

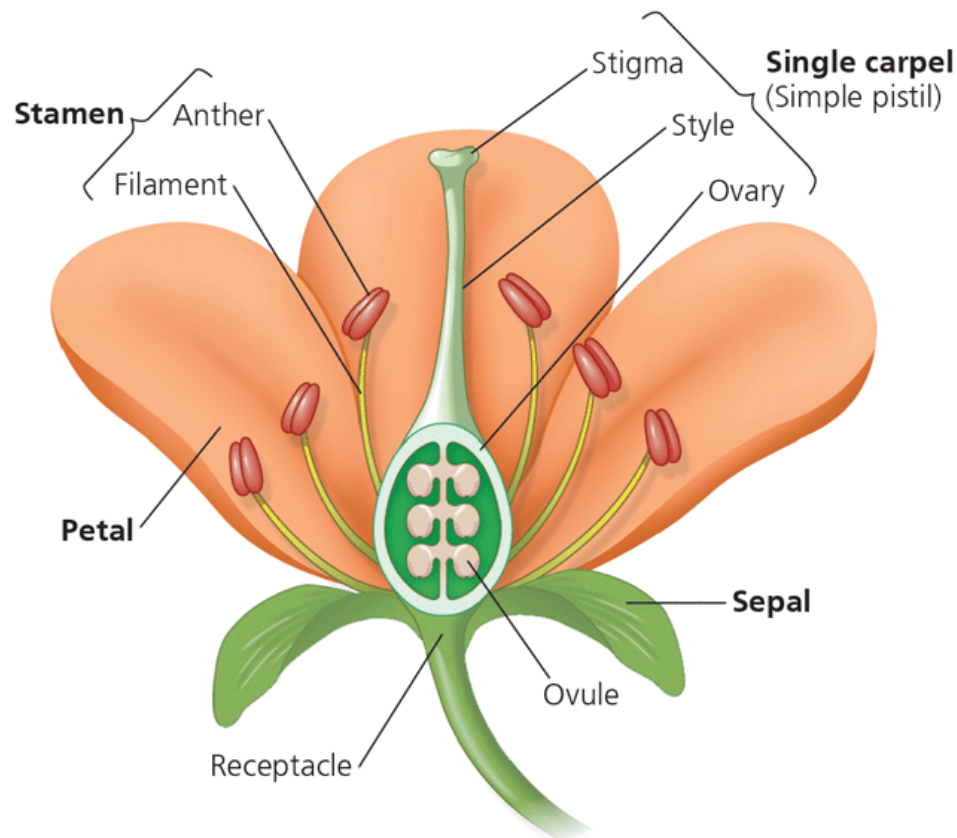
Concept 38.1 Flowers, double fertilisation, and fruits are key features of the angiosperm life cycle

The life cycles of all plants are characterised by an alternation of generations, in which multicellular haploid (n) and multicellular diploid ($2n$) generations alternately produce each other (see [Figure 13.6b](#)). The diploid plant, the *sporophyte*, produces haploid spores by meiosis. These spores divide by mitosis, giving rise to multicellular *gametophytes*, the male and female haploid plants that produce gametes (sperm and eggs). Fertilisation, the fusion of gametes, results in a diploid zygote, which divides by mitosis and forms a new sporophyte. In angiosperms, the sporophyte is the dominant generation: It is larger, more conspicuous, and longer-lived than the gametophyte. The key traits of the angiosperm life cycle can be remembered as the “three Fs”—*f*lowers, double *f*ertilisation, and *f*ruits. We’ll begin by discussing flowers.

Flower structure and function

The [flower](#), the sporophytic structure of angiosperms specialised for sexual reproduction, is typically composed of four types of floral organs: [carpels](#), [stamens](#), [petals](#), and [sepals](#) ([Figure 38.2](#)). When viewed from above, these organs take the form of concentric whorls. Carpels form the first (innermost) whorl, stamens the second, petals the third, and sepals the fourth (outermost) whorl. All are attached to a part of the stem called the [receptacle](#). Flowers are determinate shoots; they cease growing after the flower and fruit are formed.

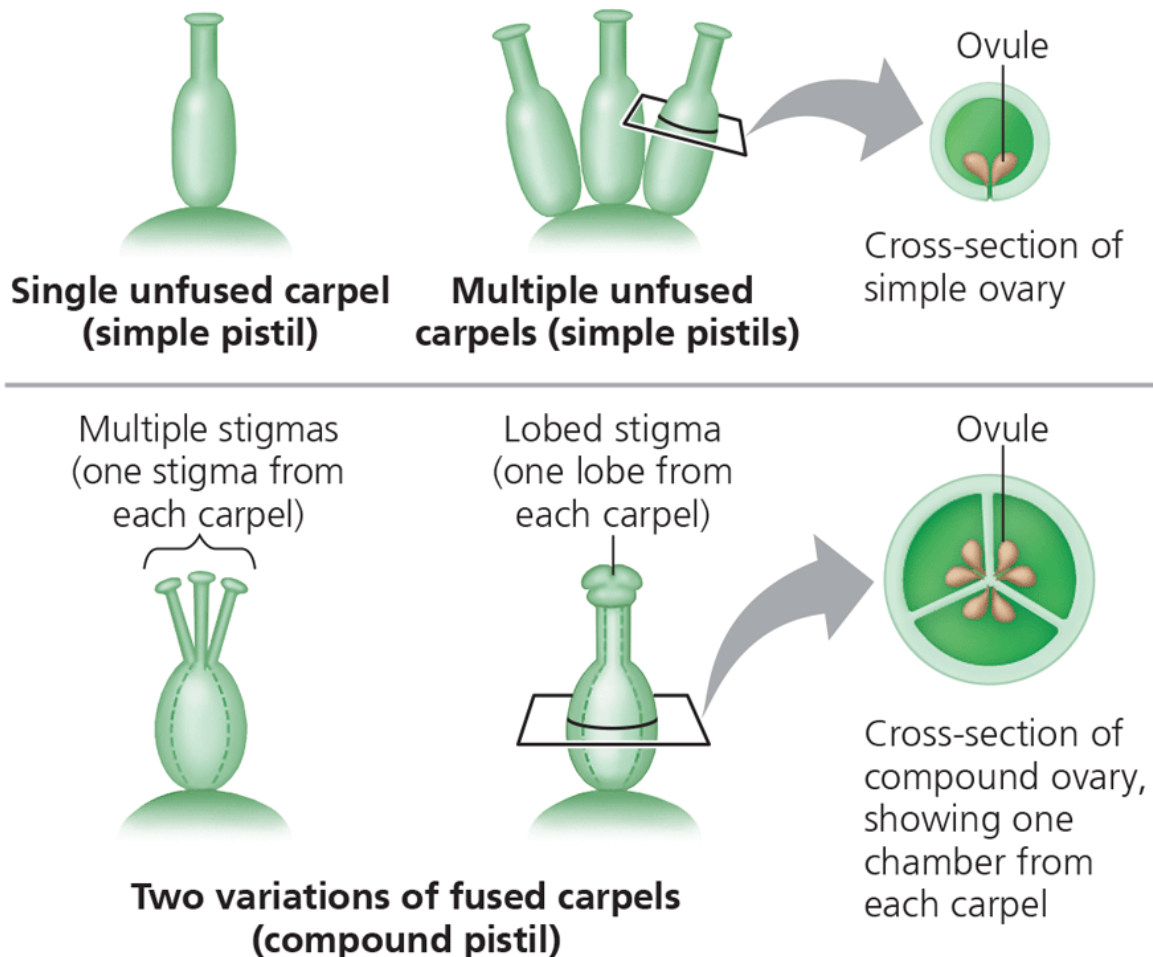
Figure 38.2 The structure of an idealised flower.



Carpels and stamens are sporophylls—modified leaves specialised for reproduction (see [Concept 30.1](#)); sepals and petals are sterile modified leaves. A carpel (megasporophyll) has an [ovary](#) at its base and a long, slender neck called the [style](#). At the top of the style is a sticky structure called the [stigma](#) that captures pollen. Within the ovary are one or more [ovules](#), which become seeds if fertilised; the number of ovules depends on the species. The flower in [Figure 38.2](#) has a single carpel, but many species have multiple carpels. In most species, the carpels are fused, resulting in a compound ovary with two or more chambers, each containing one or more ovules. The term [pistil](#) is sometimes used to refer to a single carpel or two or more fused carpels ([Figure 38.3](#)). A stamen (microsporophyll) consists of a stalk called the filament and a terminal structure called the [anther](#); within the anther are chambers called microsporangia (pollen sacs) that produce pollen. Petals are typically more brightly coloured than sepals and advertise the flower to insects and other animal pollinators. Sepals, which enclose and protect unopened floral buds, usually resemble leaves more than the other floral organs do.

Figure 38.3 The relationship between the terms *carpel* and *pistil*.

A simple pistil consists of a single, unfused carpel. A compound pistil consists of two or more fused carpels. Some types of flowers have only a single pistil, while other types have many pistils. In either case, the pistils may be simple or compound.



Description

Complete flowers have all four basic floral organs (see [Figure 38.2](#)). Some species have **incomplete flowers**, lacking sepals, petals, stamens, or carpels. For example, most grass flowers lack petals. Some incomplete flowers are sterile, lacking functional stamens and carpels; others are *unisexual* (sometimes called *imperfect*), lacking either stamens or carpels. Flowers also vary in size, shape, colour, fragrance, organ arrangement, and time of opening. Some are borne singly, while others are arranged in showy clusters called **inflorescences**. For example, a sunflower consists of a central disc composed of hundreds of tiny incomplete flowers, surrounded by sterile, incomplete flowers that look like yellow petals (see [Figure 40.24](#)). Much of floral diversity represents adaptation to specific pollinators.

Methods of pollination

Pollination is the transfer of pollen to the part of a seed plant containing the ovules. In angiosperms, this transfer is from an anther to a stigma. Pollination can occur by wind, water, or animals ([Figure 38.4](#)). In wind-pollinated species, including grasses and many trees, the release of enormous quantities of smaller-sized pollen compensates for the randomness of dispersal by the wind. At certain times of the year, the air is loaded with pollen grains, as anyone plagued with pollen allergies can attest. Some species of aquatic plants rely on water to disperse pollen. Most angiosperm species, however, depend on insects, birds, or other animal pollinators to transfer pollen directly from one flower to another.

Figure 38.4 Exploring Flower Pollination

Most angiosperm species rely on a living (biotic) or nonliving (abiotic) pollinating agent that can move pollen from the anther of a flower on one plant to the stigma of a flower on another plant.

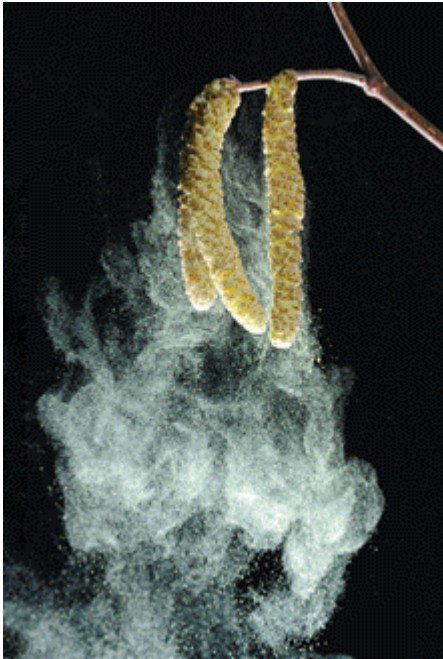
Approximately 80% of all angiosperm pollination is biotic, employing animal go-betweens. Among abiotically pollinated species, 98% rely on wind and 2% on water. (Some angiosperm species can self-pollinate, but such species are limited to inbreeding in nature.)

Abiotic pollination by wind

About 20% of all angiosperm species are wind-pollinated. Since their reproductive success does not depend on attracting pollinators, there has been no selective pressure favouring colourful or scented flowers. Accordingly, the flowers of wind-pollinated species are often small, green, and inconspicuous, and they produce neither scent nor the sugary solution called nectar. Most temperate trees and grasses are wind-pollinated. The relative inefficiency of wind pollination is compensated for by production of copious amounts of pollen grains. Wind tunnel studies reveal that wind pollination is often more efficient than it appears because floral structures can create eddy currents that aid in pollen capture.



Carpellate flower (carpels only)



Staminate flowers (stamens only) releasing clouds of pollen

Pollination by bees



Common dandelion under normal light



Common dandelion under ultraviolet light

About 65% of all flowering plants require insects for pollination; up to 80% of commercially important crops rely on insects for pollination. Bees are the most important insect pollinators, and there is great concern throughout the world that native and honeybee populations continue to decline at alarming rates. Many biologists believe that pesticides are responsible for the decline. Collapse of bee populations will lead to many fruits and vegetables disappearing from supermarket shelves. Pollinating bees depend on nectar and pollen for food. Typically, bee-pollinated flowers have a delicate, sweet fragrance. Bees are attracted to bright colours, primarily yellow and blue. Red appears dull to them, but they can see ultraviolet radiation. Many bee-pollinated flowers, such as the common dandelion (*Taraxacum vulgare*), have ultraviolet markings called “nectar guides” that help insects locate the nectaries (nectar-producing glands) but are only visible to human eyes under ultraviolet light. New Zealand’s native solitary bee (*Hylaeus* spp.) is the first recorded vertebrate capable of prising open an explosive- bird-pollinated flower (*Peraxilla tetrapetalla*). *P. tetrapetalla* is a parasitic mistletoe endemic to New Zealand. It is generally bird pollinated, unless a bee gets there first.



New Zealand’s red mistletoe (*Peraxilla tetrapetala*) is most frequently bird pollinated, although bees occasionally provide that service.

Pollination by mammals

Flowers pollinated by bats and non-flying mammals are lightcoloured and aromatic, attracting their nocturnal pollinators. The southern blossom bat (*Syconycteris australis*) and little pygmy possums (*Cercartetus lepidus*), throughout most of Australia, drink the nectar and eat the pollen of many *Banksia* species and other members of the family Proteaceae. New Zealand's lesser short-tailed bat (*Mystacina tuberculata*) pollinates the vanishingly rare woodrose (*Dactylanthus taylorii*). In feeding, the bats transfer pollen from plant to plant.



Southern blossom bat feeding on the flowers of *Banksia integrifolia* at night.

Pollination by birds

Bird-pollinated flowers, such as this New South Wales waratah (*Telopea speciosissima*), are usually large and bright-red or yellow, but they have little odour. Since birds, like this New Holland honeyeater (*Phylidonyris novaehollandiae*), often do not have a welldeveloped sense of smell, there has been no selective pressure favouring scent production. However, the flowers produce the sugary nectar that helps meet the high energy demands of the pollinating birds. The primary function of nectar, which is produced by nectaries at the base of many flowers, is to “reward” the pollinator. The petals of such flowers are often fused, forming a bent floral tube that fits the curved beak of the bird.



New Holland honeyeater drinking nectar of a New South Wales waratah (*Telopea speciosissima*)

Pollination by flies

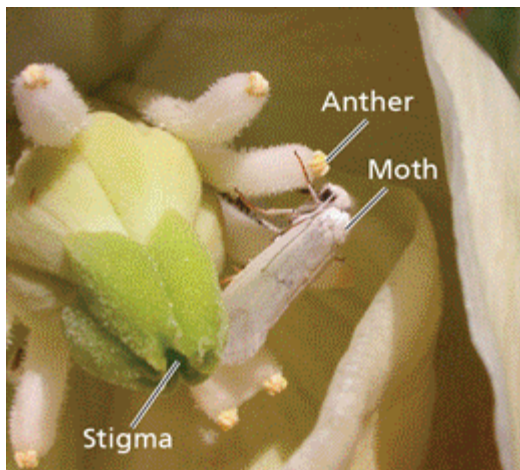
Many fly-pollinated flowers are reddish and fleshy, with an odour like rotten meat. Blowflies visiting carrion flowers (*Stapelia* spp.) mistake the flower for a rotting corpse and lay their eggs on it. In the process, the blowflies become dusted with pollen that they carry to other flowers. When the eggs hatch, the larvae find no carrion to eat and die. The orchids benefit from receiving cross pollen (pollen from a different plant). Fruit flies may benefit from collecting the orchid's chemical scents, because they represent precursors for the production of male pheromones.



Fruit flies on an orchid

Pollination by moths and butterflies

Moths and butterflies detect odours, and the flowers they pollinate are often sweetly fragrant. Butterflies perceive many bright colours, but moth-pollinated flowers are usually white or yellow, which stand out at night when moths are active. Moth on yucca flower



Moth on yucca flower

Evolution

Animal pollinators are drawn to flowers for the food they provide in the form of pollen and nectar. Attracting pollinators that are loyal to a given plant species is an efficient way to ensure that pollen is transferred to another flower of the same species. Natural selection, therefore, favours deviations in floral structure or physiology that make it more likely for a flower to be pollinated regularly by an effective animal species. If a plant species develops traits that make its flowers more prized by pollinators, there is a selective pressure for pollinators to become adept at harvesting food from these flowers. The joint evolution of two interacting species, each in response to selection imposed by the other, is called [coevolution](#). For example, some species have fused flower petals that form long, tubelike structures bearing nectaries tucked deep inside. Charles Darwin suggested that a race between flower and insect might lead to correspondences between the length of a floral tube and the length of an insect's proboscis, a straw-like mouthpart. Based on the length of a long, tubular flower that grows in Madagascar, Darwin predicted the existence of a pollinating moth with a 28-cm-long proboscis. Such a moth was discovered two decades after Darwin's death ([Figure 38.5](#)).

Figure 38.5 Coevolution of a flower and an insect pollinator.

The long floral tube of the Madagascar orchid *Angraecum sesquipedale* has coevolved with the 28-cm-long proboscis of its pollinator, the hawk moth *Xanthopan morgani praedicta*. The moth is named in honour of Darwin's prediction of its existence.



Climate change may be affecting long-standing relationships between plants and animal pollinators. For example, two species of Rocky Mountain bumblebees now have tongues that are about one-quarter shorter than those of bees of the same species 40 years ago. Flowers that require long-tongued

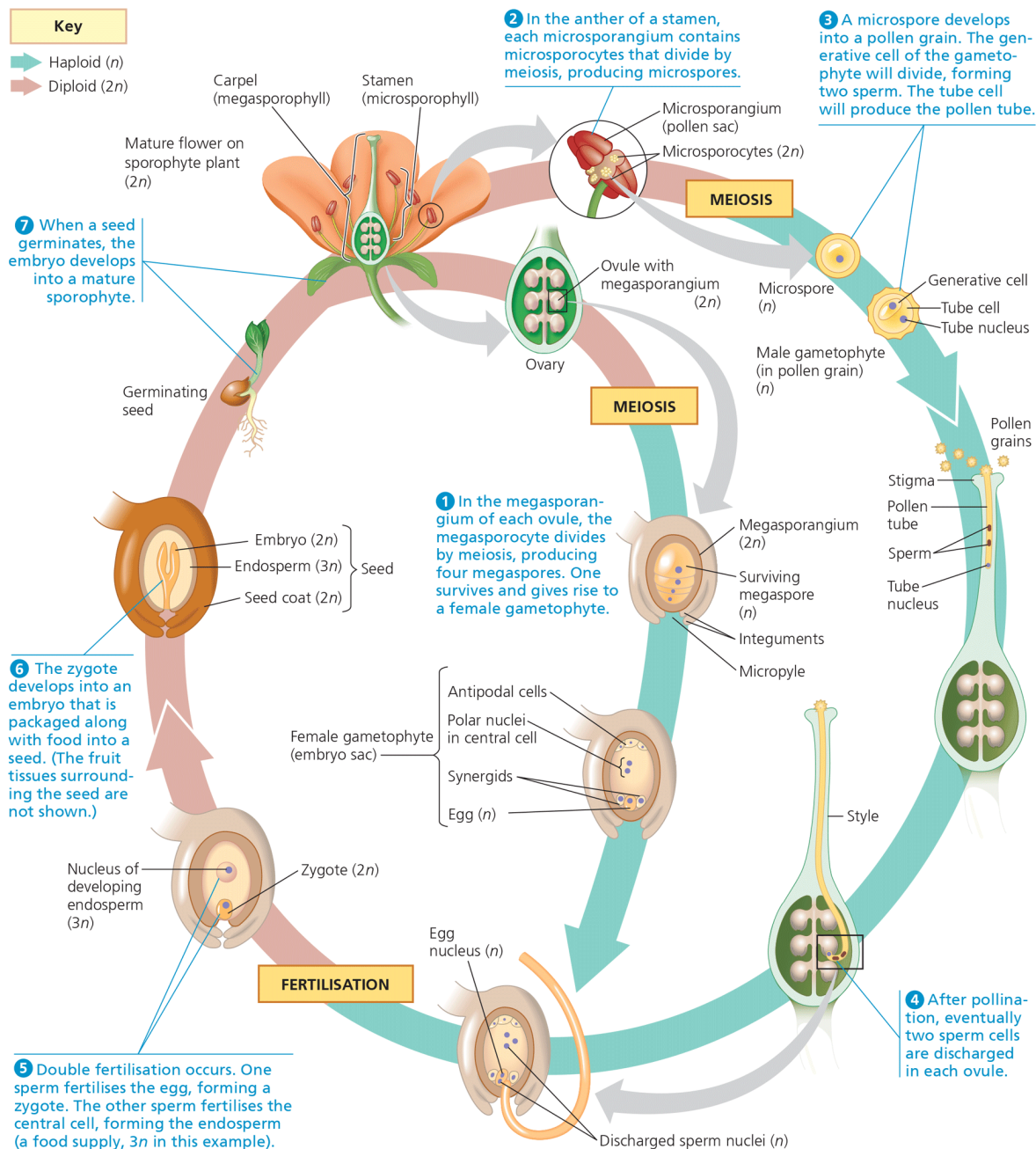
pollinators have declined under the warmer conditions in the Rockies. As a result, there has been selective pressure favouring bumblebees with shorter tongues.

The angiosperm Life Cycle: An overview

Pollination is one step in the angiosperm life cycle. [Figure 38.6](#) provides a complete overview of the life cycle, focusing on gametophyte development, sperm delivery by pollen tubes, double fertilisation, and seed development.

Figure 38.6 The life cycle of angiosperms.

For simplicity, a flower with a single carpel (simple pistil) is shown. Many species have multiple carpels, either separate or fused.



Description

Visual Skills

Where in this life cycle would the most mitotic divisions be occurring?

Over the course of seed plant evolution, gametophytes became reduced in size and wholly dependent on the sporophyte for nutrients (see [Figure 30.2](#)). The gametophytes of angiosperms are the most reduced of all plants, consisting of only a few cells: They are microscopic, and their development is obscured by protective tissues.

Development of female gametophytes (Embryo Sacs)

As a carpel develops, one or more ovules form deep within its ovary, its swollen base. A female gametophyte, also known as an [embryo sac](#), develops inside each ovule. The process of embryo sac formation occurs in a tissue called the megasporangium 1 within each ovule. Two *integuments* (layers of protective sporophytic tissue that will develop into the seed coat) surround each megasporangium, except at a gap called the *micropyle*. Female gametophyte development begins when one cell in the megasporangium of each ovule, the *megasporocyte* (or megaspore mother cell), enlarges and undergoes meiosis, producing four haploid [megaspores](#). Only one megaspore survives; the others degenerate.

The nucleus of the surviving megaspore divides by mitosis three times without cytokinesis, resulting in one large cell with eight haploid nuclei. The multinucleate mass is then divided by membranes to form the embryo sac. Near the micropyle of the embryo sac, two cells called synergids flank the egg and help attract and guide the pollen tube to the embryo sac. At the opposite end of the embryo sac are three antipodal cells of unknown function. The other two nuclei, called polar nuclei, are not partitioned into separate cells but share the cytoplasm of the large central cell of the embryo sac. The mature embryo sac thus consists of eight nuclei contained within seven cells. The ovule, which will become a seed if fertilised, now consists of the embryo sac, enclosed by the megasporangium (which eventually withers) and two surrounding integuments.

Development of male gametophytes in pollen grains

As the stamens are produced, each anther 2 develops four microsporangia, also called pollen sacs. Within the microsporangia are many diploid cells called *microsporocytes*, or microspore mother cells. Each microsporocyte undergoes meiosis, forming four haploid [microspores](#), 3 each of which eventually gives rise to a haploid male gametophyte. Each microspore then undergoes mitosis, producing a haploid male gametophyte consisting of only two cells: the *generative cell* and the *tube cell*. Together, these two cells and the spore wall constitute a [pollen grain](#). The spore wall, which consists of material produced by

both the microspore and the anther, usually exhibits an elaborate pattern unique to the species. During maturation of the male gametophyte, the generative cell passes into the tube cell: The tube cell now has a completely free-standing cell inside it.

Sperm delivery by pollen tubes

After the microsporangium breaks open and releases the pollen, a pollen grain may be transferred to a receptive surface of a stigma—the act of pollination. At the time of pollination, the pollen grain typically consists of only the tube cell and the generative cell. After landing on a receptive stigma, the pollen grain absorbs moisture, generally exuded by the stigma; the grain then hydrates and germinates. Pollen grains produce a [pollen tube](#) when they germinate. This tube is a long cellular protuberance that delivers sperm to the female gametophyte. As the pollen tube elongates through the style, the nucleus of the generative cell divides by mitosis and produces two sperm, which remain inside the tube cell. The tube nucleus leads ahead of the two sperm as the tip of the pollen tube grows towards the micropyle in response to chemical attractants produced by the synergids. The arrival of the pollen tube initiates the death of one of the two synergids, thereby providing a passageway into the embryo sac. The tube nucleus and the two sperm are then discharged from the pollen tube 4 in the vicinity of the female gametophyte.

Double fertilisation

[Fertilisation](#), the fusion of gametes, occurs after the two sperm reach the female gametophyte. One sperm fertilises the egg, forming the zygote. The other sperm combines with the two polar nuclei, forming a triploid ($3n$) nucleus in the centre of the large central cell of the female gametophyte. This cell will give rise to the [endosperm](#), a food-storing tissue of the seed. 5 The union of the two sperm cells with different nuclei of the female gametophyte is called [double fertilisation](#). Double fertilisation ensures that endosperm develops only in ovules where the egg has been fertilised, thereby preventing angiosperms from squandering nutrients on infertile ovules. Near the time of double fertilisation, the tube nucleus, the other synergid, and the antipodal cells degenerate.

Seed development

6 After double fertilisation, each ovule develops into a seed. Meanwhile, the ovary develops into a fruit, which encloses the seeds and aids in their dispersal by wind or animals. As the sporophyte embryo develops from the zygote, the seed stockpiles proteins, oils, and starch to varying degrees, depending on the species. This is why seeds are such a major nutrient drain. Initially, carbohydrates and other nutrients are stored in the seed's endosperm, but later, depending on the species, the swelling cotyledons (seed leaves) of the embryo may take over this function. When a seed germinates, 7 the embryo develops into a new sporophyte. The mature sporophyte produces its own flowers and fruits: The life cycle is now complete, but it is necessary to examine more closely how an ovule develops into a mature seed.

Seed development and Structure: *A Closer Look*

After successful pollination and double fertilisation, a seed begins to form. During this process, both the endosperm and the embryo develop. When mature, a [seed](#) consists of a dormant embryo surrounded by stored food and protective layers.

Endosperm development

Endosperm usually develops before the embryo does. After double fertilisation, the triploid nucleus of the ovule's central cell divides, forming a multinucleate "supercell" that has a milky consistency. This liquid mass, the endosperm, becomes multicellular when cytokinesis partitions the cytoplasm by forming membranes between the nuclei. Eventually, these "naked" cells produce cell walls, and the endosperm becomes solid. Coconut "milk" and "meat" are examples of liquid and solid endosperm, respectively. The white fluffy part of popcorn is another example of endosperm. The endosperms of just three grains—wheat, corn, and rice—provide much of the food energy for human sustenance.

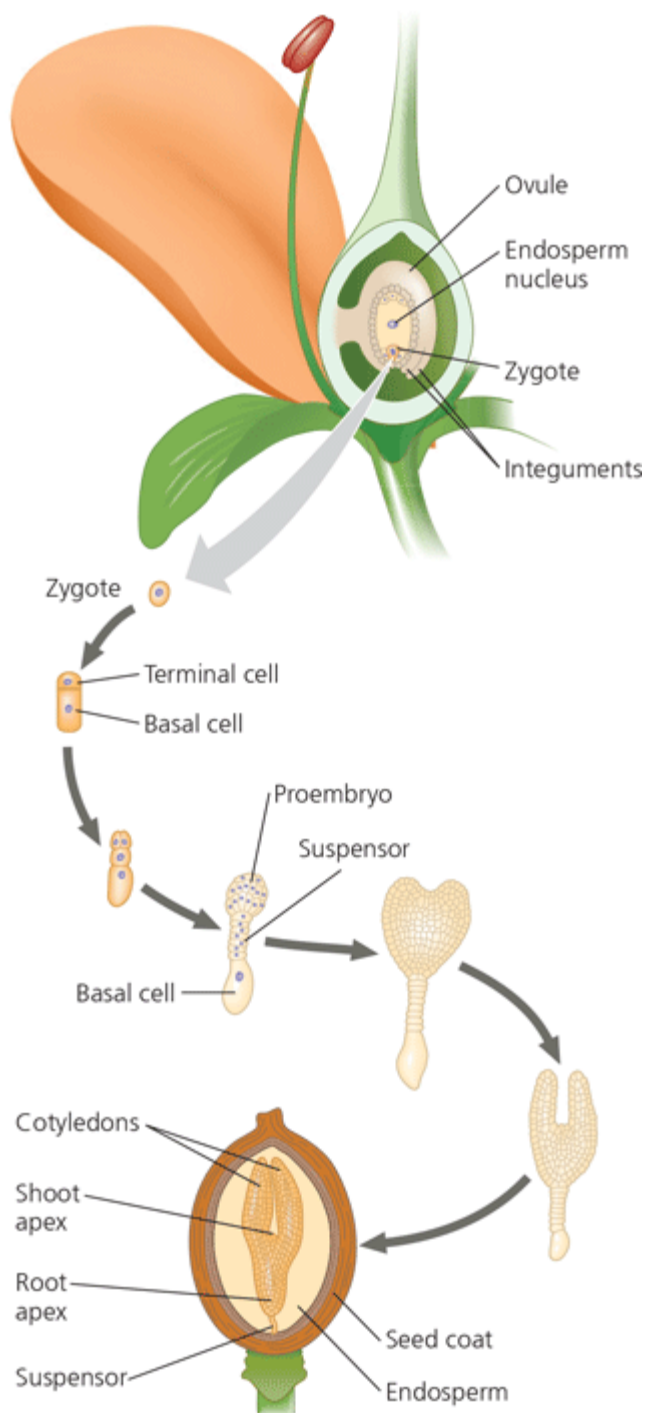
In grains and most other species of monocots, as well as many eudicots, the endosperm stores nutrients that can be used by the seedling after germination. In other eudicot seeds, the food reserves of the endosperm are completely exported to the cotyledons before the seed completes its development; consequently, the mature seed lacks endosperm.

Embryo development

The first mitotic division of the zygote is asymmetrical and splits the fertilised egg into a basal cell and a terminal cell ([Figure 38.7](#)). The terminal cell eventually gives rise to most of the embryo. The basal cell continues to divide, producing a thread of cells called the suspensor, which anchors the embryo to the parent plant. The suspensor helps in transferring nutrients to the embryo from the parent plant and, in some species, from the endosperm. As the suspensor elongates, it pushes the embryo deeper into the nutritive and protective tissues. Meanwhile, the terminal cell divides several times and forms a spherical proembryo (early embryo) attached to the suspensor. The cotyledons begin to form as bumps on the proembryo. A eudicot embryo, with its two cotyledons, is heart-shaped at this stage.

Figure 38.7 The development of a eudicot plant embryo.

By the time the ovule becomes a mature seed and the integuments harden and thicken into the seed coat, the zygote has given rise to an embryonic plant with rudimentary organs.



Description

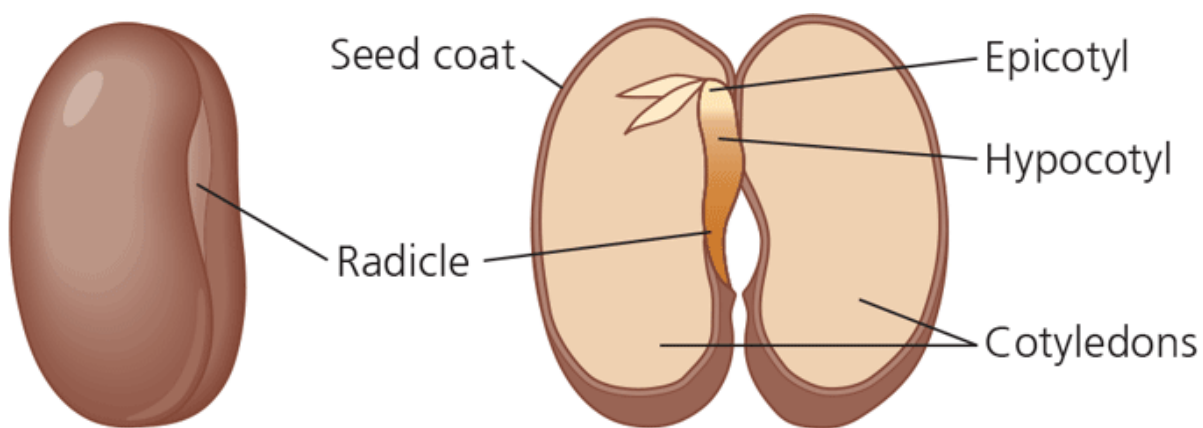
Soon after the rudimentary cotyledons appear, the embryo elongates. Cradled between the two cotyledons is the embryonic shoot apex. At the opposite end of the embryo's axis, where the suspensor attaches, an embryonic root apex forms. After the seed germinates—indeed, for the rest of the plant's life—the apical meristems at the apices of shoots and roots sustain primary growth (see [Figure 35.12](#)).

Structure of the mature seed

During the last stages of its maturation, the seed dehydrates until its water content is only about 5–15% of its weight. The embryo, which is surrounded by a food supply (cotyledons, endosperm, or both), enters [dormancy](#); that is, it stops growing and its metabolism nearly ceases. The embryo and its food supply are enclosed by a hard, protective [seed coat](#) formed from the integuments of the ovule. In some species, dormancy is imposed by the presence of an intact seed coat rather than by the embryo itself.

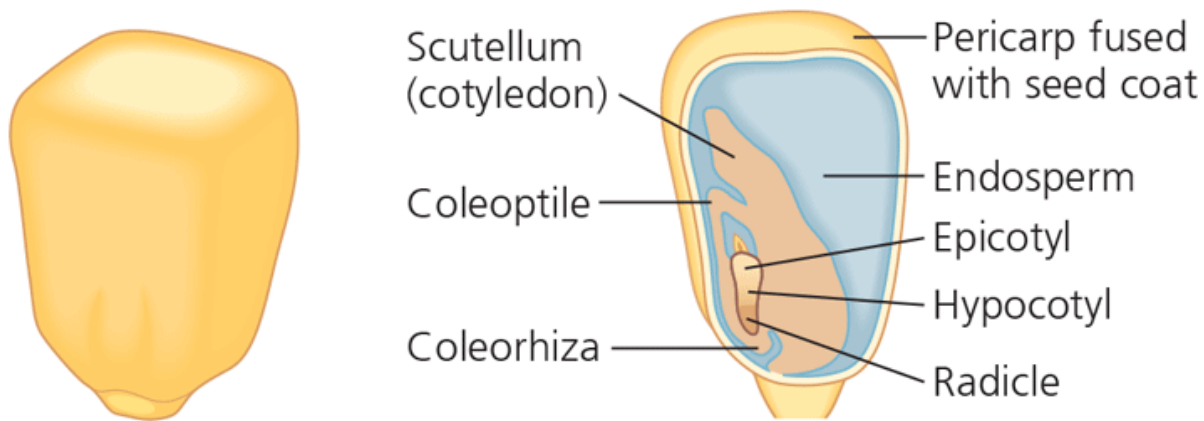
If you split apart a seed of the garden bean, a type of eudicot, you can see that the embryo consists of an elongate structure, the embryonic axis, attached to two thick, fleshy cotyledons ([Figure 38.8a](#)). Below where the cotyledons are attached, the embryonic axis is called the [hypocotyl](#) (from the Greek *hypo*, under). The hypocotyl terminates in the [radicle](#), or embryonic root. The portion of the embryonic axis above where the cotyledons are attached and below the first pair of miniature leaves is the [epicotyl](#) (from the Greek *epi*, on, over). The epicotyl, young leaves, and shoot apical meristem are collectively called the *plumule*.

Figure 38.8 Seed structure.



(a) Common garden bean, a eudicot with thick cotyledons. The fleshy cotyledons store food absorbed from the endosperm before the seed germinates.

[Description](#)



(b) Corn, a monocot. Like all monocots, corn has only one cotyledon. Corn and other grasses have a large cotyledon called a scutellum. The rudimentary shoot is sheathed in a structure called the coleoptile, and the coleorhiza covers the young root.

[Description](#)

Make Connections

In addition to cotyledon number, how do the structures of monocots and eudicots differ? (See [Figure 30.16](#).)

Visual Skills

Which mature seed lacks an endosperm? What happened to it?

The cotyledons of the common garden bean are packed with starch before the seed germinates because they absorbed carbohydrates from the endosperm when the seed was developing. However, the seeds of some eudicot species, such as castor beans (*Ricinus communis*), retain their food supply in the endosperm and have very thin cotyledons. The cotyledons absorb nutrients from the endosperm and transfer them to the rest of the embryo when the seed germinates.

The embryos of monocots possess only a single cotyledon ([Figure 38.8b](#)). Grasses, including corn and wheat, have a specialised cotyledon called a *scutellum* (from the Latin *scutella*, small shield, a reference to its shape). The scutellum, which has a large surface area, is pressed against the endosperm, from which it absorbs nutrients during germination. The embryo of a grass seed is enclosed within two

protective sheathes: a [coleoptile](#), which covers the young shoot, and a [coleorhiza](#), which covers the young root. Both structures aid in soil penetration after germination.

Seed Dormancy: An adaptation for tough times

The environmental conditions required to break seed dormancy vary among species. Some seed types germinate as soon as they are in a suitable environment. Others remain dormant, even if sown in a favourable place, until a specific environmental cue causes them to break dormancy.

The requirement for specific cues to break seed dormancy increases the chances that germination will occur at a time and place most advantageous to the seedling. Seeds of many desert plants, for instance, germinate only after a substantial rainfall. If they were to germinate after a mild drizzle, the soil might soon become too dry to support the seedlings. Where natural fires are common, many seeds require intense heat or smoke to break dormancy; seedlings are therefore most abundant after fire has cleared away competing vegetation. Where winters are harsh, seeds may require extended exposure to cold before they germinate; seeds sown during summer or autumn will therefore not germinate until the following spring, ensuring a long growth season before the next winter. Certain small seeds, such as those of some lettuce varieties, require light for germination and will break dormancy only if buried shallow enough for the seedlings to poke through the soil surface. Some seeds have coats that must be weakened by chemical attack as they pass through an animal's digestive tract and thus are usually carried a long distance before germinating from faeces.

The length of time a dormant seed remains viable and capable of germinating varies from a few days to decades or even longer, depending on the plant species and environmental conditions. The oldest carbon-14-dated seed that has grown into a viable plant was a 2,000-year-old date palm seed from Israel. Most seeds are durable enough to last a year or two until conditions are favourable for germinating. Thus, the soil has a bank of ungerminated seeds that may have accumulated for several years. This is one reason vegetation reappears so rapidly after an environmental disruption such as fire.

Sporophyte development from seed to mature plant

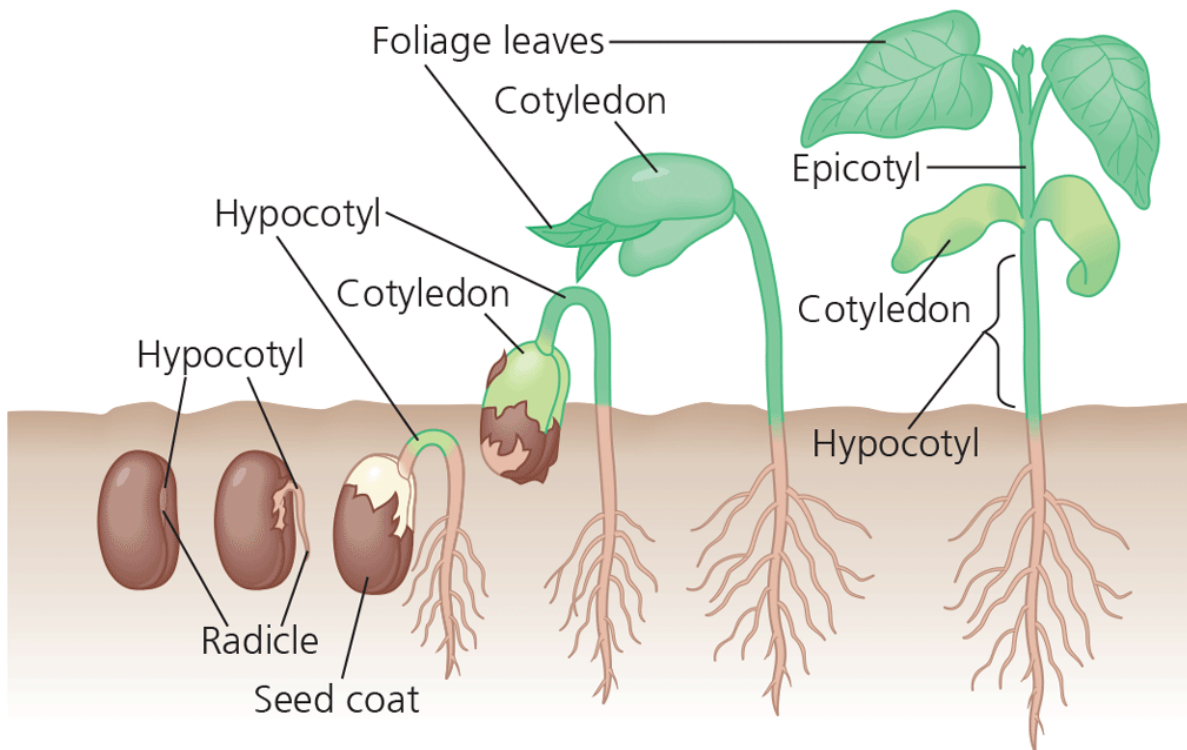
When environmental conditions are conducive for growth, seed dormancy is lost and germination proceeds. Germination is followed by growth of stems, leaves, and roots, and eventually by flowering.

Seed germination

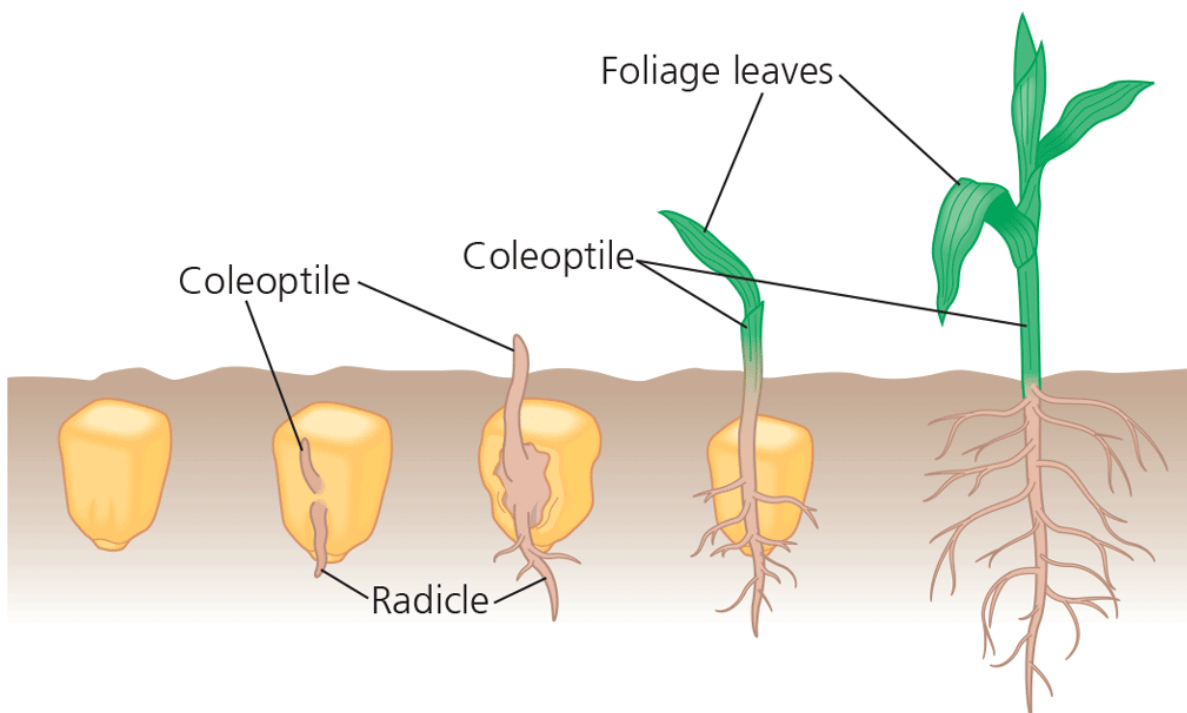
Seed germination is initiated by [imbibition](#), the uptake of water due to the low water potential of the dry seed. Imbibition causes the seed to expand and rupture its coat and triggers changes in the embryo that enable it to resume growth. Following hydration, enzymes digest the storage materials of the endosperm or cotyledons, and the nutrients are transferred to the growing regions of the embryo.

The first organ to emerge from the germinating seed is the radicle, the embryonic root. The development of a root system anchors the seedling in the soil and supplies it with water necessary for cell expansion. A ready supply of water is a prerequisite for the next step, the emergence of the shoot tip into the drier conditions encountered above ground. In garden beans, for example, a hook forms in the hypocotyl, and growth pushes the hook above ground ([Figure 38.9a](#)). In response to light, the hypocotyl straightens, the cotyledons separate, and the delicate epicotyl, now exposed, spreads its first true leaves (as distinct from the cotyledons, or seed leaves). These leaves expand, become green, and begin making food by photosynthesis. The cotyledons shrivel and fall away, their food reserves having been exhausted by the germinating embryo.

Figure 38.9 Two common types of seed germination.



(a) Common garden bean. In common garden beans, straightening of a hook in the hypocotyl pulls the cotyledons from the soil.



(b) Corn. In corn and other grasses, the shoot grows straight up through the tube of the coleoptile.

Visual Skills

How do bean and corn seedlings protect their shoot systems as they push through the soil?

Some monocots, such as corn and other grasses, use a different method for breaking ground when they germinate ([Figure 38.9b](#)). The coleoptile pushes up through the soil and into the air. The shoot tip grows through the tunnel provided by the coleoptile and breaks through the coleoptile's tip upon emergence.

Growth and flowering

Once a seed has germinated and started to photosynthesise, most of the plant's resources are devoted to the growth of stems, leaves, and roots (also known as *vegetative growth*). This growth, including both primary and secondary growth, arises from the activity of meristematic cells (see [Concept 35.2](#)). During this stage, usually the best strategy is to photosynthesise and grow as much as possible before flowering, the reproductive phase.

The flowers of a given plant species typically appear suddenly and simultaneously at a specific time of year. Such timing promotes outbreeding, the main advantage of sexual reproduction. Flower formation involves a developmental switch in the shoot apical meristem from a vegetative to a reproductive growth mode. This transition into a *floral meristem* is triggered by a combination of environmental cues (such as day length) and internal signals, as we'll explain in [Concept 39.3](#). Once the transition to flowering has begun, the order of each organ's emergence from the floral meristem determines whether it will develop into a sepal, petal, stamen, or carpel (see [Figure 35.36](#)).

Fruit structure and function

Before a seed can germinate and develop into a mature plant, it must be deposited in suitable soil. Fruits play a key role in this process. A [fruit](#) is the mature ovary of a flower. While the seeds are developing from ovules, the flower develops into a fruit ([Figure 38.10](#)). The fruit protects the enclosed seeds and, when mature, aids in their dispersal by wind or animals. Fertilisation triggers hormonal changes that cause the ovary to begin its transformation into a fruit. If a flower has not been pollinated, fruit typically does not develop, and the flower usually withers and dies.

Figure 38.10 The flower-to-fruit transition.

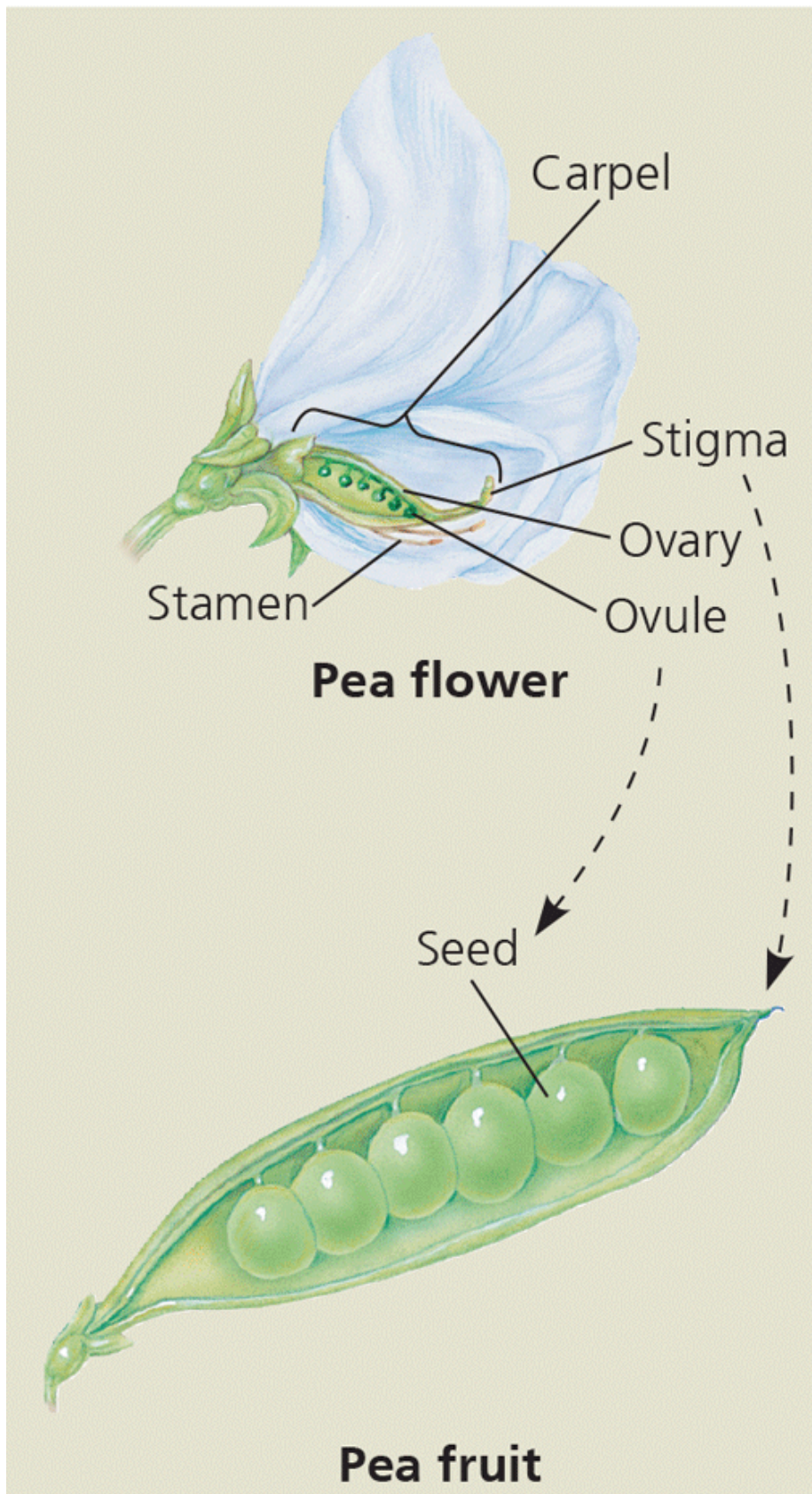
After flowers, such as those of the American pokeweed, are fertilised, stamens and petals fall off, stigmas and styles wither, and the ovary walls that house the developing seeds swell to form fruits. Developing seeds and fruits are major sinks for sugars and other carbohydrates.



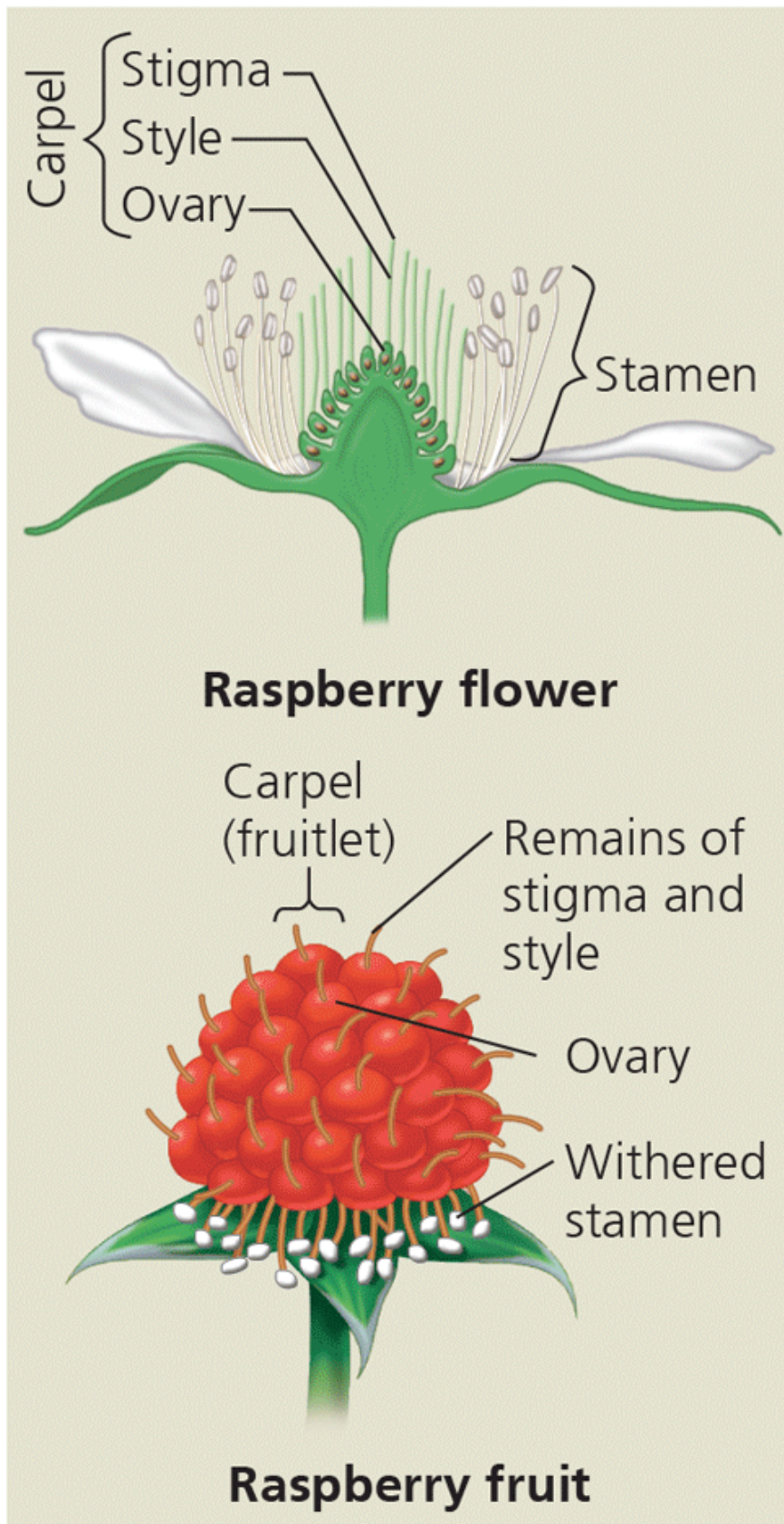
During fruit development, the ovary wall becomes the *pericarp*, the thickened wall of the fruit. In some fruits, such as soybean pods, the ovary wall dries out completely at maturity, whereas in other fruits, such as grapes, it remains fleshy. In still others, such as peaches, the inner part of the ovary becomes stony (the pit) while the outer parts stay fleshy. As the ovary grows, the other parts of the flower usually wither and are shed.

Fruits are classified into several types, depending on their developmental origin. Most fruits are derived from a single carpel or several fused carpels and are called [simple fruits](#) ([Figure 38.11a](#)). An [aggregate fruit](#) results from a single flower that has more than one separate carpel, each forming a small fruit ([Figure 38.11b](#)). These “fruitlets” are clustered together on a single receptacle, as in a raspberry. A [multiple fruit](#) develops from an inflorescence, a group of flowers tightly clustered together. When the walls of the many ovaries start to thicken, they fuse together and become incorporated into one fruit, as in a pineapple ([Figure 38.11c](#)).

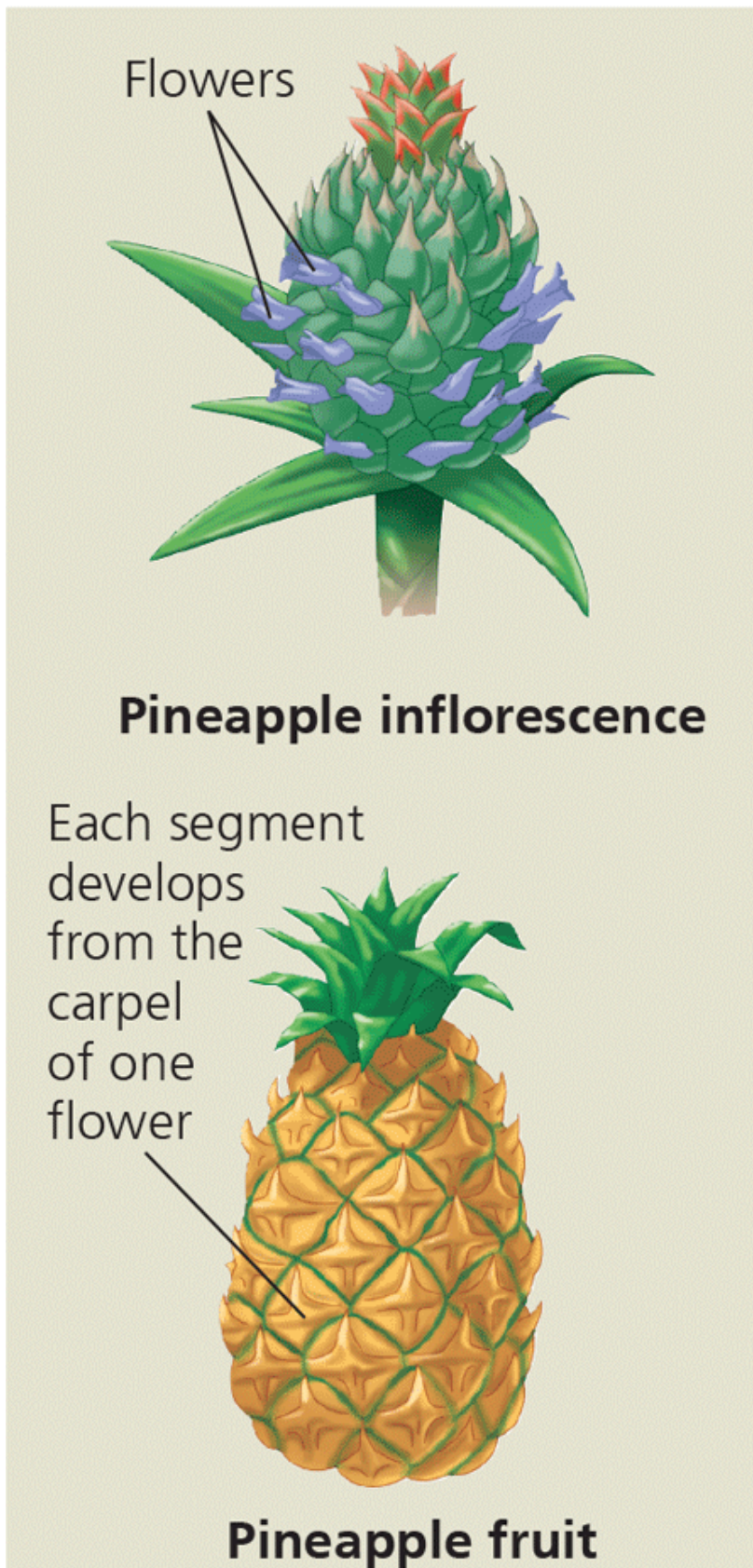
Figure 38.11 Developmental origin of different classes of fruits.



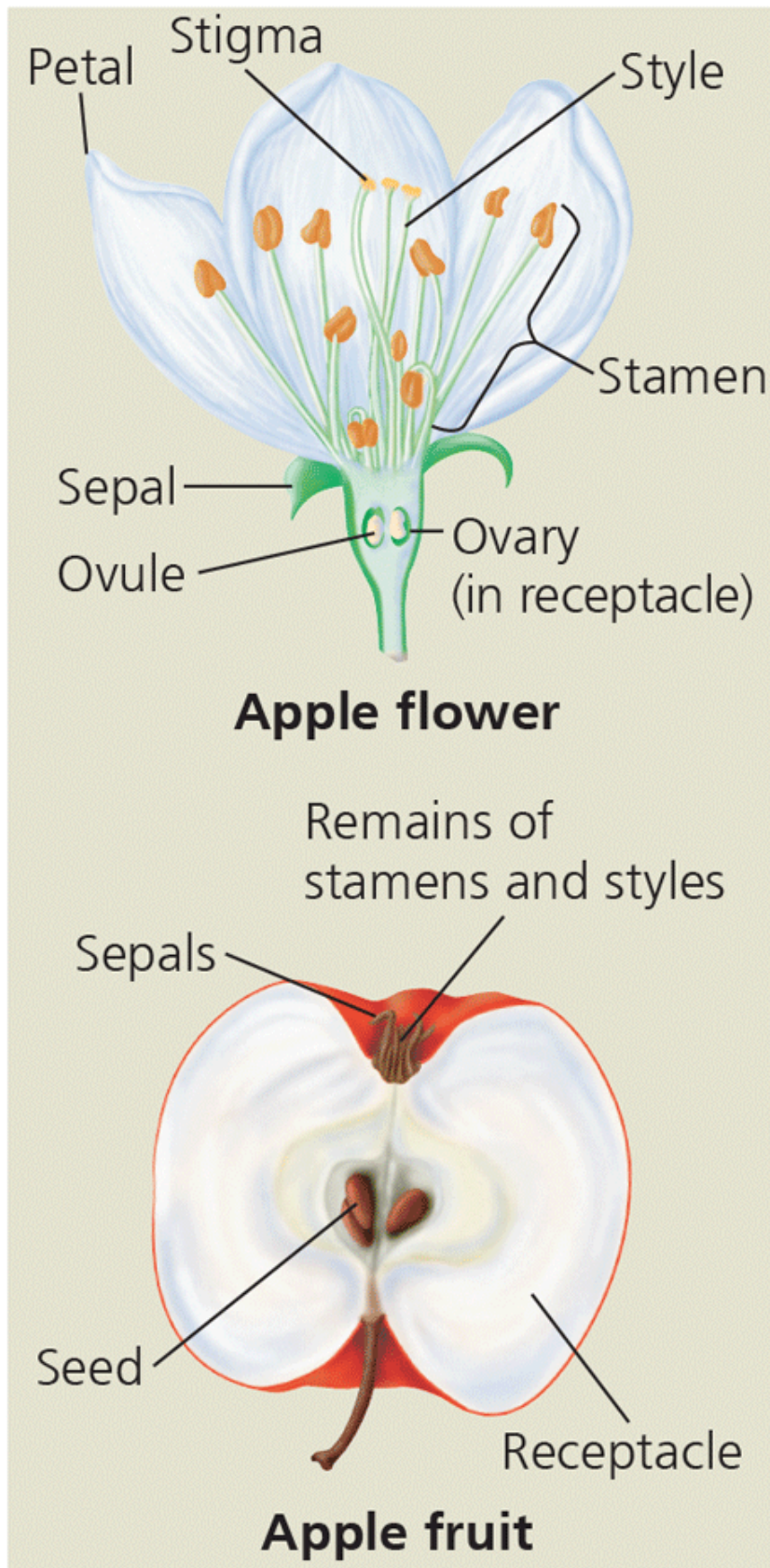
(a) Simple fruit. A simple fruit develops from a single carpel (or several fused carpels) of one flower (examples: pea, lemon, peanut).



(b) Aggregate fruit. An aggregate fruit develops from many separate carpels of one flower (examples: raspberry, blackberry, strawberry).



(c) **Multiple fruit.** A multiple fruit develops from many carpels of the many flowers that form an inflorescence (examples: pineapple, fig).



(d) Accessory fruit. An accessory fruit develops largely from tissues other than the ovary. In the apple fruit, the ovary is embedded in a fleshy receptacle.

In some angiosperms, other floral parts contribute to what we commonly call the fruit. Such fruits are called [accessory fruits](#). In apple flowers, the ovary is embedded in the receptacle, and the fleshy part of this simple fruit is derived mainly from the enlarged receptacle; only the apple core develops from the ovary ([Figure 38.11d](#)). Another example is the strawberry, an aggregate fruit consisting of an enlarged receptacle studded with tiny, partially embedded fruits, each bearing a single seed.

A fruit usually ripens about the same time that its seeds complete their development. Whereas the ripening of a dry fruit, such as a soybean pod, involves the ageing and drying out of fruit tissues, the process in a fleshy fruit is more elaborate. Complex interactions of hormones result in an edible fruit that entices animals that disperse the seeds. The fruit's "pulp" becomes softer as enzymes digest components of cell walls. The colour usually changes from green to another colour, making the fruit more visible among the leaves. The fruit becomes sweeter as organic acids or starch molecules are converted to sugar, which may reach a concentration of 20% in a ripe fruit. [Figure 38.12](#) examines some mechanisms of seed and fruit dispersal in more detail.

Figure 38.12 Exploring Fruit and Seed Dispersal

A plant's life depends on finding fertile ground. But a seed that falls and sprouts beneath the parent plant will stand little chance of competing successfully for nutrients. To prosper or competing successfully for Plants use biotic dispersal agents as well as abiotic agents such as water and wind.

Dispersal by water



Some buoyant seeds and fruits can survive months or years at sea. In a coconut, the seed embryo and fleshy white “meat” (endosperm) are within a hard layer (endocarp) surrounded by a thick and buoyant fibrous husk.

Dispersal by wind



With a wingspan of 12 cm, the giant seed of the tropical Asian climbing gourd *Alsomitra macrocarpa* glides through the air of the rainforest in wide circles when released.



The winged fruit of a maple spins like a helicopter blade, slowing descent and increasing the chance of being carried further by horizontal winds.



Hairy panic grass breaks off at the ground and tumbles across the terrain, scattering its seeds.



Some seeds and fruits are attached to umbrellalike “parachutes” that are made of intricately branched hairs and often produced in puffy clusters. These dandelion “seeds” (actually one-seeded fruits) are carried aloft by the slightest gust of wind.

Dispersal by animals



The sharp, tack-like spines on the fruits of bindii (*Tribulus terrestris*) can pierce bicycle tyres and injure animals, including humans. When these painful “tacks” are removed and discarded, the seeds are dispersed.



Some animals, such as this giant white-tailed rat (*Uromys caudimaculatus*), hoard seeds or fruits in underground caches. If the animal dies or forgets the cache’s location, the buried seeds are well positioned to germinate.



Seeds in edible fruits are often dispersed in faeces, like those shown here from the endangered cassowary (*Casuarius casuarius*) from North Queensland. The cassowary disperses the seeds of over 40 rain forest trees. In some cases, passage through the cassowary's gut is necessary before the seeds can germinate.



Ants are chemically attracted to seeds with “food bodies” rich in fatty acids, amino acids, and sugars. The ants carry the seed to their underground nest, where the food body (the lighter-coloured portion shown here) is removed and fed to larvae. Due to the seed’s size, unwieldy shape, or hard coating, the remainder is usually left intact in the nest, where it germinates.

In this section, you have learned about the key features of sexual reproduction in angiosperms—flowers, double fertilisation, and fruits. Next, we’ll examine asexual reproduction.

CONCEPT CHECK 38.1

1. Distinguish between pollination and fertilisation.
2. WHAT IF? If flowers had shorter styles, pollen tubes would more easily reach the embryo sac. Suggest an explanation for why very long styles have evolved in most flowering plants.
3. MAKE CONNECTIONS Does the life cycle of humans have any structures analogous to plant gametophytes? Explain your answer. (See [Figures 13.5](#) and [13.6](#).)

For suggested answers, see [Appendix A](#).