seem to change in a clocklike fashion and that different lineages, even sister lineages, may change at different rates. New techniques are being developed that account for rate variation in a molecule's evolution over time.

This technique has been applied to plants. Some molecular clock estimates suggest that land plants originated about 1 billion years ago and vascular plants separated from bryophytes as early as 700 million years ago. These estimates are controversial because they do not correspond with estimates derived from the fossil record.

Molecular clock estimates of the origin of angiosperms also have been proposed. Research using chloroplast genes has yielded dates ranging from 79 to 220 million years ago. Some of the dates determined in molecular clock studies agree with those determined by dating fossils. (Note that the range of dates given in this chapter for *Archaeofructus* fossils is 125-140 million years.) New methods of analysis, expanded data sets, and better calibration with known fossils promise to yield molecular clock ages that we can accept with confidence.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *We Live on a Changing Surface*

Currently, the climate of the John Day Basin is semiarid. But in geological terms, this climate has only just arrived, and in earlier times, the climate was wetter and the vegetation more lush.

In the Eocene epoch, which began about 57 million years ago (Fig. 25.5), the dominant vegetation of the John Day Basin consisted of tropical vegetation of the type currently found in the mountain forests of Central America, where annual rainfall is more than 150 cm and there is no winter frost.

Twenty million years later, in the Oligocene epoch, rainfall decreased to perhaps 120 cm per year, summers were wet and mild, and winters were drier and cold, but with little snow. The fossil record shows a change to a rich, mixed conifer-hardwood forest. Leaves had become smaller, with dentate (toothed) or convoluted margins, indicating a drier habitat (because smaller leaves with lobed or uneven margins can be cooled directly by wind instead of by transpiration). Deciduousness implies a colder winter. This type of mixed forest is not found anywhere on Earth today because the component species have been fragmented and separated. The closest approximations are along the cool, wet Oregon-California coast, in the Great Smoky Mountains of Tennessee, and in parts of China and Japan.

Twelve million years later, in the Miocene epoch, the shift to deciduous trees was even more pronounced, and conifers became less abundant. Species richness declined. Paleobotanists imagine that the climate was much like that in modern Ohio: 100 cm of annual precipitation, with half of that falling as snow in winter when freezing temperatures were common.

By the Pliocene epoch, fir and spruce--conifers that we associate today with cold climates--were common, along with winter-deciduous hardwoods. Some leaves were quite small and hard, indicating adaptation to a cold and arid climate.

Currently, the John Day Basin is dominated by sagebrush (*Artemisia tridentata*). Trees are absent except along watercourses. Annual precipitation is only 25 cm per year, most of that falling as snow in winter. The area is a semiarid cold desert.



Fossil leaves from John Day Basin.

ECONOMIC BOTANY: *Botanical Gardens, Smuggling, and Colonialism*



Figure. Kew Gardens, London. Palm House and Parterre.

Botanical gardens are collections of living plants. They began as places where plants that were new to science, having been collected on voyages of discovery in the sixteenth and seventeenth centuries, could be propagated and studied. The first botanical garden, established in 1545, was the Royal Botanic Garden at Padua, Italy. Other Italian gardens at Pisa, Florence, and Bologna soon followed. In the seventeenth century, gardens were constructed in France, the Netherlands, England, Germany, Sweden, Scotland, and Japan. Early botanical gardens were small and formally laid out; the English were the first to plant larger, more naturally landscaped gardens.

The Royal Botanic Gardens at Kew, England, are the finest botanical gardens in the world (Figure). They began on 4 hectares (10 acres) in 1759, but they have expanded to occupy more than 100 hectares (250 acres) today. More than 28,000 species of plants from around the world are growing in the garden. Major sections include an arboretum (trees), tropical plants maintained in warm greenhouses, a rock garden, alpine plants in refrigerated greenhouses, and a grass collection. Libraries, research laboratories, collections of botanical art, and a herbarium of 6 million pressed specimens also are on the grounds. Kew Gardens exemplifies several activities common to most botanical gardens. They conduct basic taxonomic research on living specimens, investigate plants for potential economic value, propagate horticultural plants that have ornamental value, educate the public, provide the public with a place to enjoy nature, and provide a secure location to maintain rare plants.

Sometimes the collection of plants for botanical gardens has involved questionable activities. For example, by the mid-nineteenth century, rubber had become a valuable, desired plant product. The industrial process of vulcanization had enormously expanded the use of rubber. Rubber comes from tropical plants of the New World, and the best rubber trees (*Hevea brasiliensis*) were native to Brazil. The Brazilian government wished to maintain its monopoly and prohibited the export of rubber tree cuttings or seeds.

The British India Office, however, was determined to start rubber plantations in the new British colony of Ceylon. The India Office believed that Ceylon soils and climate were similar enough to those of Brazil to provide a suitable new home for rubber production. In 1876, the India Office secretly commissioned the English rubber worker H.A. Wickham to smuggle out rubber tree seeds, agreeing to pay him the equivalent of \$50 per 1,000 seeds.

Wickham proved to be efficient. He collected 70,000 seeds, packing them in covered baskets, labeled simply "Botanical Specimens for Her Majesty's Gardens at Kew." He eventually found a willing ship captain with available space who slipped the seeds past the customs office. Once in England, the seeds were turned over to botanists at Kew Gardens, who carefully germinated and nurtured 2,400 seedlings from the 70,000 seeds. Most of these plants were shipped within a year to plantations that had been made ready in Ceylon. By 1912, these plantations were producing a princely income of \$45,000 per hectare (2.5 acres) per year. Not surprisingly, Wickham was knighted in 1920. Currently, 95% of the world's rubber comes from Southeast Asia, and plantations also have been established in Africa.

Many other economically valuable plants were moved to new homes during the imperialist and colonialist times of the seventeenth to nineteenth centuries. Trade in plants was one of the driving economic forces during those centuries. For example, profits in brokering spice between Southeast Asia and Europe were every bit as attractive to investors as trade in gold, cotton, or slaves. Cornering the market of a spice or any other important plant species was a reward for aggressive imperialism. Consequently, coffee was taken from Africa to Central and South America, to Indonesia, and to Hawaii; tea was moved from China to India; chili peppers were transplanted from the Caribbean to Europe; pineapples were hijacked from South America to Hawaii; rice was taken from Asia to Texas and California; and oranges were brought from China to Florida. Sugarcane originated on the Pacific islands. In all these cases, modern centers of production are far from the places where the plants were once native and restricted. Truly, humans are homogenizing the Earth's edible landscape.

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