Chapter 14

Seeds and Fruits

KEY CONCEPTS

1. In flowering plants, seeds are the structures containing the embryo plant for the next generation. Seeds are surrounded by a seed coat and contain the embryo axis and the cotyledons. They contain either one cotyledon (monocotyledonous plants) or two (dicotyledonous plants). Cotyledons contain stored food.

2. Germination of seeds involves the activation of processes in the embryo, such as mobilization of food reserves and starting cell division and elongation. The embryo radicle becomes the root system of the seedling plant, and the epicotyl becomes the shoot system.

3. There are several different types of seeds. Seeds have differing mechanisms and specialized structures for dispersal.

4. A fruit is a ripened ovary. There are several different types of fruits.

5. The function of the fruit is to aid in dispersal of the seeds. Several different vectors--wind, water, and animals--are involved in fruit and seed dispersal.

14.1 SEEDS

Seeds and fruits are without doubt the most important source of food for people and other animals, and they always have been. Seeds and fruits are filled with stored foods intended to help the embryo germinate and grow--or to attract an animal to eat the fruit and inadvertently carry the seeds away to spread them elsewhere. Rice (*Oryza sativa*), corn (*Zea mays*), and barley (*Hordeum vulgare*) grains are used for food by the majority of the people in the world. Early people recognized the nutritional value of seeds and fruits, and they harvested them from wild plants, and later they figured out how to grow them for food.

Biologically, seeds are mature ovules that contain the embryonic plants of the next generation. The tremendous production of seeds ensures the renewal of plant populations. Each seed is constructed and packaged to ensure its dispersal to a favorable site for successful germination and growth. The fruit is the packaging structure for the seeds of flowering plants. In this chapter we will discuss the structure and development of seeds and fruits and their adaptations for dispersal.

The Seed Is a Mature Ovule

The seed completes the process of reproduction initiated in the flower. Following fertilization, the zygote develops into an embryo, the primary endosperm nucleus develops the endosperm, and the integuments of the ovule develop into the seed coat.

For a short time after fertilization (Fig. 14.1b, d), the zygote nucleus divides frequently while the primary endosperm nucleus divides rapidly to form the **endosperm**, the nutrient-rich storage tissue that will feed the seed when it germinates. After the
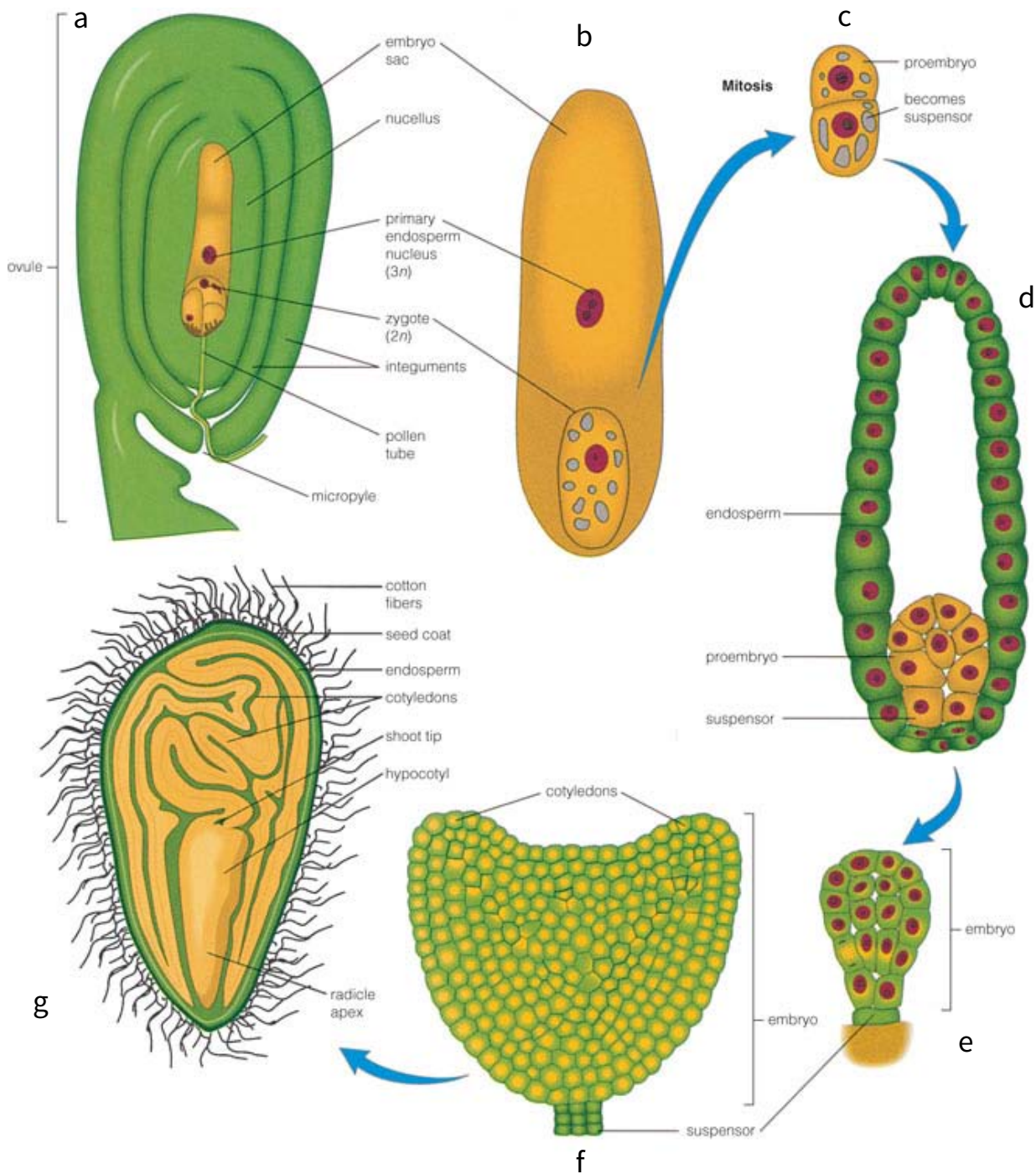
Figure 14.1. Embryo and seed development in cotton (*Gossypium hirsutum*). (a) Ovule after double fertilization. (b) Embryo sac after fertilization. (c) The zygote divides by mitosis, one of the two cells is destined to become the embryo and the other the suspensor. (d) Early stage of embryo (proembryo) and endosperm development. (e) Early embryo as a small globe of cells. (f) Heart-shaped stage of the embryo with newly formed cotyledons. (g) The cotton seed is the mature embryo, with highly folded cotyledons, surrounded by a seed coat. Note the seed coat fibers (really epidermal hairs), for which cotton is harvested.

endosperm has developed, the zygote nucleus divides to form a filament of several cells (Fig. 14.1c). The cell farthest from the micropyle begins a series of divisions that produces the early stage embryo or proembryo. At about the same time, the cell closest to the micropyle elongates and divides, becoming the **suspensor**, which supports the embryo in the endosperm (Fig. 14.1d, e). Further divisions result in a globular stage (Fig. 14.1e) and, finally, a heart-shaped stage, after the two **cotyledons** have developed (Fig. 14.1f). In addition, the embryo develops a radicle (the embryonic root) at one end and a shoot tip at the other (Fig. 14.18).

The specific steps just described apply to cotton (*Gossypium hirsutum*); there are many variations in the details of embryo development for other plants. For example, the major distinction between embryos of **dicotyledonous** and **monocotyledonous** plants is the number of cotyledons (two or one, respectively).

While the embryo is developing, the **nucellus**, endosperm, and **integuments** are also undergoing changes that are characteristic of the group of plants to which the seed belongs. In the great majority of plants, the nucellus and endosperm are required only for the initial stages of embryo development. This is particularly true of the nucellus, which is generally used as a nutritive source in early embryo stages. It persists as a food storage tissue, the **perisperm**, in seeds of sugar beet and many other species. The endosperm persists as a food reserve in seeds of many monocot plants, such as onion (*Allium cepa*) (Fig. 14.2); these include grasses of such major economic importance as rice (*Oryza sativa*) and serious weed pests such as yellow foxtail (*Setaria lutescens*) (Fig. 14.3). Endosperm persists as a food storage tissue in relatively few dicot seeds, castor bean (*Ricinus communis*) being an exception (Fig. 14.4).
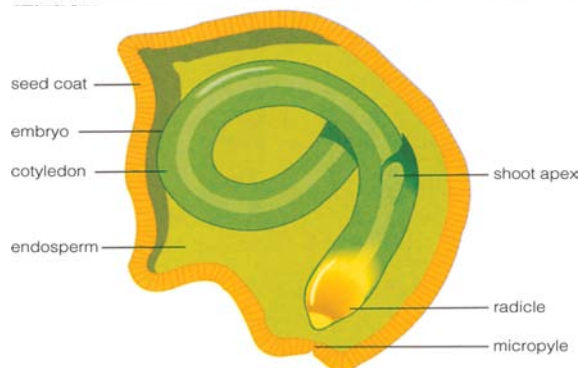

Figure 14.2. (above) External view of onion seeds (*Allium cepa*). X11. (below) A longitudinal section through an onion seed showing the embryo coiled within the endosperm.
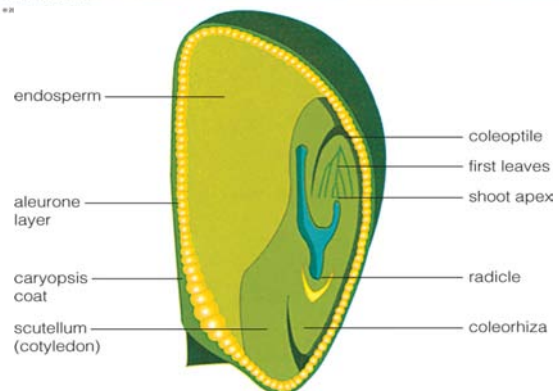
Figure 14.3. Caryopses (grains) of yellow foxtail grass (*Setaria lutescens*),. X17. (above) External views. (below) Median section.
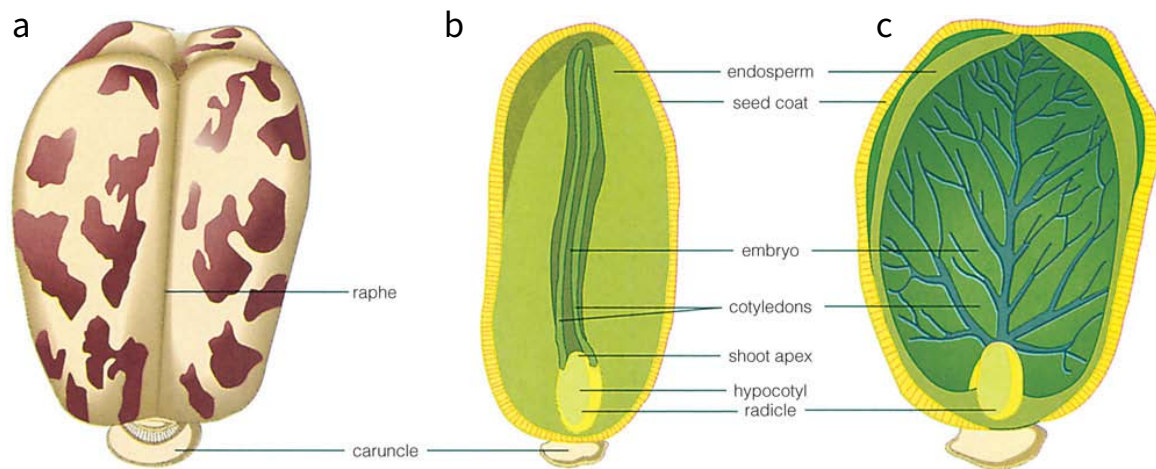
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Figure 14.4. Castor bean (*Ricinus communis*) seed, a dicot with endosperm in the mature seed. (left) External view. (center) Section showing edge view of embryo. (right) Section showing flat view of embryo.

When food storage occurs within the embryo, the normal vascular tissues of the embryo convey the solubilized food to the meristems of the emerging plant, where it is required for growth. Food stored in the endosperm, outside the embryo, is absorbed through epidermal cells of the embryo axis.

The integuments become the **seed coats** in the mature seed. Scanning electron microscopy shows the seed coats to be variously and sometimes beautifully sculptured (Fig. 14.5). The seed coat acts as a protective shell around the embryo and sometimes contains chemical substances that inhibit the seed from germinating until the temperature, light, or moisture conditions are exactly right for germination.

Seed Structures Vary

Seed structure varies widely between species. This means that plants have evolved many solutions to propagating themselves successfully. We will briefly describe, as examples of variations in seed structure, the seeds of two dicot plants--
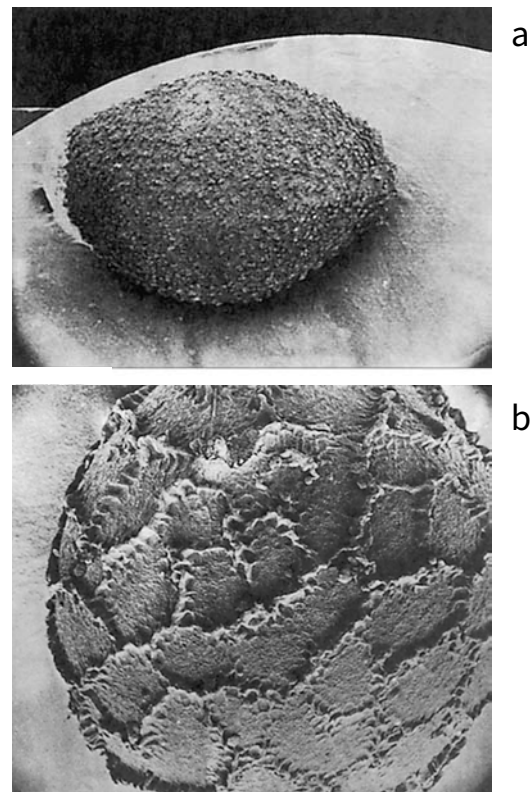

Figure 14.5. Sculptured seed coats. (a) Field bindweed (*Convolvulus arvensis*). X19. (b) California poppy (*Eschscholtzia californica*). X118.

bean and castor bean--and two monocot plants--a grass and onion.

COMMON BEAN   The bean *(Phaseolus vulgaris)* seed is kidney-shaped in outside view. External structures on the seed are the hilum, micropyle, and raphe (Fig. 14.6). The **hilum** is a large oval scar left when the seed breaks away from its placental connection, the funiculus. The **micropyle** is a small opening in the seed coat at one end of the hilum; it is the opening through which the pollen tube enters the ovule. The **raphe** is a ridge at the end of the hilum opposite the micropyle and is the base of the funiculus.

When the seed coat of a soaked bean is removed, what remains is the embryo; no endosperm is present. The bean embryo consists of two fleshy cotyledons and the *embryo axis.* The embryo axis is composed of the embryonic root or **radicle** at one end and the embryonic shoot or **epicotyl** at the other end. The **hypocotyl** is just below the cotyledons.

Figure 14.6. Bean (*Phaseolus vulgaris*), a typical dicot seed lacking an endosperm when mature. (a) External side view. (b) External face view. (c) Opened to expose embryo.

CASTOR BEAN   The castor bean (*Ricinus communis*) seed has an external structure called the **caruncle**, which is a spongy outgrowth of the outer seed coat. The hilum and micropyle of the castor bean are covered by the caruncle, and the raphe runs the full length of the seed (see Fig. 14.4). The caruncle functions in absorbing water, which is needed during germination.

The castor bean embryo is embedded in a massive endosperm. The embryo consists of two thin cotyledons, a very short hypocotyl, a small epicotyl, and a small radicle. Castor bean oil was used by the Egyptians as a laxative; a paste made from the seeds was also used as a treatment for toothache. These seeds should be handled with care, however, because they contain a very toxic substance, called *ricin.* If ingested, ricin causes nausea, muscle spasms, and convulsions; as few as eight seeds can cause death in sensitive people.

GRASSES The so-called seed of grasses is really a fruit, the caryopsis or grain (see Fig. 14.3). It is a one-seeded, dry fruit in which the pericarp or ovary wall is firmly attached to
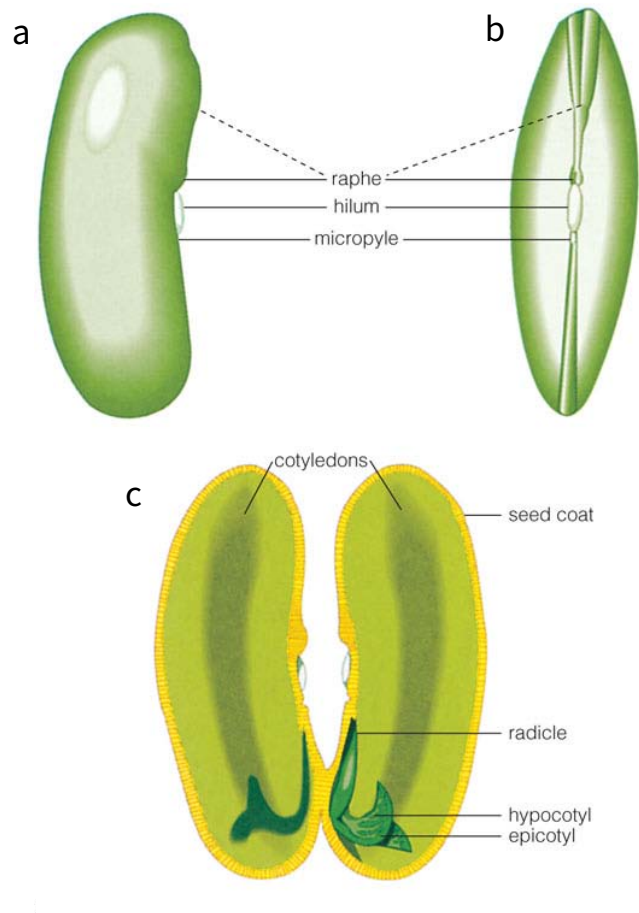
the seed coat and seed. The starchy endosperm constitutes the bulk of the caryopsis and is surrounded by a layer of cells, the **aleurone layer**, that contain proteins and fats but little or no starch.

The grass embryo has an axis with a shoot apex and a root apex. The shoot apex, together with several rudimentary leaves, is ensheathed by a **coleoptile**. The radicle is surrounded by the **coleorhiza**. A relatively large part of the grass embryo is a very specialized, shield-shaped cotyledon called the **scutellum**. The outer cells of the scutellum secrete enzymes that digest the adjacent stored foods in the endosperm upon germination. These digested foods move from the endosperm through the scutellum to the growing parts of the embryo.

The process of milling to make polished white rice removes the caryopsis fruit coat, the entire protein-rich aleurone layer, and the outer layers of the endosperm. This means that most of the nutritious protein of the grain is removed before the rice is packaged for human consumption. The milled material, called *bran,* is now itself a popular food.

Popcorn is also the fruit of a grass plant. Americans love popcorn and we eat billions of gallons of it every year. Have you ever wondered why popcorn pops? Have you ever wondered why so many kernels are left unpopped at the bottom of the kettle? Scientists at the University of Illinois conducted experiments to answer these questions. Popcorn pops when heated because steam builds up inside the grain. The resistance of the fruit coat holds the steam back until the pressure becomes so high that the grain bursts. All the starch inside becomes fluffy. The "duds" don't pop because their fruit coat has cracks in it that allow the steam to escape.

ONION Like grasses, the onion *(Allium cepa)* is a monocot; but unlike grasses, its seed coat encloses only a small amount of endosperm. The embryo is very simple, the radicle and single cotyledon being quite prominent. The shoot apex is located close to the midpoint of the axis and appears as a notch. The embryo is coiled, with the radicle end usually pointing toward the micropyle (see Fig. 14.2).

14.2 GERMINATION

Germination, the first step in the growth of the embryo, begins with the uptake or **imbibition**, of water. This is a critical step because seeds are quite dry, containing only 5 to 10% water. The cells of dry seeds are tightly packed with stored proteins, starch, and lipids (Fig. 14.7a). This stored food is packaged into cytoplasmic organelles called *protein bodies, lipid bodies,* and *amyloplasts,* which store starch (see Chapter 3). After imbibition, enzymes are activated and rapidly released to digest the stored food into smaller molecules which can then be transported and converted into energy needed for growth. Consequently, the cells of imbibed embryos contain fewer storage organelles and more mitochondria, ribosomes, and endoplasmic reticulum which are organelles involved in metabolism (Fig. 14.7b).

The first indication that germination has begun is generally the swelling of the radicle. It imbibes water rapidly and, bursting the seed coat and other coverings that may be present, starts to grow downward into the soil.
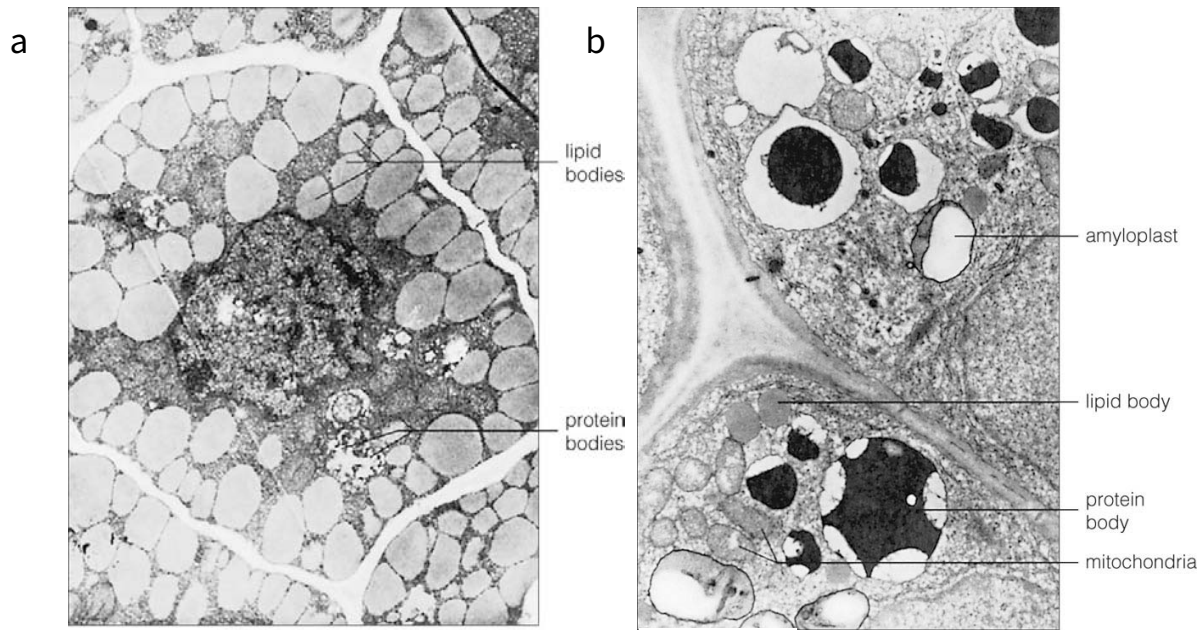
Figure 14.7. Cellular changes brought about by germination, demonstrated in transmission electron micrographs of yellow foxtail grass (*Setaria lutescens*). (a) Scutellum cell in dry caryopsis before germination; note the abundance of storage organelles such as lipid bodies and protein bodies. X8,600. (b) Root cell after 65 hours of germination; the cell now has fewer storage organelles and more organelles involved in metabolism such as mitochondria and leucoplasts. X6,500.

The Germination Process Differs Among Plants

Although the succeeding steps of germination are essentially similar in all plants, there are variations. In the germination of beans, peas, castor beans, and onions, a structure with a sharp hook is first forced upward through the soil. The structure forming the hook is different in each case. In bean (*Phaseolus vulgaris*), the hypocotyl elongates (Fig. 14.8). In pea (*Pisum sativum*), the epicotyl elongates (Fig. 14.9). In both cases, cotyledons and shoot apex remain below ground at first. The hook straightens once it is above ground and exposed to light. In the case of bean, the straightening of the hypocotyl raises the cotyledons and shoot apex toward the light. This is called **epigeal** germination. When the pea epicotyl straightens, the cotyledons remain below ground, and only the apex and first leaf are raised upward. This is called **hypogeal** germination (Fig. 14.9).

Castor bean (*Ricinus communis*) has epigeal germination (Fig. 14.10). It is different from common beans in that its cotyledons first function as absorbing organs, facilitating the transfer of food from the endosperm to the rest of the seedling. When the reserve food supply in the endosperm is exhausted, the cotyledons of the castor bean embryo emerge from the seed coat. They enlarge, become green, carry out photosynthesis for a time, and then eventually wither and die.

In onion (*Allium cepa*), a sharply bent cotyledon breaks the soil surface and slowly straightens out. The cotyledon of the onion is tubular, and its base encloses the shoot apex (Fig. 14.11). The first leaf finally emerges through a small opening at the base of the cotyledon.

In grasses such as corn (*Zea mays*), the situation is more complex. The shoot and root are enveloped by tubular sheaths of the coleoptile (Fig. 14.12) and coleorhiza. The primary root rapidly pushes through the coleorhiza. Adventitious roots then arise from the lower nodes of the stem. The coleoptile elongates and emerges above ground, becoming 2 to 4 cm (about 1 to 2 in) long. At this time, the uppermost leaf pushes its way through the coleoptile and, growing rapidly, becomes part of the photosynthesizing shoot.
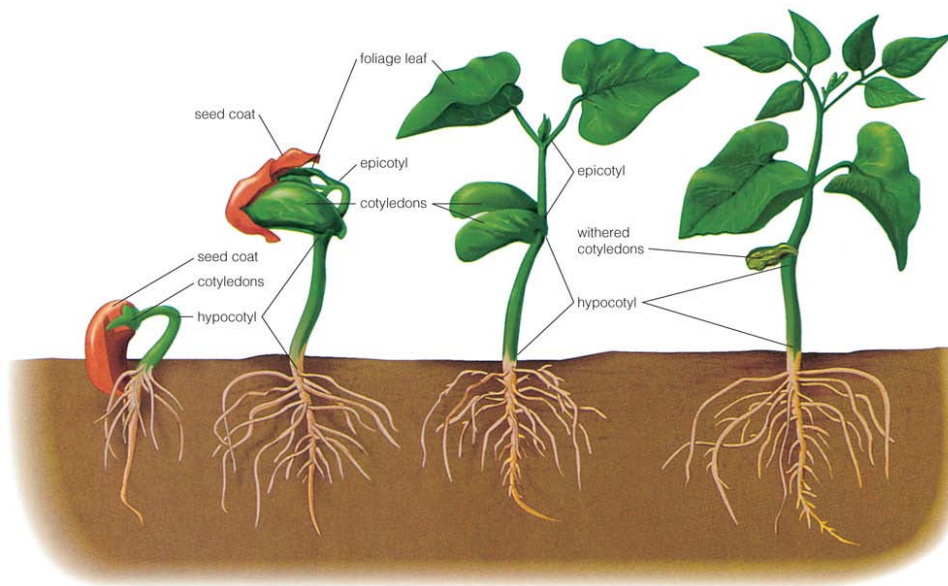

Figure 14.8. Stages in the epigeal germination of a bean (*Phaseolus vulgaris*) seed.
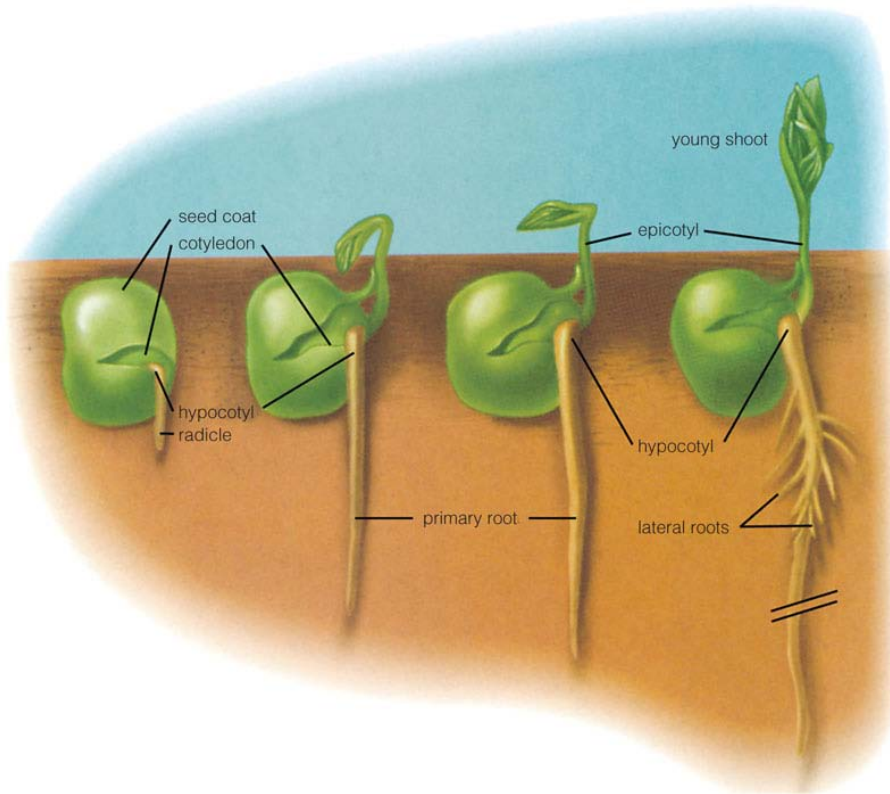
Figure 14.9. Stages in the hypogeal germination of a pea (*Pisum sativum*) seed.
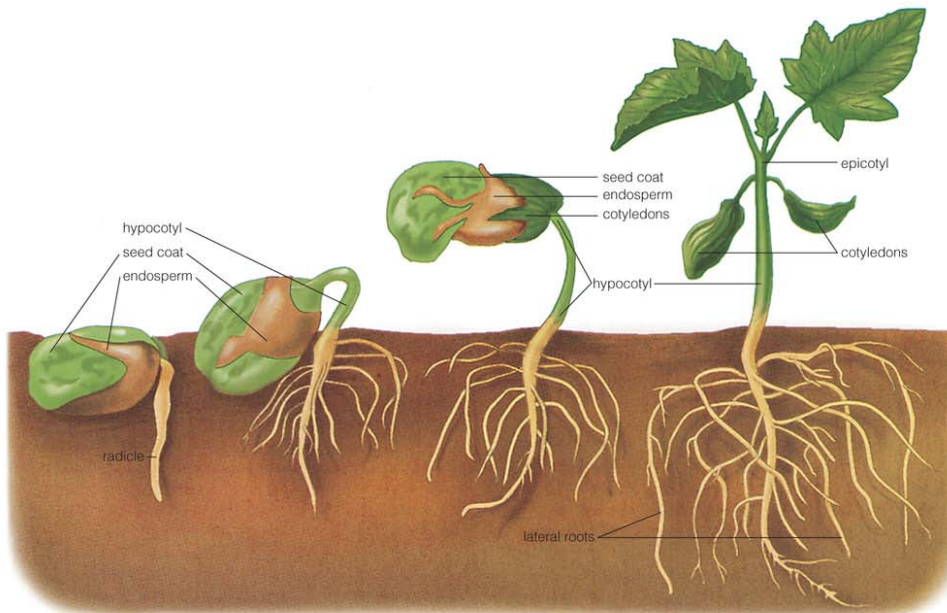
Figure 14.10. Stages in the germination of a castor bean (*Ricinus communis*) seed.
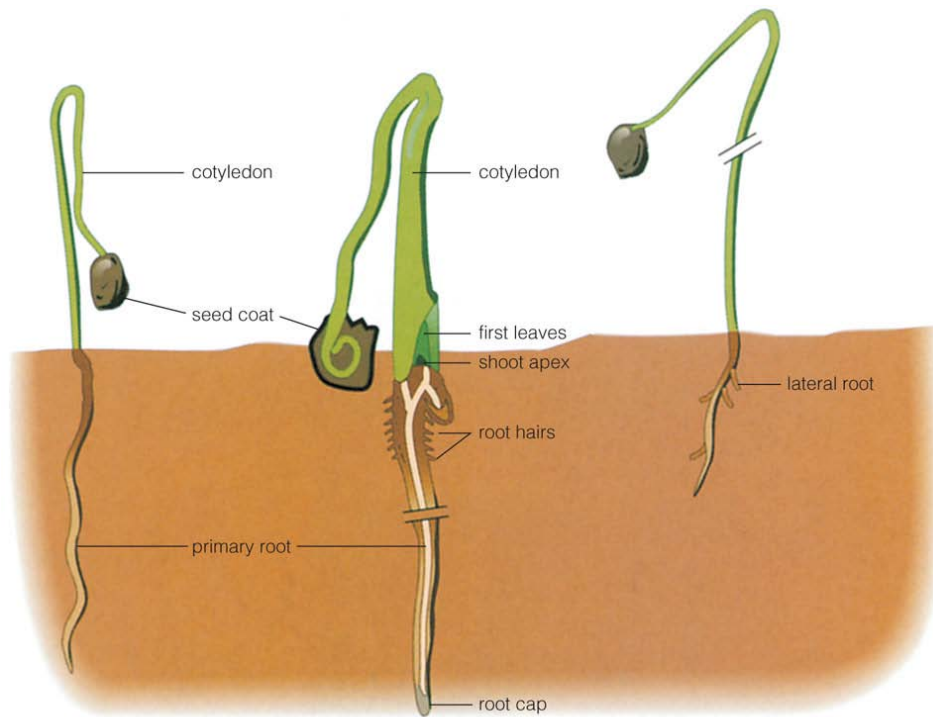
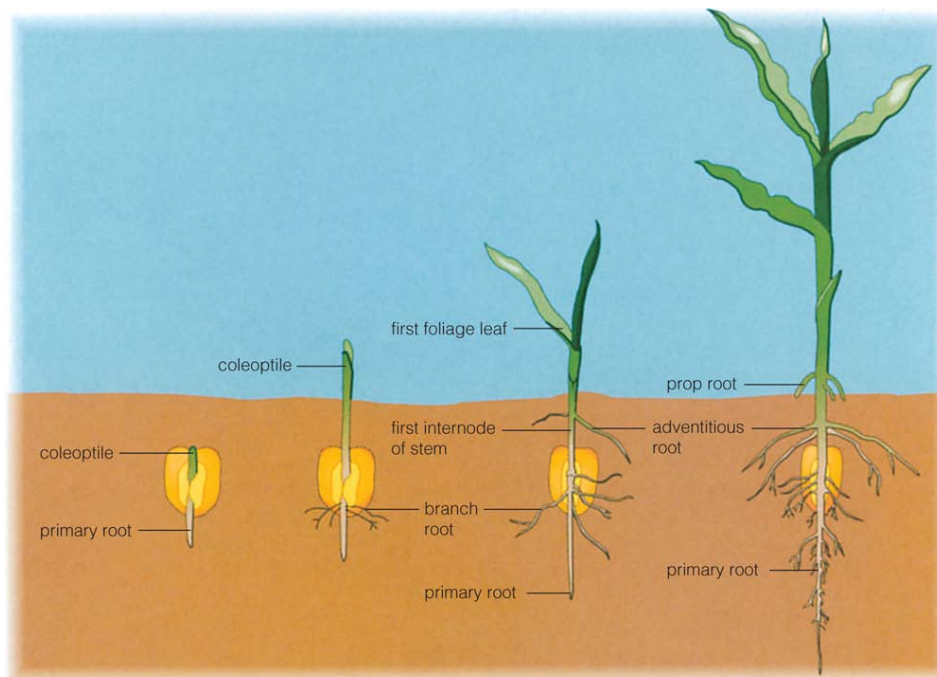Figure 14.11. Stages in the germination of an onion (*Allium cepa*) seed.

Figure 14.12. Stages in the germination of corn (*Zea mays*). After the primary root emerges, it branches to form the root system. Adventitious roots emerge from the lower stem, and prop roots form to hold the stem upright. The emerging young leaves are protected by a sheath-like coleoptile.

Germination May Be Delayed by Dormancy

Seeds can remain viable for remarkably long periods. In one study, jars containing seeds from several different plant species were buried. At 5- and 10-year intervals, the jars were opened, and the seeds were tested for germination. Most species remained viable for at least 10 years, and one species, the moth mullein (*Verbascum blattaria*), germinated after more than 100 years. This is not a record for seed longevity, however. Viable seeds from the Oriental lotus (*Nelumbo nucifera*) have been removed from archaeological sites known to be more than 1000 years old.

Many viable seeds will not germinate even when supplied with water, oxygen, and a favorable temperature, because they are in a state of dormancy (inability to germinate because of reduced physiological activity). Various factors can break dormancy. For instance, light is necessary for the germination of some lettuce (*Lactuca*) species. Scarring or breaking through the seed coat is required before the seeds of some plants (including many kinds of legumes) will germinate; their hard, dense seed coats restrict the movement of water and gases. In orchids, seeds are dispersed while the embryos are immature, and they must develop further before germinating. Seeds of some cool-temperate zone plants, (for instance, gooseberry, *Ribes speciosum*), will not germinate unless they are first subjected for a time to temperatures close to freezing, while moist. At the other extreme, the seeds of some pines (*Pinus*) will not germinate unless they have been subjected to the rather high heat of a fire. Another type of dormancy is produced by natural chemical inhibitors, which occur in many fruits or in seed coats--for example, in yellow foxtail grass (*Setaria lutescens*).

14.3 FRUITS: RIPENED OVARIES

A **fruit**, the ripened ovary of a flower, is an important auxiliary structure in the sexual life cycle of angiosperms. Fruits protect seeds, aid in their dispersal, and may be a factor in timing their germination. Because fruits are highly constant in structure, even when grown in different environments, they play an important role in the classification of angiosperms. The kay at the end of the chapter, "Key to Fruits," will help you identify the different types of fruits described in this section.

In everyday usage, the term *fruit* usually refers to a juicy and edible structure such as an apple (*Malus* sp.), plum (*Prunus* sp.), peach (*Prunus persica*), or grape (*Vitis vinifera*). Structures that are commonly called *vegetables,* such as string beans (*Phaseolus vulgaris*), eggplant (*Solanum melongena*), okra (*Hibiscus esculentus*), squash (*Cucurbita* sp.), tomato (*Lycopersicon esculentum*) and cucumber (*Cucumis sativus*), are all fruits in a botanical sense, as are grains of corn (*Zea mays*), and oats (*Avena sativa*), and other cereals.

The Nature of the Ovary Determines the Structure of the Fruit

In spite of considerable variation along family lines, fruits share basic developmental and anatomical characteristics. For instance, all fruit development is initiated by fertilization which stimulates the ovary wall to undergo development and differentiation into three layers. The fruit wall (which develops from the ovary wall) is called the **pericarp**; its three more or less distinct layers (in order, beginning with the outermost) are **exocarp**,

mesocarp, and **endocarp** (Fig. 14.13). When the fruit is mature, floral structures--such as pedicel, calyx, withered stamens, style and stigma, and even remnants of the corolla--may also be present.

Tissues other than the ovary wall that form part of a fruit, are referred to as accessory. Much of the fruit of pineapple (*Ammas* sp.), apple (*Malus* sp.), and strawberry (*Fragaria* sp.) can be called accessory. In the strawberry, the edible portion is a thickened, pulpy central receptacle in which achenes (dry, one-seeded fruits) are embedded.
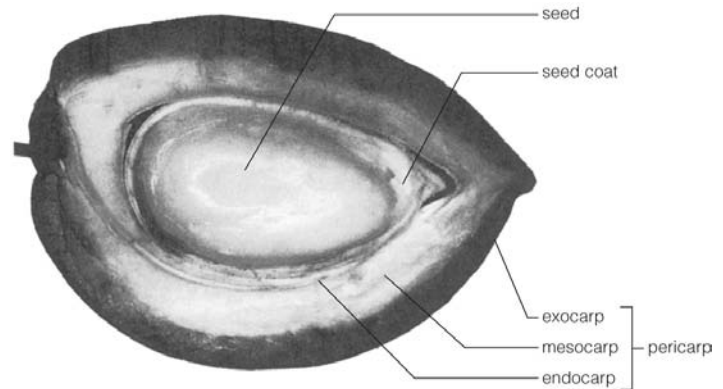

Figure 14.13. Mature almond (*Prunus amygdalus*) fruit showing split outer portion of ovary walls (pericarp)--endocarp, mesocarp and ectocarp.

Fruits May Be Simple or Compound

There are three main categories of fruits. Simple fruits are derived from a single ovary. They may be dry or fleshy; the ovary may be composed of one or more carpels, and the fruit may be **dehiscent** (splits open when mature) or indehiscent (does not split open). Compound fruits are composed of more than one fruit. There are two types: aggregate fruits and multiple fruits. **Aggregate fruits** are derived from many separate ovaries of a single flower, all attached to a single receptacle (for example, strawberry, Fig. 14.14). **Multiple fruits**, such as pineapple (Fig. 14.15), are the enlarged ovaries of several flowers grown more or less together into a single mass. The receptacle of some multiple fruits, such as fig (*Ficus* sp.), enlarges and is actually the edible part (Fig. 14.16).

In classifying the different kinds of fruits, the following criteria are taken into account:

1. the structure of the flower from which the fruit develops
2. the number of ovaries involved in fruit formation
3. the number of carpels in each ovary
4. the nature of the mature pericarp (whether the fruit wall is dry or fleshy)
5. whether or not the pericarp splits (dehisces) at maturity
6. if the pericarp dehisces, the manner of its splitting
7. the role, if any, that accessory tissues may play in formation of the mature fruit

Simple Fruits Are from Single Ovaries

Simple fruits come in several forms. Their pericarp (fruit wall) may be dry or fleshy. If dry, the pericarp may or may not dehisce.
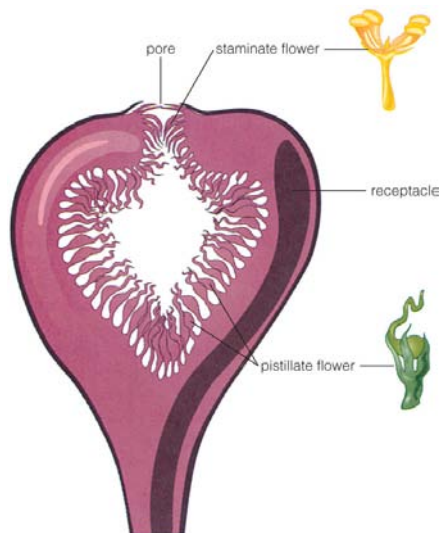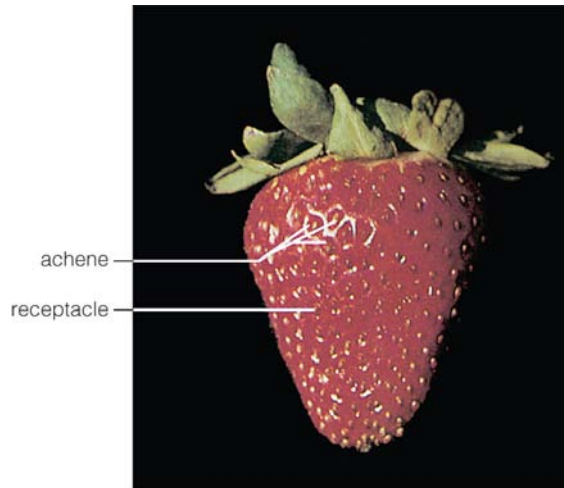
Figure 14.14 (upper left). Strawberry (*Fragaria*), an aggregate fruit. The tiny individual fruits, called achenes, are simple, dry fruits. They are embedded in an enlarged fleshy receptacle.

Figure 14.15 (upper right). Pineapple (*Ananas comosus*), a multiple fruit. The individual fruits, called berries, are embedded in the swollen edible inflorescence axis. Jagged-edged bracts extend out over the fruits.

Figure 14.16 (left). The fruit and flowers of fig (*Ficus carica*). (a) Fleshy receptacle. Internal views showing (b) staminate and (c) pistillate flowers.

PERICARP DRY AND DEHISCENT The **legume** or **pod** is the type of fruit found in nearly all members of the pea family (Fabaceae). A pod arises from a single carpel, which at maturity generally dehisces along two sides (Fig. 14.17). In the pea (*Pisum sativa*) pod, the shell is the pericarp, and the pea is the seed. Pods may be spirally twisted or curved, as in Scotch broom (*Cytissus scoparius*). However, a number of legumes such as alfalfa (*Medicago sativa*) have pods that do not dehisce.

An example of a **follicle** fruit is the magnolia (*Magnolia grandiflora*) (Fig. 14.18). The follicle develops from a single carpel and opens along only one side.

Capsules are simple fruits derived from compound ovaries (an ovary composed of more than one carpel). Each carpel produces a few to many seeds. Capsules dehisce in various ways along the top surface. Poppy (*Papaver* sp.) is an example (Fig. 14.19).

The **silique** is the characteristic fruit of members of the mustard family (Brassicaceae). The silique (Fig. 14.20) is a dry fruit derived from a superior ovary consisting of two locules. At maturity, the dry pericarp separates into three portions; the seeds are attached to the central, persistent portion.

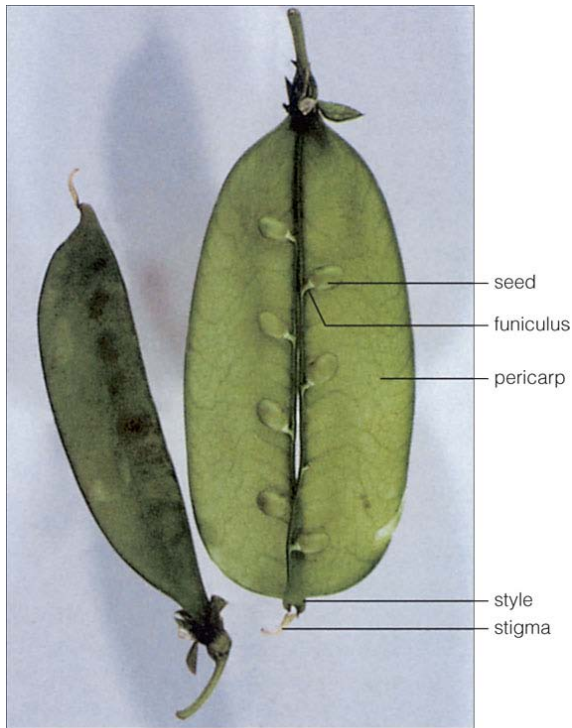Figure 14.17. Opened pea pod (*Pisum sativum*) showing developing seeds attached to carpel margins.

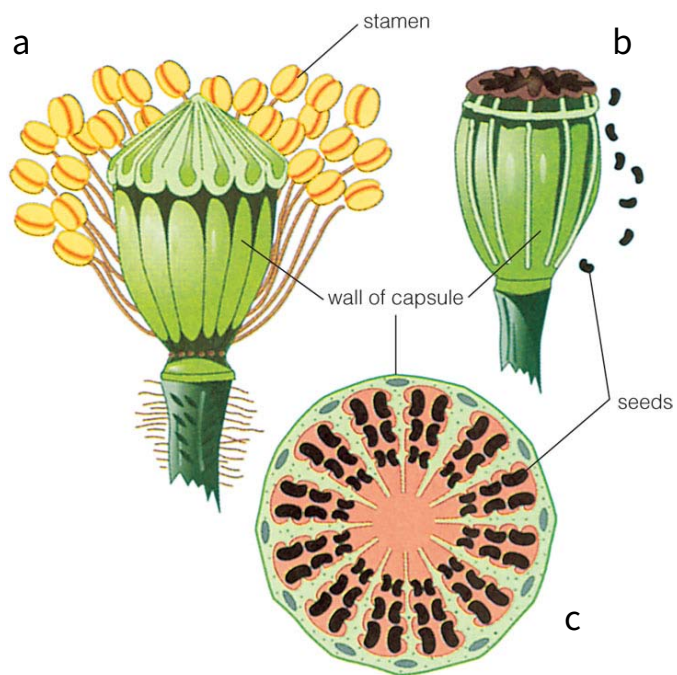Figure 14.18. Dehiscing follicle of a *Magnolia* sp.

Figure 14.19. Poppy (*Papaver* sp.) capsule. (a) Side view before dehiscence. (b) Mature poppy capsule dehiscing by pores at the top. (c) Cross section of poppy capsule showing the position of seeds.

Figure 14.20. Silique of *Mathiola* sp.

PERICARP DRY AND INDEHISCENT   The **achene** is a dry, one-seeded fruit. Sunflower (*Helianthus annuus*) achenes are usually called seeds, but carefully breaking open the pericarp reveals that the seed is inside. The pericarp is easily separated from the seed coat, which is a thin, filmy layer surrounding the sunflower embryo (Fig. 14.21).

The **caryopsis** or **grain** is the fruit of the grass family (Poaceae), which includes rice (*Oryza sativa*) and wheat (*Triticum aestivum*). The grain is a dry, one-seeded, indehiscent fruit (see Fig. 14.3). It differs from the achene in that pericarp and seed coat are firmly united all the way around the embryo.

The **samara** may be a one-seeded simple fruit, as in elm (*Ulmus* sp.), or a two-seeded one, as in maple (*Acer* sp.) (Fig. 14.22). These fruits are typified by an outgrowth of the ovary wall, which forms a winglike structure that aids in seed dispersal.

The **schizocarp** is a fruit characteristic of the carrot family (Apiaceae), which includes celery (*Apium graveolens*). The schizocarp consists of two carpels that split, when mature, along the midline into two one-seeded, indehiscent halves (Fig. 14.23).

The term **nut** is popularly applied to a number of hard-shelled fruits and seeds. Botanically speaking, a typical nut is a one-seeded, indehiscent dry fruit with a hard or stony pericarp (shell). Examples are chestnut (*Castanea* sp.) and walnut (*Juglans* sp.). An acorn, the fruit of the oak (*Quercus* sp.) (Fig. 14.24), is partially enclosed by a hardened cup. The outer husk of the walnut, which is removed during processing, is composed of bracts, perianth, and the outer layer of the pericarp. The hard shell is the remainder of the pericarp. Note that unshelled almonds (*Prunus* sp.), are really not nuts but fleshy fruits known as drupes, from which the hulls--exocarp and mesocarp--have been removed. Brazil nuts (*Bertholleda excelsa*) are seeds, not nuts, and the unshelled peanut (*Arachis hypogaea*) is really a pod.
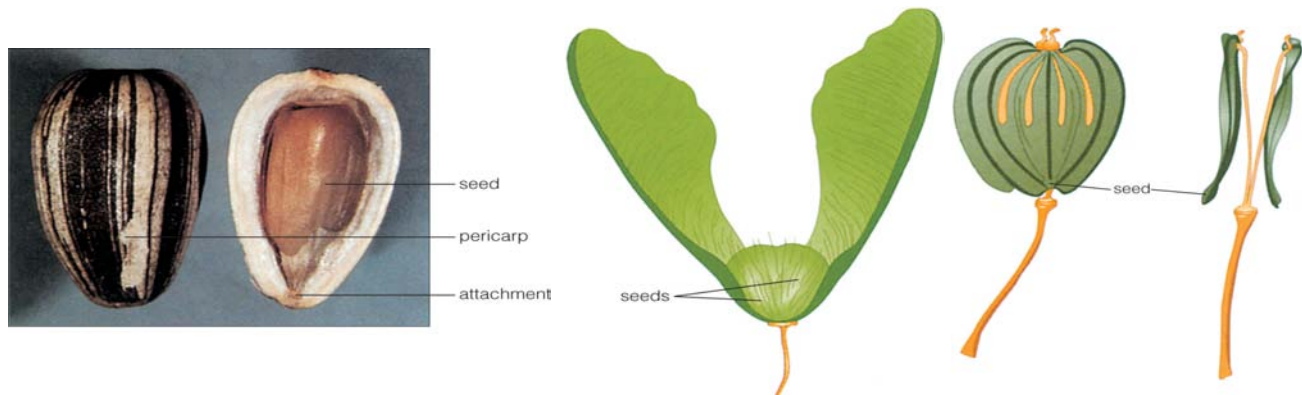

Figure 14.21 (left). Achene of sunflower (*Helianthus annuus*), unopened and opened to show attachment of seed.

Figure 14.22 (center). Two-seeded samara of maple (*Acer*).

Figure 14.23 (right). Schizocarp of cow-parsnip (*Heracleum hirsutum*); left is face view, and right is side view.
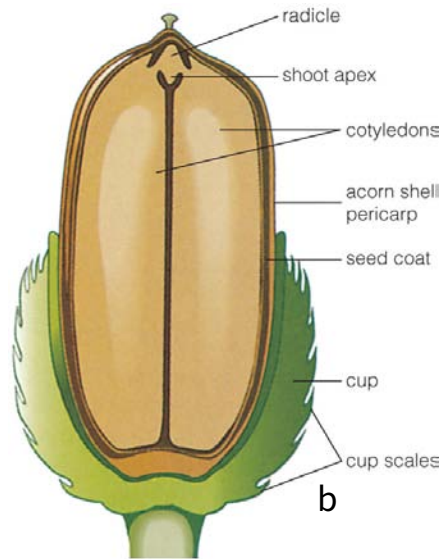
Figure 14.24. Nut. (a) An acorn of oak (*Quercus*) is actually a nut, the cup are fused bracts. (b) Internal view of acorn, showing the embryo.

PERICARP FLESHY The fruits in this category are popular for food. They feature a fleshy fruit wall (pericarp). The fleshy part is usually attractive to animals, who eat the fruit and in turn carry away the seeds. The seeds found in these fruits tend to have a hard seed coat that is not broken down as the seed passes through the animal and is deposited in its feces.

Cherry, almond, peach, and apricot (all are *Prunus* sp.), in the rose family (Rosaceae), are examples of **drupes**. The olive (*Oleo* sp.) (family Oleaceae) fruit is also a drupe. Derived from a single carpel, the drupe is usually one-seeded. It has a hard endocarpconsisting of thick-walled sclereids (see Chapter 4), and a thin exocarp forms the skin. The mesocarp is the edible fleshy portion. The pit of a cherry is a seed, with a thin seed coat, plus the stony inner layer (endocarp) of the ovary wall. I n almond fruit (see Fig. 14.13), the mesocarp is fleshy like a typical drupe when the fruit is young. As it develops, however, the mesocarp becomes hard and dry and forms the hull. The shell of the almond is endocarp. This is an instance in which the seed, not the outer part, is the edible part of a drupe.

A **berry** is a fleshy type of fruit that is derived from a compound ovary. Usually, many seeds are embedded in the flesh (Fig. 14.25), which is pericarp, although the line of demarcation may be difficult to see. It comes as a surprise to many that tomatoes, lemons (*Citrus limon*)*,* and cucumbers (*Cucurbita* sp.) are berries, but strawberries (*Fragaria* sp.) and blackberries (*Rubus* sp.)*,* in spite of their common names, are not. These are good examples of botanical names and common names that don't match.

Lemons, oranges, limes, and grapefruits (all *Citrus* sps.) are a type of berry called a **hesperidium**. The thick, leathery rind (peel) with numerous oil cavities is exocarp and mesocarp; the thick, juicy pulp segments (endocarp) are composed of several wedge-shaped locules (Fig. 14.26). The juice forms in juice sacs or vesicles that are outgrowths from the endocarp walls. Each mature juice sac is composed of many living cells filled with juice. The fruits of watermelon (*Citrullus vulgaris*), cucumber, and squash--all members of the cucumber family (Cucurbitaceae)--are a kind of berry called a **pepo** (Fig. 14.27). The outer wall (rind) of the fruit consists of receptacle tissue that surrounds and is fused with the exocarp. The flesh of the fruit is principally mesocarp and endocarp.

Apples (*Malus* sp.) and pears (*Pyrus* sp.), both in the Rosaceae family, are examples of **pomes**. This fruit is derived from a flower with an inferior ovary (Fig. 14.28). The flesh is enlarged hypanthium (a fleshy floral tube), and the core is from the ovary.
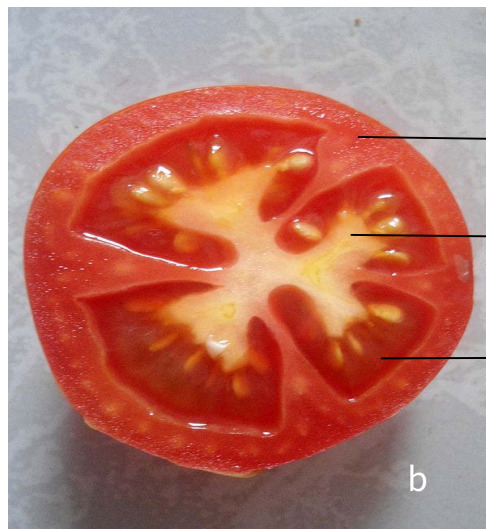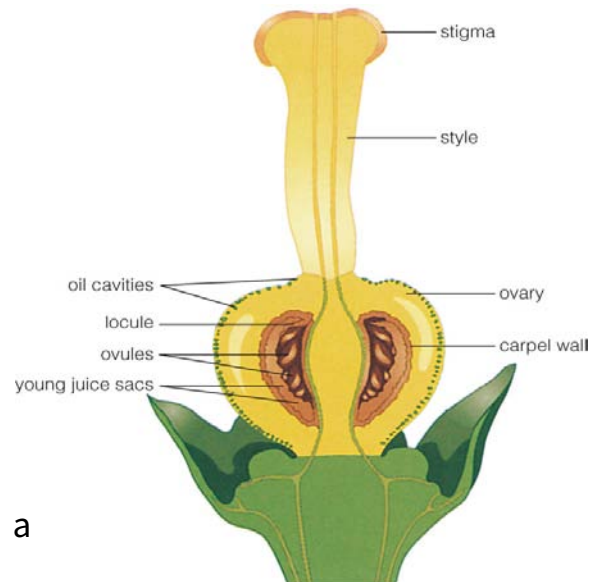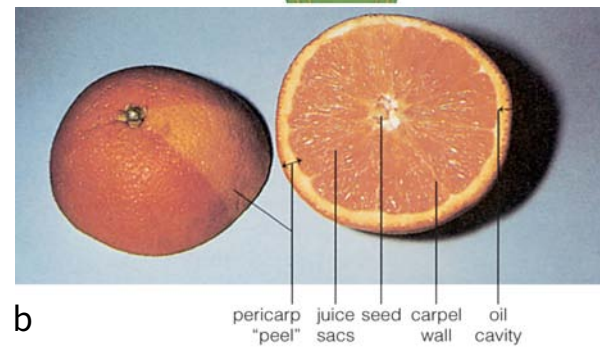
Figure 14.25 (above left). Berry of tomato (*Lycopersicon esculentum*). (a) External view. (b) Cross section.

Figure 14.26 (above right) A citrus fruit is a hesperidium. (a) Flower of organge (Citrus sinensis), showing a lengthwise section of maturing ovary. (b) Cross section and external view of mature fruit.

Figure 14.27. Cucumber (*Cucumis sativus*) fruit is a berry.

Figure 14.28. Pome fruit of apple (*Malus sylvestris*). (a) Median longitudinal section of flower showing maturing fruit. (b) Median section of fruit. (c) Cross section of fruit.
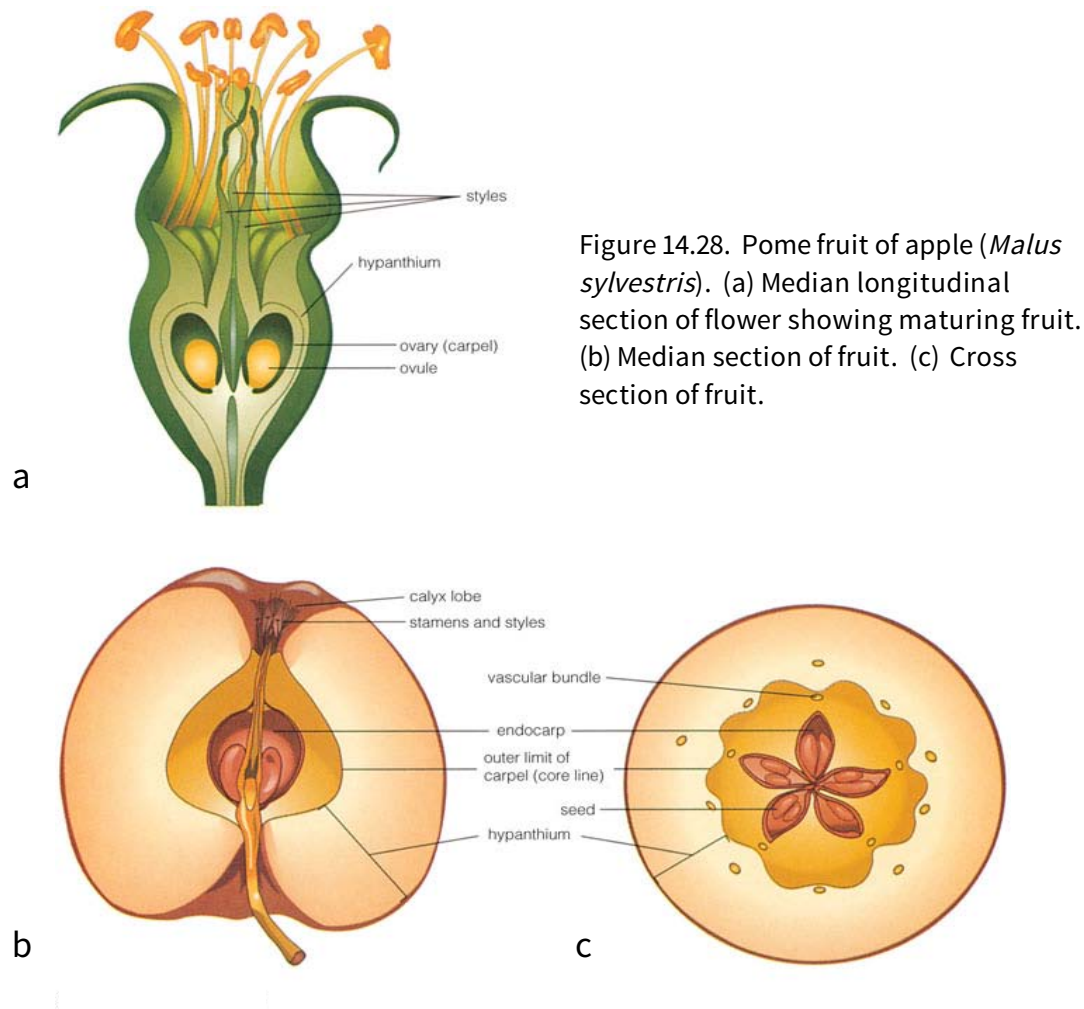
Compound Fruits Develop from Several Ovaries

An aggregate fruit is formed from numerous carpels of one individual flower. These fruits are made up of many simple fruits attached to a fleshy receptacle. The strawberry flower has numerous separate carpels on a single receptacle. Each carpel develops into an achene (see Fig. 14.14). Flowers of raspberry, blackberry, and other species of *Rubus* have essentially the same structure as strawberry, except that the attached fruits are small drupes (Fig. 14.29).

A multiple fruit is formed from individual ovaries of several flowers, all clumped together. The fig (*Ficus* sp.) (see Fig. 14.16) and the pineapple (*Ananas comosus*) (see Fig. 14.15) are examples of multiple fruits; the individual fruits composing them are drupes in fig and berries in pineapple. The fig fruit we eat is an enlarged, fleshy receptacle. Its flowers are small and attached to the inner wall of the receptacle.

Not All Fruits Have Seeds

In some plants, normal fruit may develop without seeds being enclosed. Fruits that develop without fertilization are called **parthenocarpic**; consequently, such

fruits are seedless. Thompson seedless grapes (*Vitis* sp.) were thought to be parthenocarpic until it was shown that fertilization does take place but that the ovules fail to mature into seeds. Such situations have led to a broader use of the word *parthenocarpy* to mean simply, seedless fruits.

Parthenocarpic (seedless) fruits are quite regularly produced in such cultivated plants as eggplant, navel orange, banana, pineapple, and some varieties of apple and pear. In certain plants, seedless fruits may be induced by pollen that is incapable of fertilizing the ovules. For example, in some orchids, placing dead pollen or a water extract of pollen upon the stigma may start fruit development. Parthenocarpy is commercially induced in some plants by spraying the blossoms with dilute aqueous solutions of growth substances like auxin.

Figure 14.29. Aggregate fruit of the blackberry (*Rubus ursinus*). The individual fruits are drupes.

14.4 ADAPTATIONS FOR SEED DISPERSAL

The role of ripe fruit is threefold: to aid in the dispersal of the seeds inside; to deter inappropriate seed-dispersing animals from taking the fruit or seed; and to protect the seeds from herbivores who merely consume seeds but do not disperse them. It is important to realize that there is no nutritional relationship between the fruit and the seeds within it. That is, the stored food in the fruit cannot be utilized by dormant seeds or by germinating seedlings. The only stored food available to seedlings is in the endosperm and cotyledons within the seed itself.

Both seeds and fruits are rich in a variety of chemical resources: sugar, starch, protein, lipid, amino acids, and a variety of secondary compounds. The average caloric value of this material is about 5100 kilocalories (kcal) per gram dry weight, a value approaching that of healthy animal tissue (about 6000 kcal per gram). In contrast, leaf, root, stem, and other vegetative tissues average only 4000 kcal per gram. This means that it costs the plant more to make seeds and fruits than it does to make vegetative organs. This expense is necessary to ensure that the materials present inside seeds and fruits will guarantee the successful dissemination of the seeds. Several different mechanisms have c), float in seawater, attract the eye and the stomach of a bird (Fig. 14.30g), entice an ant to carry a seed, or permit the fruit to hook onto the hairs of a passing mammal (Fig. 14.30d-f). Just as in pollination, the animal vectors used are sometimes rewarded,

sometimes exploited; in other words, the relationship is sometimes mutualistic, sometimes parasitic.
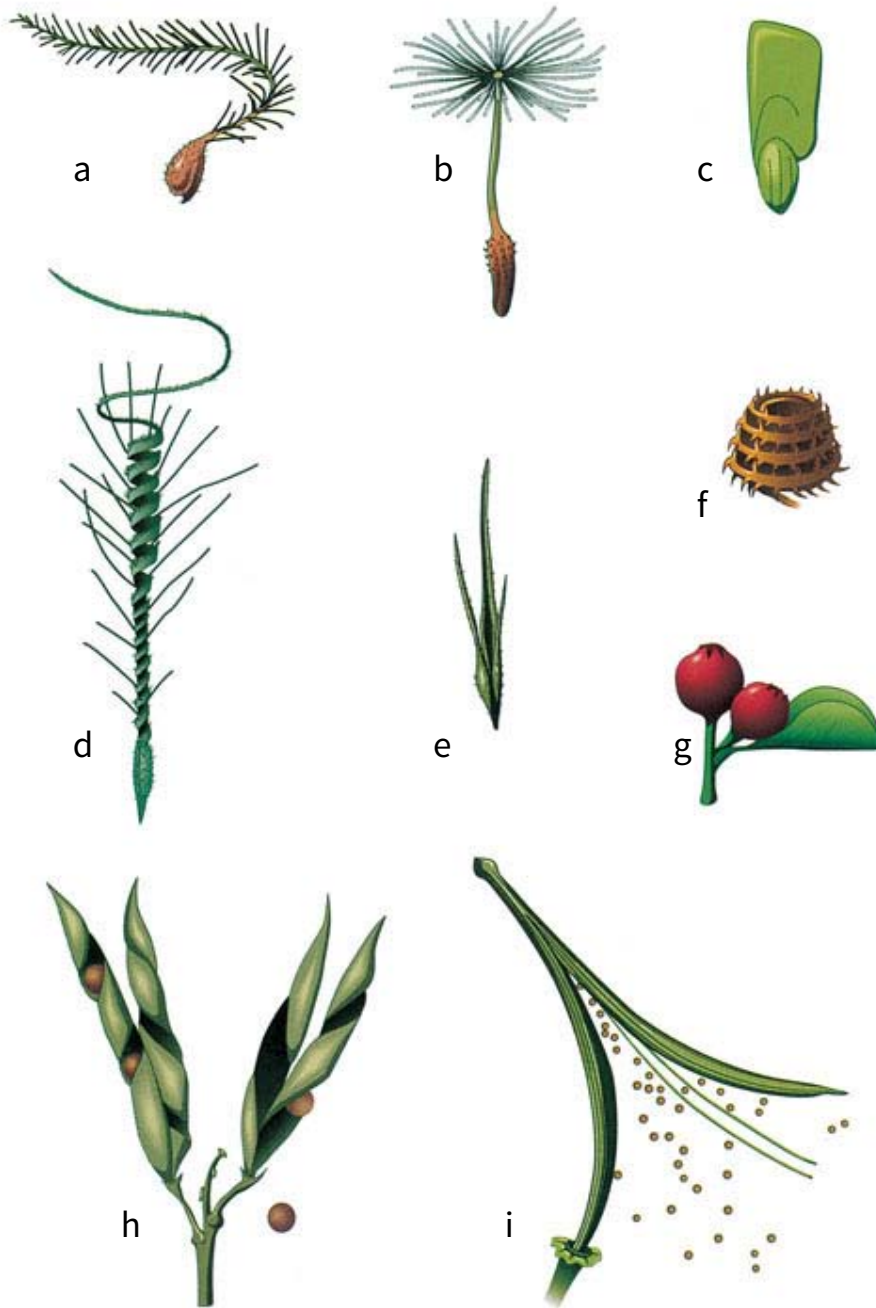
Figure 14.30. Fruits and seeds showing various devices aiding in dispersal. Wind: (a) *Clematis*. X4. (b) Dandelion (*Taraxacum vulgare*). X5. (c) Seed of Coulter's big-cone pine (*Pinus coulteri*). X1. Attachment: (d) Cranesbill (*Geranium*). X3. (e) foxtail (*Hordeum hispida*). X3. (f) Bur clover (*Medicago denticulata*). X4. (g) Fleshy edible fruit of *Cotoneaster*. X2. Violent dehiscence of pericarp. (h) Vetch (*Vicia sativa*). X2. (i) California poppy (*Eschscholtzia californica*). X2.

Dispersal May Be by Wind, Water, and Animals

Common **abiotic** vectors for fruit and seed dispersal are wind and water. Winged and plumed fruits (Fig. 14.30a-c) are common adaptations for wind dispersal. In some cases, the seeds are ballistically exploded by a violent dehiscence of the pericarp (Fig. 14.30h, i).

Some sedges (*Carex* sp.) have a fruit with a membranous envelope containing air, and these are spread by floating on water. The coconut (*Cocos* sp.) is a tropical group of plants famous for growing on midoceanic islands thousands of miles from other land. The coconut fruit is capable of floating for many days and then germinating when washed onto a sandy beach and leached of salt by rainwater (Fig. 14.31a). Many other tropical beach plants have similar (although much smaller) floating fruits. A number of weed species of irrigated farmland are dispersed by water along irrigation canals. In deserts the smoke tree (*Dalea*) and desert willow (*Chilopsis*) growing along arroyos (dry stream beds) have hard seeds that are carried away from the parent by flash floods (Fig. 14.31b). The rushing water also pushes the seeds against rocks, scraping the seed coats and scarifying them. Without that scarification, the seeds would remain dormant. Water in this case is more than a dispersal agent; it pretreats the seed and makes it receptive to germination cues.
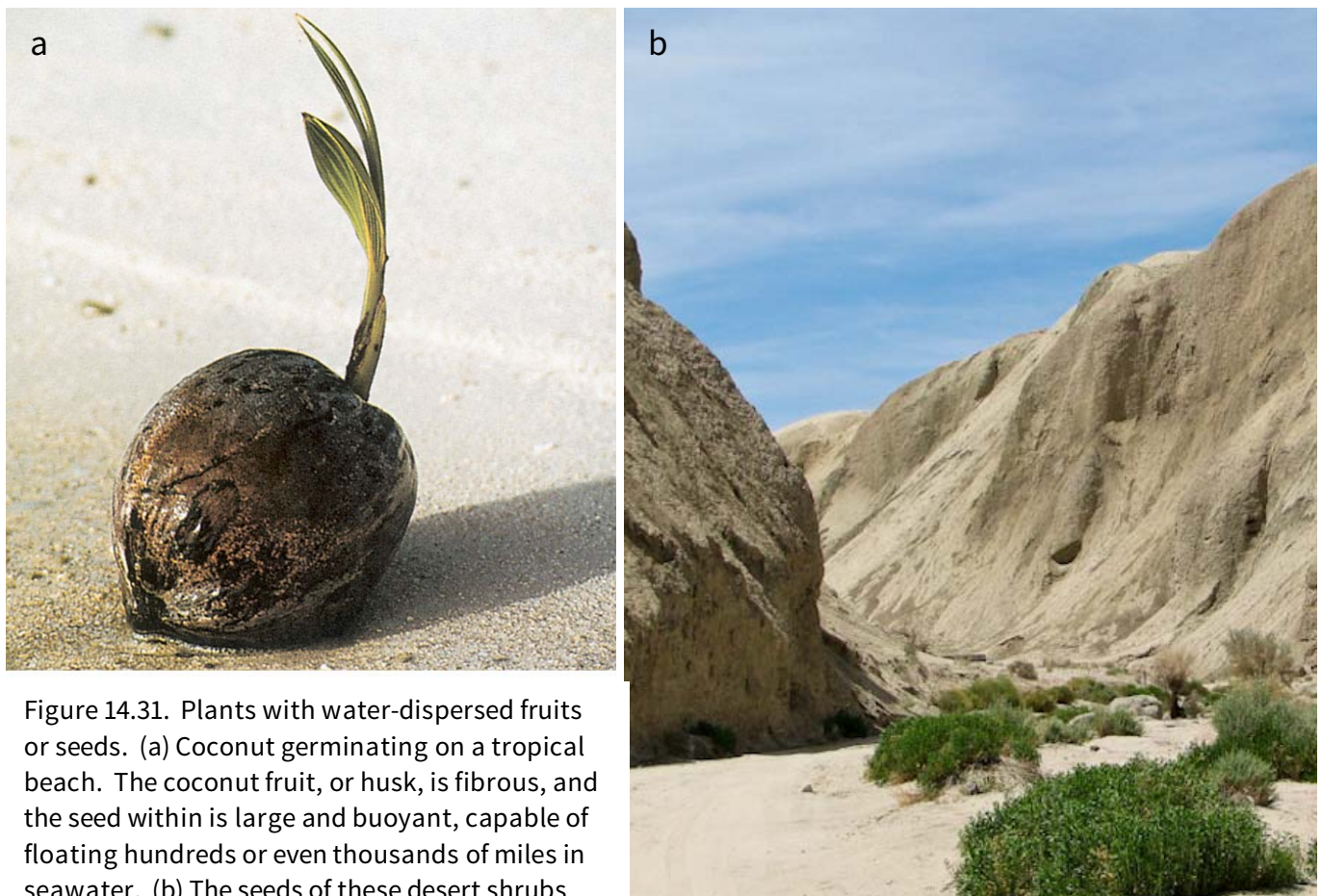
Figure 14.31. Plants with water-dispersed fruits or seeds. (a) Coconut germinating on a tropical beach. The coconut fruit, or husk, is fibrous, and the seed within is large and buoyant, capable of floating hundreds or even thousands of miles in seawater. (b) The seeds of these desert shrubs are carried away from the parents by flash flood waters in the arroyo.

Common animal (**biotic**) vectors include ants, birds, bats, rodents, fish, ruminants, and primates. They are attracted to fruit by its color, position, seasonal availability, odor, and taste. Sometimes, the vector eats only the fruit and discards the seeds; this is true of some primates. In other cases, the vector swallows the seeds unchewed; after passing

unharmed through the gut, the seeds are excreted some distance from where they were consumed. This is often the case with birds. Birds are attracted to fleshy, colored berries and, after dining on them, may fly long distances before regurgitating or excreting the hard seeds. Cattle eat legume pods of mesquite (*Prosopis fuliflora*) and *Acacia* in southwestern grasslands and later pass many undamaged seeds out in their excrement. These germinate, and the seedlings grow well in their fertilized microenvironment. In yet other cases, the animals eat many seeds but cache others. Squirrels and jays, for example, may carry walnuts, hickory nuts, acorns, and pine seeds from parent trees to distant hiding places. Apparently, they forget some of the caches and never revisit them; in effect, they have planted these seeds, and clusters of seedlings will emerge later.

Ants are responsible for dispersing many seeds of herbs in temperate-zone forests and grasslands. They harvest the hard, small seeds and deposit them in granaries below ground. Some seeds escape consumption and germinate. Other plant species have **elaiosomes**, or food bodies, at one end of their seeds (Fig. 14.32). Ants harvest the seeds only for that reward and then toss them out. Discarded outside the ant nest (several meters from the parent plant), the unharmed seed may then germinate.

The relationships above are mutualistic because there is some reward for the animal. Plants can also use animals in a more parasitic fashion; in such cases, there is no reward. For instance, seeds of some aquatic and marsh plants stick to the feet of birds in mud and are carried for long distances. Mistletoe (*Phoradendron* sp.), a parasite of other plants, has naturally sticky seeds, and birds can carry them on their feet to new host trees. Seeds with beards, spines, hooks, or barbs catch a ride to a new site by adhering to animal hair and human clothing (see Fig. 14.30e, f).

Figure 14.32. Elaisomes. (left) Flannel bush (*Fremontodendron californicum*), a chaparral shrub of California. (right) Each seed of the flannel bush has an elaiosome at one end of each seed. The seeds are harvested by ants, taken to their nests, and stripped of their elaisomes, and discarded, whereupon the seeds are free to germinate without competing with the parent plant.

Some Plants Have Evolved Anti-herbivore Mechanisms

At the same time that the fruit attracts dispersal vectors, it must repel herbivores. Mechanisms to discourage herbivores include reducing the time of fruit availability, making the fruit or seed coat physically hard, and making the fruit or endosperm chemically repellent.

Many perennial plant species do not reproduce every year, or at least the magnitude of their reproduction varies from year to year. Such species produce fruit and seed abundantly only during what are called mast years. Because food supply is a limiting factor in population size, the relatively low amount of seed produced in off years keeps the number of seed eaters in check. As a result, seed-eating mammal, bird, and insect populations are not large enough to consume all the seeds available during a mast year, so some seeds escape consumption and germinate.

Those species of plants that do reproduce every year often limit the time when ripe fruit is available. Large fruits that require a long time to develop remain green, hard, and relatively small until just before the final maturation stages. Then color, texture, size, and sweetness change suddenly, and the fruit is available to herbivores for only a brief time. This limits the number of fruits (and seeds) they can consume before dispersal.

Our common notion of *fruit* is a juicy, soft organ, but many plants produce fruits that are partly or completely dry and hard. Examples include drupes, which have a hard endocarp, and such completely hard fruits as nuts. Biting or boring insects are prevented from invading the fruit or seed by the sclerenchyma tissue (usually sclereids), which also prevents the seed from being damaged by the grinding action in the crops of birds or the mouths of chewing mammals. Legume seed coats are notoriously hard and often pass through animal guts unharmed.

Chemical protection mechanisms are widespread and diverse. Many fruits are rich in secondary compounds, chemicals produced by a plant partly or entirely for the effect they have on other organisms. In the case of herbivore defense, the effect is negative and often toxic. Secondary compounds in fruits and seeds include lectins (which cause red blood cells to clump), enzyme inhibitors, cyanogens (which release cyanide, a potent nerve toxin), saponins (a detergent), alkaloids (like opium), and unusual amino acids. When present in the endosperm, these secondary compounds may later have a primary function as well; that is, they may be metabolized by the seedling into valuable nontoxic resources.

During the course of evolution, it appears that the metabolic quirks of at least one species of animal have successfully defused each chemical defense originated by seeds and fruits. This is referred to as *coevolution.* Thus, there are specialized insects capable of eating plant tissue toxic to nearly every other animal. In some cases--as in the larvae of the monarch butterfly, which is able to feed on milkweeds rich in metabolic by-products called cardiac glycosides--the animal not only eats the plant but uses the toxin for its own benefit, to deter a predator.

An excellent example of plant-herbivore coevolution is the series of plant defenses and herbivore responses summarized in Table 14.1 for a group of closely related tropical legumes. The plants exhibit a range of herbivore defenses, involving chemistry, texture, size, and timing. For each defense, however, some species of weevil has evolved a solution.

Table 14.1 Legume Defenses and Seed Weevil Adaptations

Plant Defense	Weevil Adaptation
Gum production by seed pods after penetration of first larva from egg mass; this may push off remaining eggs or drown or otherwise obstruct young larvae.	A period of quiescence in embryonic development in the egg until seed maturation is completed. Eggs laid singly instead of in clusters.
Dehiscence, fragmentation, or explosion of pods, scattering the seeds to escape from larvae coming through the pod walls.	Eggs laid on seeds only after they have been scattered. Attachment of seeds to one another or to the pod valve.
Production of a pod free of surface cracks, which prevents eggs from adhering. Also, indehiscent pods, excluding weevils, which lay eggs only on exposed seeds.	Eggs laid into the soft, fleshy exocarp. Chewing holes in the pod walls, in which eggs are then laid. Gluing the eggs to the pod surface.
A layer of material on the seed surface that swells when the pod opens and detaches the attached eggs.	Attachment of the eggs by anchoring strands to allow for substrate expansion. Entry of the larva through the pod into the seed before the pod opens.
Production of allelochemic substances.	Mechanisms for avoidance and detoxification.
Flaking of the seed pod surface, which may remove eggs laid on that surface.	Eggs laid beneath the flaking exocarp. Rapid embryonic development or feeding on immature seeds so that entry occurs before flaking begins.
Immature seeds remaining small throughout the year and then abruptly growing to maturity just before being dispersed.	Entry and feeding on immature seeds. Delay of embryonic maturation until seeds are mature.
Seeds so small or thin that weevils cannot mature in them.	Use of seed contents more completely. Feeding on several seeds.

Distant Dispersal of Seeds Is Not a Universal Aim

The benefit of fruit and seed dispersal is the spread of a species far from its parent. There is a cost as well, however. Many fruits and seeds are wasted because they are eaten and deposited in places inappropriate for successful germination and seedling establishment. In some stressful habitats, only a very few safe sites exist, and these are scattered within a large, hostile area. Because parent plants ordinarily already reside within one of the safe sites, it is advantageous to prevent or limit dispersal away from the parents.

One method of limiting dispersal is self-planting. The morphology of the fruit lends itself to lodging near the parent and drilling into the ground. Many grasses have long, bent *awns* (slender bristles) that twist as air humidity fluctuates. The awns function as levers that drive the grain into the soil. Stiff hairs at the base of the grain prevent it from pulling backwards, out of the soil. A few nongrass herbs, such as cranesbill (see Fig. 14.30d), employ a similar technique.

The peanut (*Arachis hypogaea*) inclines its fertilized flowers down to the ground, and the fruits become buried as they mature. Seeds never leave the immediate proximity of the parent.

Sea rocket, a common annual beach plant of temperate-zone shores, has a bipartite fruit. The top half is easily dislodged when mature, and its corky texture allows the enclosed seed to float and be carried to distant beaches via ocean currents. The bottom half is firmly attached to the parent, and its seed is buried with the dead parent by shifting sand at the end of the growing season (Fig. 14.33). The following year, hundreds of seedlings mark the place where the parent plant grew the year before. This two-

pronged dispersal strategy serves both to spread the species and to maintain it in safe sites year after year, even though it is an annual plant.

Plant species of isolated islands, when compared to close relatives that grow on distant continents, often exhibit a loss of dispersal mechanisms. It is possible that they evolved on continents first and then by rare chance were spread to islands, where the process of evolution modified their seeds and fruits so that dispersal became very limited, in keeping with the limited size of the islands.

Figure 14.33. Two-pronged seed-dispersal strategy. (a) Sea rocket (*Cakile maritima*) is a common, succulent annual plant along many coastlines. Note the immature, green fruits along some stems. (b) Diagram of the fruit. Each part has one seed. The top half is carried away by ocean currents, and the bottom half stays with the parent.

KEY TERMS

abiotic	endosperm	multiple fruits
achene	epicotyl	nucellus
aggregate fruits	epigeal	nut
aleurone layer	exocarp	parthenocarpic
berry	follicle	pepo
biotic	fruit	pericarp
capsules	grain	perisperm
caruncle	hesperidium	pod
caryopsis (grain)	hilum	pomes
coleoptile	hypocotyl	radicle
coleorhiza	hypogeal	raphe
cotyledons	imbibition	samara
dehiscent	integuments	schizocarp
dicotyledonous	legume (pod)	scutellum
drupes	mesocarp	seed coats
elaiosomes	micropyle	silique
endocarp	monocotyledonous	suspensor

SUMMARY

1. A seed consists of a plant embryo surrounded by a seed coat. Seeds may store food within or outside the embryo. In most dicotyledonous plants such as bean, food is stored in the two cotyledons. Cotyledons may also serve as absorbing and, later, as photosynthesizing organs. Food may be stored in an endosperm rather than in the cotyledons.

2. In seeds of monocotyledonous plants, food is usually stored in an endosperm. In grasses, such as corn, the single cotyledon-like structure (scutellum) is a specialized organ that absorbs the nutrients from the endosperm. In seeds such as those of onion, the cotyledon emerges from the seed coat and becomes green, but its tip continues to absorb food from the endosperm.

3. The first step in germination is the imbibition of water. This water facilitates the activation of enzymes involved in digesting stored food, which is converted to energy for growth.

4. In germination, the cotyledons may be elevated above the ground (epigeal), sometimes becoming photosynthetically active, or they may remain below the ground (hypogeal).

5. Mature seeds may be dormant and, depending on the species and the immediate environment, may remain viable and dormant from a few months to many years.

6. Dormancy is usually broken by providing the seed with moisture, oxygen, and a favorable temperature. Other factors, such as light, the removal of chemical inhibitors, or the destruction of the seed coat, may be required in some instances.

7. A fruit is a ripened ovary plus other closely associated floral parts.

8. There are three different kinds of fruits, classified on the basis of the number of ovaries and flowers involved in their formation:

   a. simple fruits, derived from a single ovary.
   b. aggregate fruits, derived from a number of ovaries belonging to a single flower and on a single receptacle.
   c. multiple fruits, derived from a number of ovaries of several flowers more or less grown together into one mass.

9. Simple fruits may have either a dry or a fleshy pericarp. If the pericarp is dry, it may be either dehiscent (splitting at maturity to allow seeds to escape) or indehiscent (not splitting).

10. The role of the fruit is to aid in the dispersal of the seeds within and to deter herbivores from eating the seeds without dispersing them. There is no nutritional link between the fruit and the seed of the germinating seedling.

11. Vectors of fruit and seed dispersal include wind, water, and animals. Common animal vectors include ants, birds, bats, rodents, ruminants, and primates. The animals are sometimes rewarded with food for their dispersal activities, but at other times they simply carry seeds and fruits to other sites.

12. Fruits protect seeds from herbivores by the timing of their ripening, their hardness, and their chemical composition. Fruits may contain secondary compounds that deter feeding by all but the most metabolically specialized herbivores.

13. Some fruits prevent or limit dispersal, thus ensuring that the site occupied by the parent plant will be occupied by its offspring well into future growing seasons.

Questions

1. A seed is actually a mature ovule. Define each of the following terms:
  integuments
  seed coat
  suspensor
  embryo
  cotyledon
  hilum
  raphe
  micropyle
  radicle
  epicotyl

2. Describe the processes that occur during germination.

3. What is seed dormancy? Why is it an important process?

4. A fruit is a ripened ovary. What are the functions of fruits?

5. What are the differences between simple, aggregate, and multiple fruits?

6. Buy several different fruits at the grocery store and use the "Key to Fruits" in this chapter to identify their fruit types.

7. One role of fruits is to aid in seed dispersal. Describe two different ways that fruits aid in dispersal by abiotic factors. Describe two different ways that fruits aid dispersal by biotic factors.

(*Echium*)

Because seeds and fruits are so important, stories, myths, and legends abound. Even the Bible describes "forbidden fruit" in the Garden of Eden. In the 1500s the Doctrine of Signatures was widely believed. The idea of the Doctrine was that the appearance of a plant or plant part would reveal its inner secrets and possible uses to people. Others expanded this idea to include shape, color, and smell as indicators of use.

(*Antirrhinum majus*)

The scales of a pinecone, for example, look like teeth, so medieval people made a concoction of pinecones mixed with vinegar to gargle for teeth and gum problems. (Actually, the vinegar probably did the trick by itself.) Seeds of viper's bugloss (*Echium*) resemble a snake's head, so the belief arose that a mixture made from these seeds could be used as a remedy for snakebite. Seeds of snapdragon (*Antirrhinum majus*) worn in a linen bag around the neck were supposed to prevent one from being bewitched. Some of these stories may have held a little truth simply by happenstance; but their real importance lies in the fact that they arose in the first place because people found plants, and their seeds and fruits, important to their very survival.

IN DEPTH: *Key to Fruits*

A key is a tool to help students identify things when there are several possible choices. This key can be used to identify the different types of fruits. It is a dichotomous key, in which there are two choices at each level. For example, the first level asks if the fruit is formed from a single ovary or from several. Progress through each level in the key to determine the fruit type.

I. Fruit formed from a single ovary of one flower: *Simple fruits*
    A. Pericarp fleshy
        1. The ovary wall fleshy and containing one or more carpels and seeds: *Berry* (tomato, *Lycopersicon* sp.)
            a. Ovary wall with a hard rind: *Pepo* (watermelon, *Cucumis melo*)
            b. Ovary wall with a leathery rind: *Hesperidium* (orange, *Citrus* sp.)
        2. Only a portion of the pericarp fleshy
            a. Exocarp thin; mesocarp fleshy; endocarp stony; single seed and carpel: *Drupe* (cherry, *Prunus* sp.)
            b. Outer portion of pericarp fleshy, inner portion papery, floral tube fleshy; several seeds and carpels: *Pome* (apple, *Malus* sp.)
    B. Pericarp dry
        1. Dehiscent fruits
            a. Composed of one carpel
                i. Splitting along two margins: *Legume* or *Pod.* (pea, *Pisum* sp.)
                ii. Splitting along one margin: *Follicle.* (individual fruits in *Magnolia* multiple fruit)
            b. Composed of two or more carpels
                i. Dehiscing in one of four different ways: *Capsule* (poppy)
                ii. Separating at maturity, leaving a persistent partition wall: *Silique* (mustard)
        2. Indehiscent fruits
            a. Pericarp bearing a winglike growth: *Samara* (maple)
            b. Pericarp not bearing a winglike growth
                i. Two or more carpels, united when immature, splitting apart at maturity: *Schizocarp* (carrot)
                ii. One carpel; if more, not splitting apart at maturity; one-seeded fruits
                    a). Seed united to the pericarp all around: *Caryopsis* or *Grain* (rice)

b). Seed not united to the pericarp all around

i). Fruit large, with thick, stony wall: *Nut* (walnut)

ii). Fruit small, with thin wall: *Achene.* (sunflower)

II. Fruits formed from several ovaries

A. Fruits developing from one flower: *Aggregate fruit* (classify the individual fruits in key for simple fruits)(strawberry)

B. Fruits formed from several flowers: *Multiple fruit* (classify individual fruits in key for simple fruits)(pineapple)

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