Fruits, Seeds, and Seedlings

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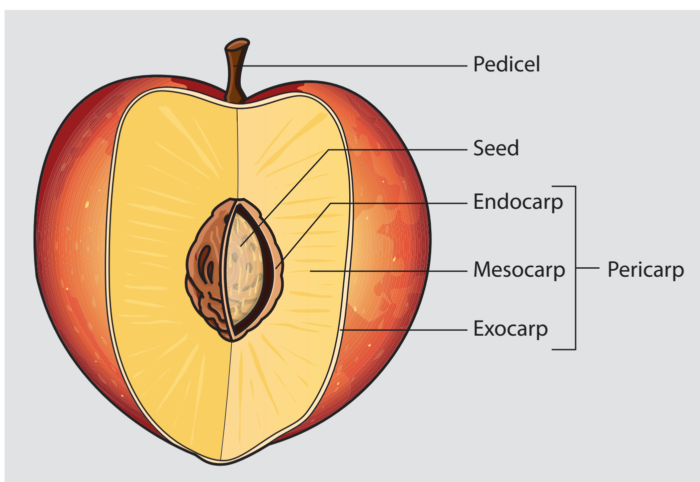
Introduction

The responsibility of the flower is to ensure fertilization; the responsibility of the fruit is seed dispersal. This chapter focuses on the anatomy and morphology of fruits, seeds, and seedlings. Like flowers, **fruits** occur only in angiosperms, not in gymnosperms; "angio" means vessel and "sperm" means seed. Therefore, angiosperms produce seeds inside a vessel (fruit). Gymnosperms (literally "naked seed") do not produce a fruit, although many such as Japanese yew (*Taxus cuspidata*) do have fleshy cones that may resemble a berry. As the angiosperm embryo and endosperm develop following double fertilization, the ovary wall increases in size and thickness and is gradually transformed into a fruit, in some cases along with the ripening of the receptacle. If the receptacle becomes a part of the mature fruit, such a fruit can be called an **accessory fruit**. The ovule enlarges into a seed, and tissues of the inner (if present) and outer integuments of the ovule become the seed coat.

19.1 Fruits Are Highly Modified Ovaries

The ovary wall typically develops into an expanded structure termed the **pericarp**. Three zones are often seen in the pericarp, an outer **exocarp**, a central **mesocarp**, and an inner **endocarp** (◘ Fig. 19.1). However, in many plants, the endocarp, the mesocarp, or both may be missing or fused with each other. In some fruit types like berries and in many dry fruits, these zones are difficult to distinguish in the mature fruit and can only be identified by carefully studying fruit development.

Following double fertilization (refer to ► Chap. 18), the ovary wall increases in size and gradually becomes a fruit. The ovule enlarges into a seed (refer to ► Chap. 18), and the tissues of the inner (if present) and outer integuments become the seed coat. The stalk of



◘ **Fig. 19.1** The three-dimensional structure of a drupe in peach (*Prunus persica*). The stony (i.e., heavily sclerified) endocarp encloses a single seed. The extensive mesocarp is fleshy and is covered by a thin skin (exocarp) comprised of epidermis and collenchyma. (Redrawn from Crang and Vassilyev 2003)

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the flower (termed a **pedicel**) remains present through the developmental process. In fruits derived from an inferior ovary, a hypanthium (a cuplike expansion of the receptacle bearing basal portions of sepals, petals, and stamens) participates in the pericarp formation.

With the exception of **parthenocarpy** (the development of fruit without seeds), fruits are developed only after double fertilization. As the embryo develops, parenchymatous extraembryonic tissues of a flower undergo complex taxon-specific modifications designed for embryo protection and seed dispersal. The other floral parts, i.e., style, perianth, and androecium, usually dry up and fall off. At the same time, both the cells of the pericarp and those of the seed coat divide and grow. The cells often contain chloroplasts capable of photosynthesis, which can provide a significant source of assimilates for the growing heterotrophic embryo.

19.2 Fruit Classification Is Based on Characters, Not Necessarily Species Relatedness

Fruits vary considerably by taxon, by means of specific dispersal and by germination strategies. Unlike taxonomic classification which is based on phylogenetic relationships, the classification of fruits is an artificial system that does not strictly recognize species relatedness. Indeed, some fruit types are restricted to a particular family or group of related plants; other fruit types are found across multiple, diverse taxa. Fruit taxonomy is based on morphological features such as the consistency of the pericarp—dry and hard or soft and fleshy (◘ Fig. 19.2a, b). Fruits may also be classified on the basis of whether they dehisce (i.e., release their seeds) or not when ripe and whether they contain a single carpel or multiple carpels. Overall, the type of fruit is important in understanding how seeds are dispersed. Not every fruit type can be discussed here, but one of several available fruit classification schemes is shown in ◘ Table 19.1, along with detail regarding the fate of the three pericarp layers (exocarp, mesocarp, and endocarp) and some information on the uses to which the fruit may be put.

◘ **Fig. 19.2** **a** Dry fruit of burdock (*Arctium* sp.) and **b** fleshy fruit of prickly pear cactus (*Opuntia* sp.). Both fruits contain the seeds of the plant. Scale bars = 1 cm in **a** and 3 cm in **b**. (**a** diablos, CC0 Creative Commons; **b** Bluesnap CC0 Creative Commons)

Table 19.1 Fruit type based on fruit characteristics and carpel number

Fruit characteristics		Number of carpels	Fruit type	Pericarp (fruit wall) layers			Examples
				Exocarp	Mesocarp	Endocarp	
Dry fruits	Indehiscent	Single carpel	Achene	All three fused together but not fused to seed			*Sunflower*—discard entire pericarp, eat seed
							Strawberry—eat receptacle (floral base) of the aggregate-accessory fruit and the fruits (achenes)
			Caryopsis	All three fused together, along with the seed coat and seed			*Wheat*—discard entire pericarp and eat seed—flour is endosperm of seed, wheat germ is embryo, bran is seed coat, whole wheat is entire seed
							Corn—yellow skin is entire pericarp; eat it and seed inside
			Samara	Papery, wing-shaped		Fused to exocarp	*Maple*, *ash*, *elm*—not eaten (maple syrup is concentrated xylem sap)
		Multiple carpels	Nut	All three thickened, highly lignified, and fused to form "shell"			*Walnut*—discard entire pericarp (nut shell); eat seed
	Dehiscent	Single carpel	Follicle	Exocarp splits open on one side only			*Milkweed*—not eaten
			Legume	Exocarp splits on both sides			*Beans*, *peas*, *peanuts*—eat seed (as in peas) or entire fruit and seed (as in pea pods, green beans)
		Multiple carpels	Capsule	Exocarp opens via holes, or a lid pops off			*Lily*, *poppy*—not eaten (heroin is extracted from the sap of the immature poppy seed capsule)

Fleshy fruits	Single carpel	Drupe	Papery	Fleshy or stringy	Hard and thick	*Peach*, *nectarine*, *cherry*, *plum*—eat exocarp and mesocarp; discard endocarp ("stone") and seed inside
						Almond—discard exo- and mesocarp, crack endocarp, and eat seed
						Coconut—endocarp is papery outer, mesocarp is thick stringy husk, and endocarp is "shell"; eat the endosperm (either liquid or solid)
	Multiple carpels	Berry	Papery	Fleshy	Fleshy	*Grape*, *eggplant*, *kiwifruit*, *tomato*—eat exo-, meso-, and endocarp
						Banana—discard exocarp (peel); eat meso- (very thick) and endocarp
						Pineapple—individual berries fused into a multiple fruit
						Blackberry, *raspberry*—individual berries fused into aggregate fruit
		Pepo	Papery	Fleshy	Fleshy or stringy	*Pumpkin*, *squash*, *cucumber*—eat mesocarp; endocarp is the stringy mass that holds the seeds
		Hesper-idium	Leathery exocarp (flavedo) fused to spongy mesocarp (albedo)		Papery	*Citrus*—each section is surrounded by the endocarp. Eat the juice-filled vesicles that fill inside of endocarp
		Pome	Papery	Fleshy	Hard or papery	*Apple*, *pear*—eat hypanthium (accessory fruit) which is derived from fusion of sepals and petals. Discard all of the fruit (core)

19.3 Dry Fruits Are Often Hard, Containing Fused Pericarp Layers and Dead Cells

At maturity, the pericarp of dry fruits consists mostly of dead, sclerified, and desiccated cells. In regions of the growing pericarp, some cells die earlier than others, and, as a result, they become crushed. Upon final maturation, one or more layers of cells undergo sclerification, giving the fruit a characteristic hardness. Dry fruits include two main groups: **indehiscent** and **dehiscent**. Dehisce (from the Latin, meaning to "split open" or "gape") means the fruit splits open and releases the seeds upon maturation of the fruit. A **schizocarp** is a dry fruit with multiple carpels that separates into individual one- or two-seeded carpels (each called a **mericarp**) upon maturity. The resulting mericarps may be indehiscent (as in carrot and mallow) or dehiscent (*Geranium* sp.).

19.3.1 Indehiscent Dry Fruits

Indehiscent fruits do not release their seeds upon maturity and are typically single-seeded. The pericarp of indehiscent fruits often resembles the seed coat in structure, and the fruits themselves are commonly called "seeds" even though this terminology is botanically incorrect. Indehiscent fruits include achenes, caryopsis, samaras, and nuts.

An **achene** is a fruit derived from superior or inferior ovaries and composed of one or more carpels. The pericarp has a leathery consistence and may be easily separated from the seed coat (◘ Fig. 19.3a, b). Examples of plants with achenes include buckwheat (Polygonaceae) and sunflowers (Asteraceae).

A **caryopsis** is similar to an achene but is derived from a superior ovary composed of a carpel in which the pericarp and the

◘ **Fig. 19.3** **a** Photograph of achenes from sunflower (*Helianthus annuus*). When mature, the entire ovary (fruit) is dried out and has a seedlike appearance. It is actually a fruit with the seed inside. **b** Sunflower seeds are contained within the achene fruit. Scale bars = 1 cm in **a** and 0.5 cm in **b**. (**a** Hans, CO0 Creative Commons; **b** F_A, CO0 Creative Commons)

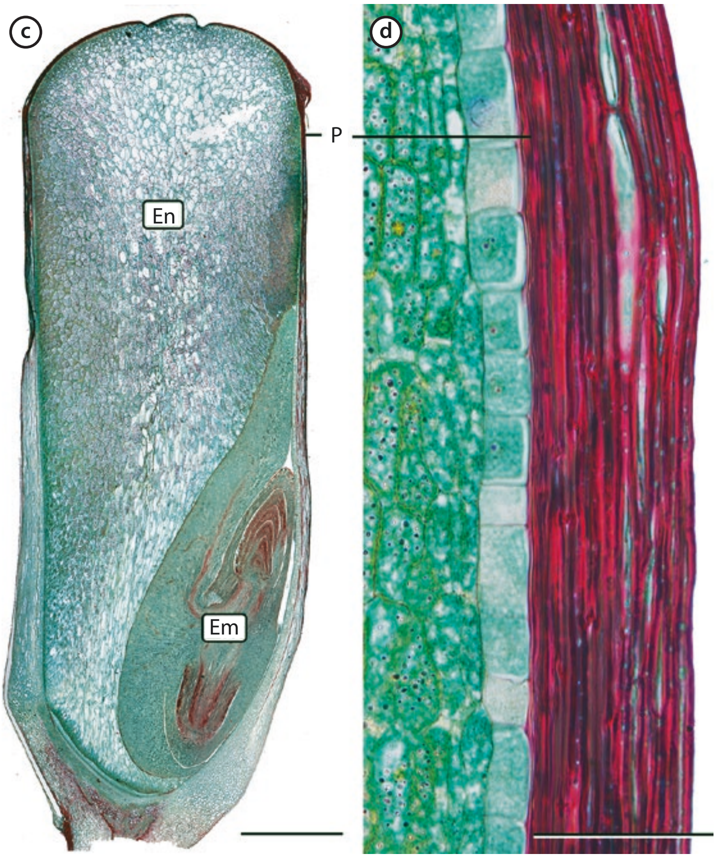


Fig. 19.3 **c** A longitudinal section of a mature maize (*Zea mays*) seed at low and **d** high magnification. The pericarp (P) is a fusion of the true pericarp tissues (exocarp, mesocarp, and endocarp) with the seed coat. The endosperm (En) and embryo (Em) are the two main parts of the seed. Scale bars = 2 mm in **c** and 50 µm in **d**. (**c**, **d** RR Wise)

remains of the integuments are completely fused (Fig. 19.3c, d). The caryopsis of grasses is in reality not a seed as it is commonly designated but a special type of a single-seeded fruit because its covering is a pericarp rather than seed coat. Examples of plants with a caryopsis-type fruit are grasses such as corn, wheat, barley, rye, and rice (Poaceae). The maize fruit is frequently referred to as a "hull" which gets lodged in the teeth of people eating popcorn.

A **samara** is similar to an achene in its basic anatomy but has a winglike outgrowth(s) of the pericarp that assists in wind-borne seed dispersal (Fig. 19.3e, f). Examples of samaras can be found in maples and box elders (Sapindaceae), tree of heaven (Simaroubaceae), and the bush willows (Combretaceae) (Fig. 19.3e, f).

A **nut** is similar to an achene, but parts or all of the pericarp is hard and stony, commonly called the "shell." In the walnuts (Fig. 19.3g, h) and hickories (Juglandaceae), the endocarp and mesocarp are shed, and the heavily sclerified endocarp is the shell. Oaks (Fagaceae) produce nuts in which all three layers of the pericarp are fused and sclerified to form the shell.

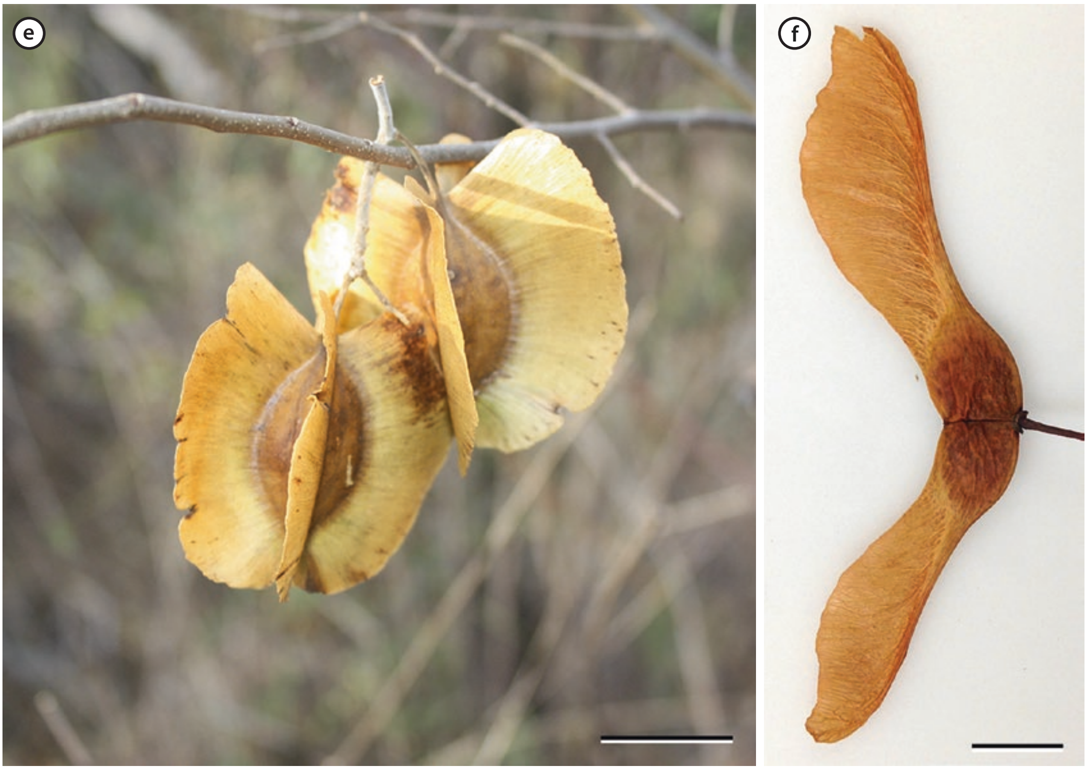


Fig. 19.3 **e**, **f** Samara fruit of **e** Zeyher's bush willow (*Combretum zeyheri*) (Marco Schmidt, CC-BY SA 3.0) and **f** silver maple (*Acer platanoides*) showing the outgrowths of the pericarp called "helicopters" that are important for seed dispersal. Scale bars = 5 cm in **e** and 1 cm in **f**. (**e** Marco Schmidt, CC-BY SA 3.0, **f** RR Wise)

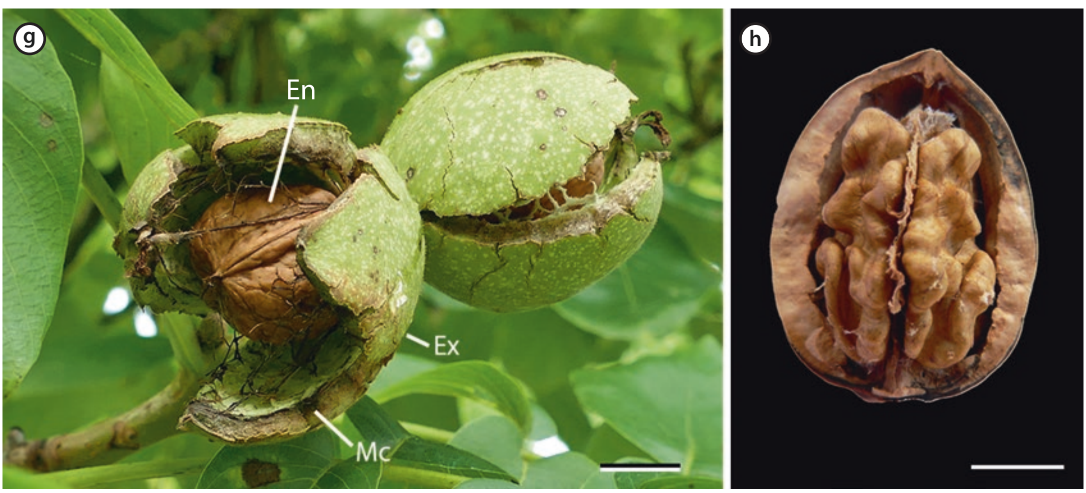


Fig. 19.3 **g**, **h** Fruit of the eastern black walnut (*Juglans nigra*). **g** The exocarp and mesocarp are shed after development of the nut. **h** The endocarp is heavily sclerified and hard. Scale bars = 1 cm in both panels. (**g** HelgaKA, CO0 Creative Commons; **h** public domain)

19.3.2 Dehiscent Dry Fruits

Dehiscent fruits are dry at maturity and usually contain several—to numerous—seeds. **Dehiscence** results in the release of seeds from the fruit and may occur in various ways from falling below mater-

Fig. 19.3 **i** Milkweed (*Asclepias syriaca*) is named for its milky sap and also contains podlike follicles at the terminal part of the shoot. The seeds within the fruit are densely packed and bearded with plumes for wind dissemination. **j** Follicle of a milkweed plant splitting and exposing seeds with plumes aiding in anemochory (wind dispersal). Scale bars = 5 cm in both panels. (**i** Marco Schmidt, CC BY-SA 3.0; **j** RR Wise)

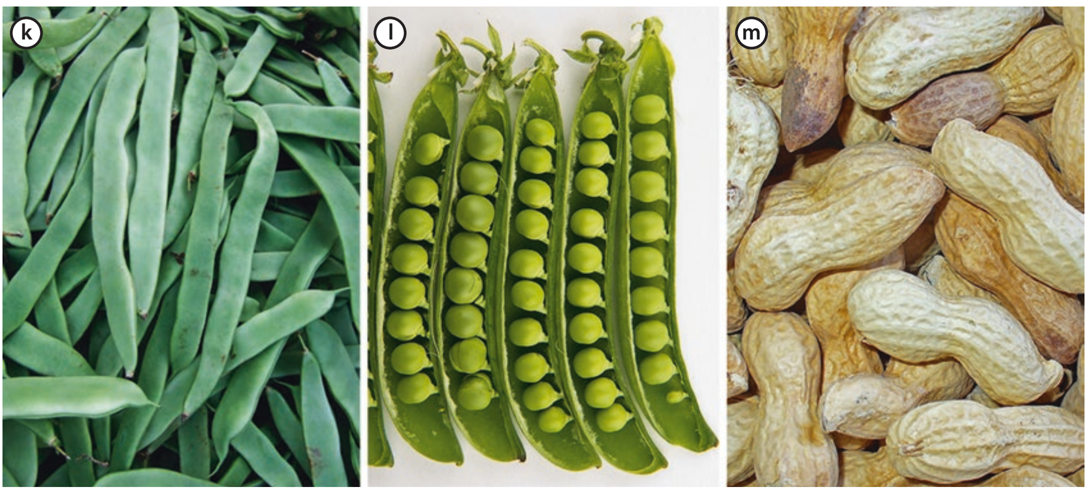


Fig. 19.3 **k**–**m** Legumes of **k** green bean (*Phaseolus vulgaris*) (Zyance – Own work, CC BY-SA 2.5), **l** sweet pea (*Pisum sativum*) (Bill Ebbesen – Own work, CC BY-SA 3.0), and **m** peanut (*Arachis hypogaea*). (H. Zell – Own work, CC BY-SA 3.0)

nal plants to wind dispersal and even ballistic dispersal. The dehiscent fruits include follicles, legumes, and capsules.

A **follicle** is a dry fruit derived from a superior ovary of a single carpel. It splits down the ventral side of the carpel. Examples of plants with follicular fruits include *Magnolia*, Christmas rose (*Helleborus niger*), and plants in the Apocynaceae—the milkweed family (Fig. 19.3i, j).

The **legume** fruit is only found in the legume family, Fabaceae. Thus, it is an exception to the rule that fruit taxonomy does not recognize species relatedness. A legume develops from a superior ovary that contains a single carpel. It splits open along both the ventral side and midrib of the carpel. At maturity, the fruit wall (pericarp) is dry and

■ **Fig. 19.3** **n** Tulip (*Tulipa* sp.) capsule is loculicidal. **o** The campion (*Silene* sp.) capsule is denticulate. **p** Seeds dehisce from the poricidal poppy (*Papaver* sp.) capsule via pores at the top. **q** The lily (*Lilium* sp.) capsule is septicidal; it sheds its seeds by forming a split down the side, between two carpels. Lily has three carpels, thus three septal splits. Scale bars = 1 cm in all panels. (**n**–**q** RR Wise)

brown, and the seeds are dehisced. However, most of us are more familiar with the immature fruit. Green beans are picked at a very early stage, before the seeds have developed. The pod/pericarp/fruit/legume wall is eaten either fresh or cooked (■ Fig. 19.3k). Snow pea pods are likewise consumed when immature. Sweet peas are picked at a slightly later developmental stage, when the seeds have developed and the pod wall, which is discarded, has dried considerably, although it is still green (■ Fig. 19.3l). Peanuts are picked at maturity after the pericarp has sclerified (■ Fig. 19.3m). The pericarp is split open and the seeds are eaten. The peanut seed has hundreds of uses (Carver 1917).

A **capsule** fruit is derived from either superior or inferior ovaries and composed of two or more carpels. The capsule wall is dry and sclerified. Tulips, lilies, irises, jimsonweed, poppies, and *Amaryllis* are all examples of plants with capsules. Capsules may be divided into different types based on where the locule splits to release the seeds. **Loculicidal** capsules split along a seam in the locule. Tulips are a common example (◘ Fig. 19.3n). **Denticulate** capsules have a large opening at the top ring by teeth, or denticles, as found in campion (◘ Fig. 19.3o). Capsules that release their seeds via pores on the top of each carpel, such as poppy, are termed **poricidal** (◘ Fig. 19.3p). Those that dehisce by a split between locules are called **septicidal**, because the split is along a septum (boundary) between the locules (◘ Fig. 19.3q).

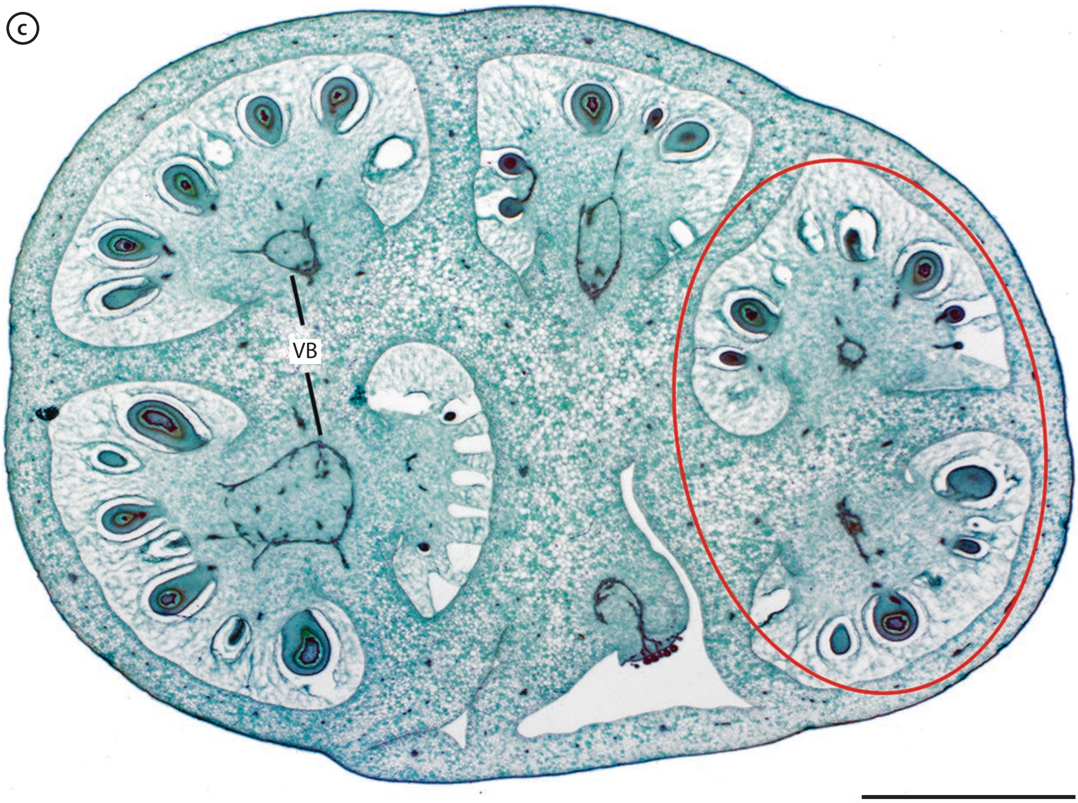
19.4 Fleshy Fruits Are Characterized by an Enlarged, Juicy Pericarp

Fleshy fruits represent what most nonbotanists mean when they use the term "fruit." Fleshy fruits are characterized by the expansion of parenchyma cells in the pericarp during fruit development and their differentiation into photosynthetic or storage tissue. Thin-walled and highly vacuolated parenchyma cells predominate in the pericarp of fleshy fruits. They are all indehiscent and do not release seeds upon fruit maturation. Many green fleshy fruits are capable of significant rates of photosynthesis. These cells remain intact and active, in one form or another, long after fruit maturation, hence the "fleshy" designation. The fleshy portion of the fruit attracts frugivores, animals that eat fruit and serve solely in seed dispersal. Fleshy fruits include the drupe, berry, pepo, hesperidium, and pome, as described below.

A **drupe** is a single-seeded fruit derived from a single carpel (◘ Fig. 19.4a, b). The drupe may also be called a stone fruit because it has a thick and hard endocarp consisting of stone cells, a fleshy mesocarp, and a thin "skin" or **exocarp** (refer to ◘ Fig. 19.1). Examples include olives, coconuts, as well as many fruits in the *Prunus* genera including peaches, cherries, nectarines, and plums.

A **berry** is a multiple-seeded fruit derived from the superior or inferior ovaries with one or more carpels (◘ Fig. 19.4c). All the ground tissue (mesocarp and endocarp) of the ovary wall expands into a fleshy or juicy tissue, and the outer layer or skin is usually the

◘ **Fig. 19.4** **a**, **b** Drupes. Cherry (*Prunus avium*) and olive (*Olea europaea*) are both drupes because they have a thin exocarp, thick mesocarp, and heavily sclerified endocarp or stone. A single seed is found within the endocarp. Scale bars = xx mm. (**a** Hans, CO0 Creative Commons, **b** ulleo, CC0 Creative Commons)

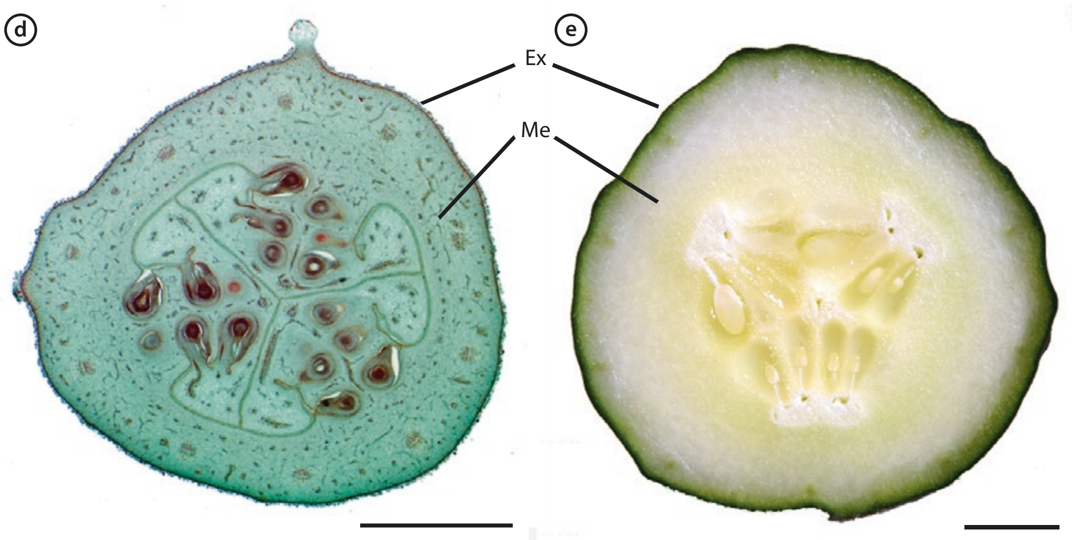


■ **Fig. 19.4** **c** Cross-section of a developing tomato (*Solanum lycopersicum*) fruit. The tomato has axile placentation, a single example of which can be seen within the red ellipse. Vascular bundles (VB) supply each seed with nutrients. Thousands of years of breeding has produced "meaty" tomato fruit with multiple, fused carpels such that the simple axile arrangement can be difficult to see. Scale bar = 500 µm. (RR Wise)

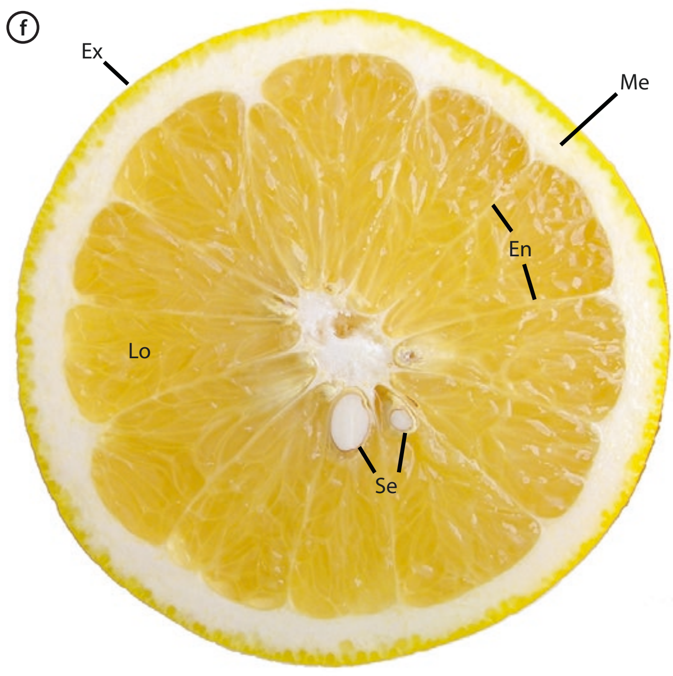
exocarp. Examples of berries include the blueberry, tomato, and peppers (*Capsicum annuum*). A developing tomato fruit is shown in ■ Fig. 19.4c. At this early stage, the fruit would green due to active chloroplasts in the exocarp. In each locule, the axial placenta bearing seeds is enlarged and contains vascular bundles. As the fruit ripens, the chloroplasts of the cells in the pericarp and placenta undergo transformation into chromoplasts, which accumulate the red carotenoid, lycopene. The seeds become mucilaginous due to slime secreted by their epidermal layers as well as from the placenta.

A **pepo** fruit typically develops from an inferior ovary with three carpels. Pepo fruits bear some resemblance to pome fruit, but they do not contain a sclerified endocarp. One of the distinguishing features of a pepo is the occlusion of its locules by the ingrowths of carpels (■ Fig. 19.4d, e). The pepo also has accessory tissue, i.e., an enlarged hypanthium, and the placentation is parietal. Examples of pepos are found in the Cucurbitaceae and include the cucumber (*Cucumis sativus*), watermelon (*Citrullus lanatus* var. *lanatus*), as well as various squashes and pumpkins (*Cucurbita pepo*).

A **hesperidium** is a multiple-seeded fruit derived from a superior ovary of about ten carpels with central-angular placentation (■ Fig. 19.4f). The exocarp, sometimes called the **flavedo**, is a brightly colored rind that consists of compact parenchyma with oil



■ **Fig. 19.4** **d**, **e** As seen here in cucumber (*Cucumis sativus*), a pepo, numerous seeds are connected to the parietal placentae and enclosed in a pulpy tissue. The pericarp consists of the green exocarp (Ex) that is composed of the epidermis, several layers of supporting tissue, and fleshy parenchymatous mesocarp (Me). No well-defined endocarp is present. Scale bars = 1 mm in **d** and 1 cm in **e**. (**d** RR Wise; **e** S Lyons-Sobaski)



■ **Fig. 19.4** **f** A hesperidium of a lemon (*Citrus limon*) fruit. The thick exocarp and white, spongy mesocarp are characteristic of this fruit type. The locules (Lo) are formed by the radial partitions of the endocarp (En) that represent fused and invaginated margins of adjacent carpels. The locules are filled with stalked, spindle-shaped multicellular juice sacs. Seeds (Se) are also present in the locules. Scale bar = 2 cm. (CO0 Creative Commons)

Fig. 19.4 **g**, **h** Photographs of a **g** longitudinal and **h** cross-section of an apple pome. In the pome of cultivated varieties of apple (*Malus pumila*), the border between the accessory part of the fruit and pericarp proper is not clearly demarcated. A boundary line may be drawn along vascular bundles (VB) that have supplied five petals. The "membranes" that line the five unoccluded locules (L) with seeds are morphologically a cartilaginous-like endocarp. Note the pedicel (P) and, on the opposite side, the withered remains of sepals (S). Scale bar = 2 cm. (**g**, **h** RR Wise)

cavities. The white spongy tissue underneath the rind is the mesocarp (a.k.a. **albedo**). It consists of loosely arranged colorless cells. This tissue appears white because of numerous air spaces. The locules are formed by the radial partitions that represent fused and invaginated margins of adjacent carpels. The locules are occluded with juice sacs that are modified trichomes and are the derivatives of the inner epidermis and subepidermis (collectively known as endocarp). Examples of plants with hesperidium fruit can be found in the Rutaceae, the citrus family.

A **pome** is a multiple-seeded fruit derived from an inferior ovary of five carpels. The fruit includes carpellary tissue from the hypanthium (floral tube). The flesh is mainly derived from an enlarged hypanthium rather than from the ovary wall. The hypanthium in the pome is the enlarged basal portion of the perianth and stamens, which are fused to the ovary (Fig. 19.4g, h). The endocarp is thin and sclerified and covered with a waxy cuticle. Sepals are often preserved on the top of the fruit, confirming that it originated from an inferior ovary. Examples of pome fruits include apples and pears. The hypanthium is the portion eaten, and the true fruit (the layers of the pericarp) is discarded as the "core."

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19.5 Fruit Structure Can Include Aggregations of Flowers into One Fruit or Many Small Fruits Within a Larger Assembly

Aggregate and multiple fruits are complicated combinations of one of the fruit types described above. **Aggregate fruits** are derived from the ovaries of numerous free carpels of one individual flower.

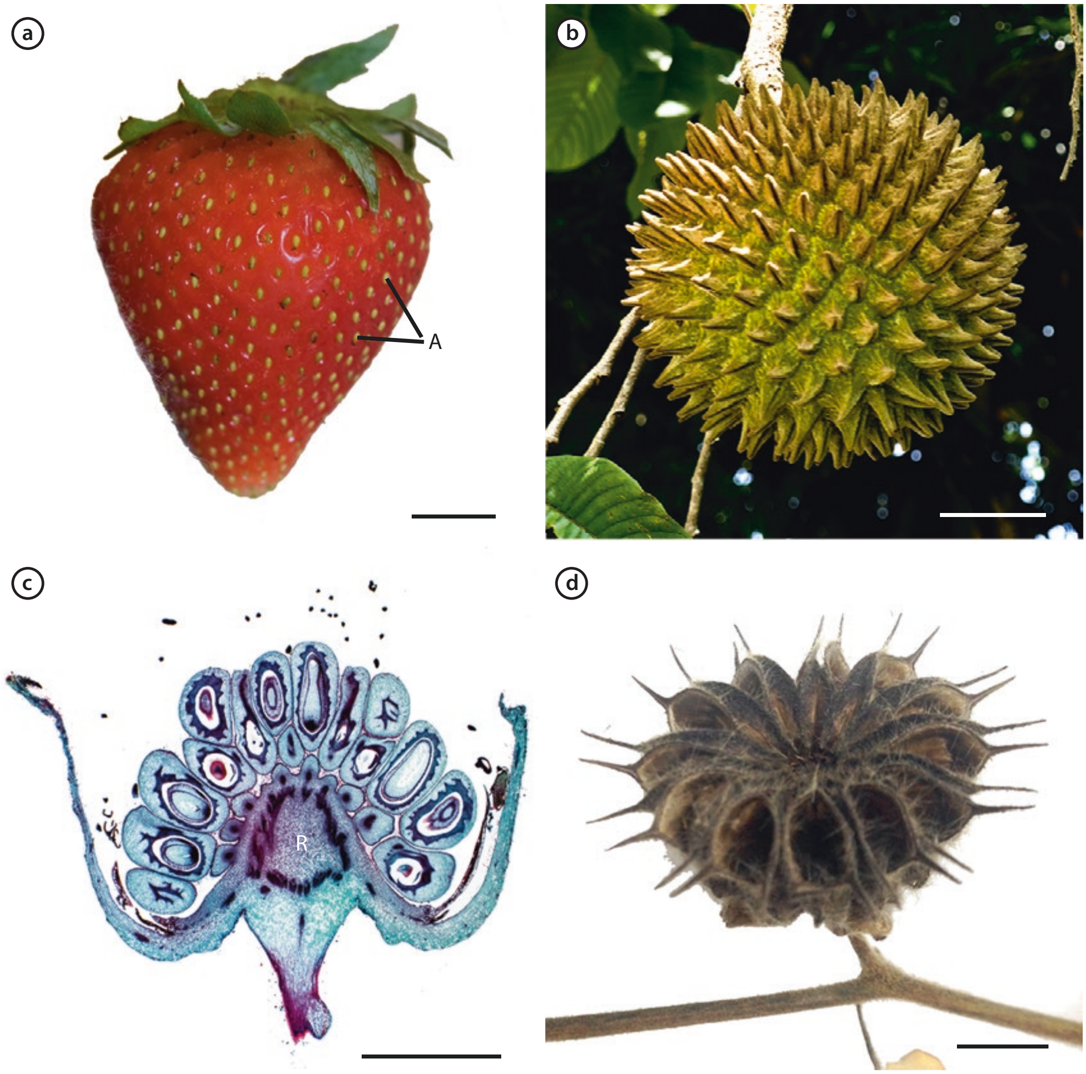
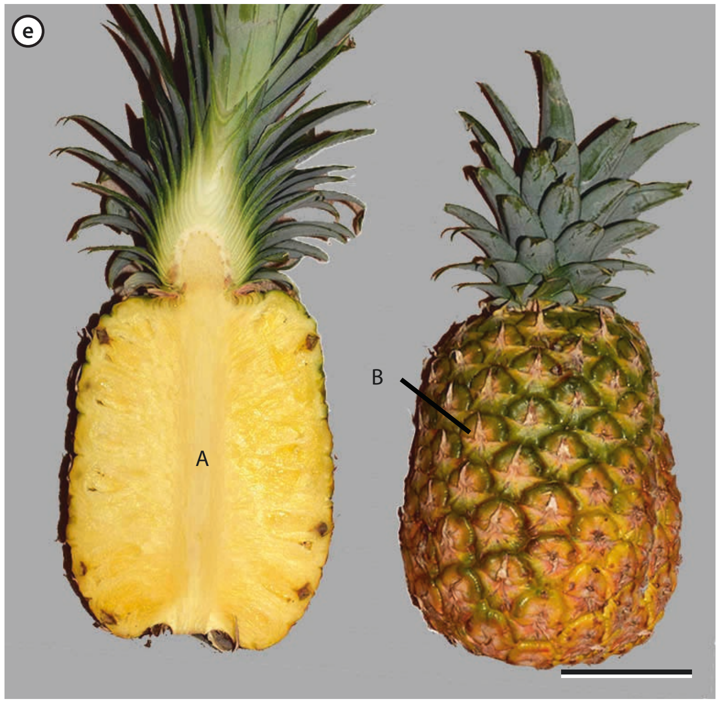


Fig. 19.5 **a**–**d** Four examples of aggregate fruit representing achenes, berries, drupes, and follicles. They all develop from the numerous ovaries of a single flower, with each superior ovary containing a single ovule. **a** The strawberry (*Fragaria* sp.) fruit is an aggregate of many achenes (dry, indehiscent fruits), attached to an enlarged and fleshy receptacle. The receptacle is the floral part that is selected for eating, with the accompanying achenes (A). **b** The custard apple (*Annona purpurea*) fruit is an aggregate of berries (fleshy fruits). **c** Raspberries (*Rubus* sp.) are aggregates of drupes (fleshy fruits). The receptacle (R) is a small, tasteless knob that remains on the plant when the fruits are picked. The individual fruits are called drupelets. **d** Velvetleaf (*Abutilon theophrasti*) fruits represent an aggregate of follicles (dry, dehiscent fruits). Scale bars = 1 cm in **a**, 5 cm in **b**, 2 mm in **c**, and 1 cm in **d.** (**a** S Lyons-Sobaski; **b** LI1324, CC0, Creative Commons; **c**, **d** RR Wise)

The receptacle enlarges and becomes fleshy. Examples of aggregate fruit include strawberries (achene), custard apple (berries), raspberry (drupes) and velvet leaf (follicles) (Fig. 19.5a–d). Such fruits may be aggregates of dry indehiscent, dry dehiscent, or fleshy fruits. In contrast, **multiple fruits** differ from aggregate fruits because each multiple fruit is derived from individual ovaries of multiple flowers. The classic example of a multiple fruit is the berries of the pineapple (Fig. 19.5e). Another example includes plants within the mulberry family, the Moraceae, where the multiple fruit often



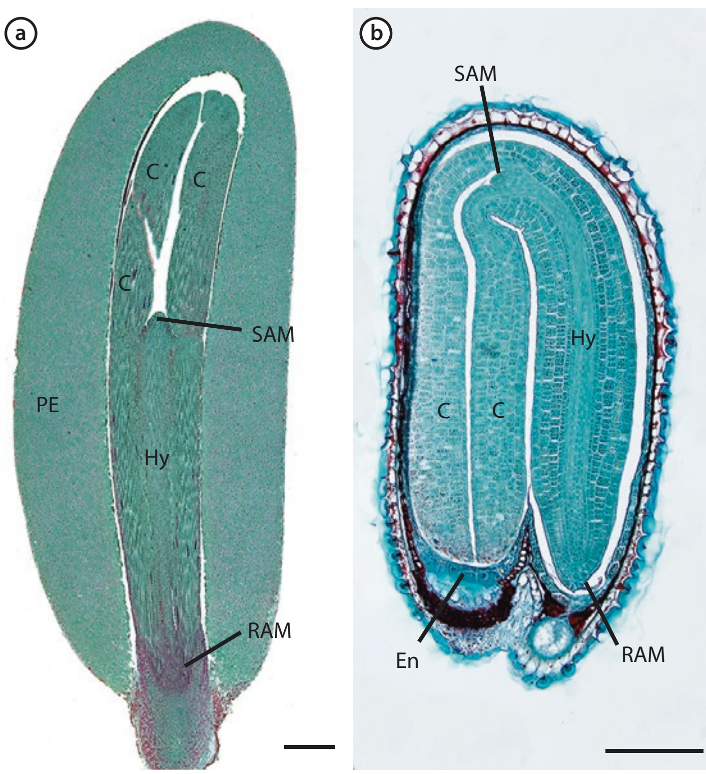
◘ Fig. 19.5 **e** The multiple fruit of pineapple (*Ananas comosus*) develops from a compact inflorescence. In the internal view, the fleshy inflorescence axis (A) is shown cut lengthwise, and numerous swollen and coalesced fruits arise laterally from it. In cultivated varieties, each fruit develops parthenocarpically (without fertilization) from an inferior ovary. In the external view, numerous spirally arranged fruits, specifically berries (B), are visible. After flower production, the inflorescence apex reverts to vegetative growth. The leafy crown is used to propagate this crop by vegetative means. Scale bar = 5 cm. (S Lyons-Sobaski)

contains many drupelets or achenes that are united with a common receptacle. Fig trees (*Ficus*) produce another type of multiple fruit called a **synconium**. Fig fruits differ from all others discussed thus far, as the flowers are located within the developing fruit structure, with each flower potentially giving rise to a drupelet. Some species of fig must be pollinated by fig wasps that enter the fruit structure.

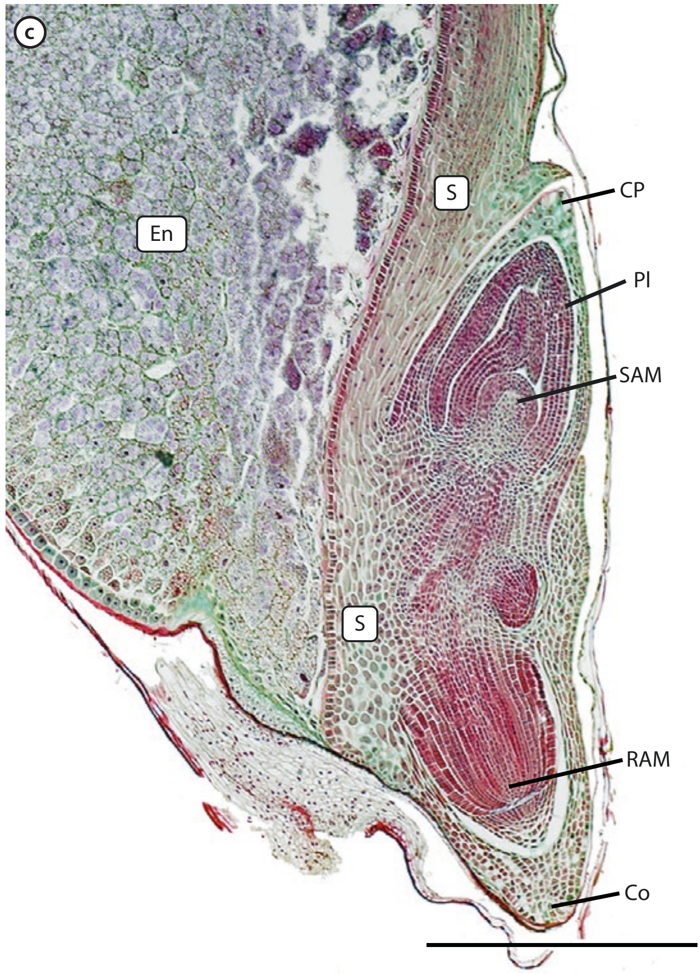
19.6 The Seed Is an Individual Plant Containing Nutrition for the Embryo

The **seed** is the main reproductive unit in both angiosperms and gymnosperms and provides continuity between the successive generations. Seeds are the means of plant dissemination (dispersal) through space. Dormancy (refer to ► Sect. 1.7) allows plants to disperse through time. Seeds help the tender embryo survive under cold, dry, and other unfavorable conditions and supply the embryo with nutritive materials for germination and prior to autotrophic growth. Plants that possess seeds are called spermatophytes (a.k.a. also known as phanerogams). They include the four taxa of gymnosperms (cycads, *Ginkgo*, conifers, and gnetophytes) and the angiosperms. The spermatophyte seed is composed of three main parts: (1) the embryo, (2) a source of stored nutrients (endosperm or pseudoendosperm), and (3) a protective seed coat. The conifer, eudicot, and monocot seed will be discussed in this section.

The embryo (the incipient sporophyte) is the most important part of the seed (◘ Fig. 19.6a–c). It consists of many (gymnosperms), two (eudicotyledons), or one (monocotyledons) leaflike cotyledons and a **hypocotyl** ("below cotyledons")—the stemlike axis between the cotyledons and the root crown. The hypocotyl forms two apical meristems at its poles, the root apical meristem (RAM) at the lower pole and the shoot apical meristem (SAM) at the upper pole. If a short stem or embryonic leaves are present, they are called the **epicotyl** ("above cotyledons") or **plumule**. However, not all spermatophyte species, have seeds that contain a well-developed plumule. The RAM and SAM give rise to all postembryonic structures in the primary growth of the plant. In conifers and eudicotyledons, the SAM is situated between the cotyledons at their



◘ **Fig. 19.6** **a** Longitudinal section of a pine (*Pinus* sp.) seed. Multiple cotyledons (C, three are marked) surround the shoot apex of the embryo. Food reserves are stored in the large pseudoendosperm (PE). The shoot apical meristem (SAM) and root apical meristem (RAM) represent the top and bottom of the hypocotyl (Hy). **b** Longitudinal section of a non-endospermic shepherd's purse (*Capsella bursa-pastoris*) seed. Most of food reserves in the endosperm (En) have been broken down and moved into the large cotyledons (C). Scale bars = 500 µm in **a** and 100 µm in **b**. (**a**, **b** RR Wise)



◘ **Fig. 19.6** **c** Longitudinal section of an endospermic caryopsis (or grain) of oats (*Avena sativa*). The lateral position of the embryo in the fruit is characteristic of the caryopsis, with the endosperm (En) occupying the majority of the seed volume. The scutellum (S) is almost twice as large as the remainder of the embryo (called the embryonic *axis*). The embryo contains a well-differentiated plumule (Pu) arising from the shoot apical meristem (SAM) with the primordium of the first leaf, termed a coleoptile (CP), protecting the plumule. The root apical meristem (RAM) is enclosed in a specific multilayered sheath, the coleorhiza (Co). Scale bar = 0.5 mm. (RR Wise)

bases, whereas in monocotyledons, it occupies a lateral position with respect to the vertically oriented cotyledon (scutellum).

Conifers lack double fertilization and therefore do not produce a true endosperm. The seeds do, however, have a seed coat, contain a developing diploid embryo, and possess a food storage tissue derived from haploid cells of the female gametophyte (◘ Fig. 19.6a). In spite of its different ontogenetic origin but in keeping with its common function, this storage tissue is typically called a pseudoendosperm.

Eudicot and monocot seeds are more complex because the angiosperm embryo and food-storing endosperm are separate products of double fertilization. The seed coat has a maternal

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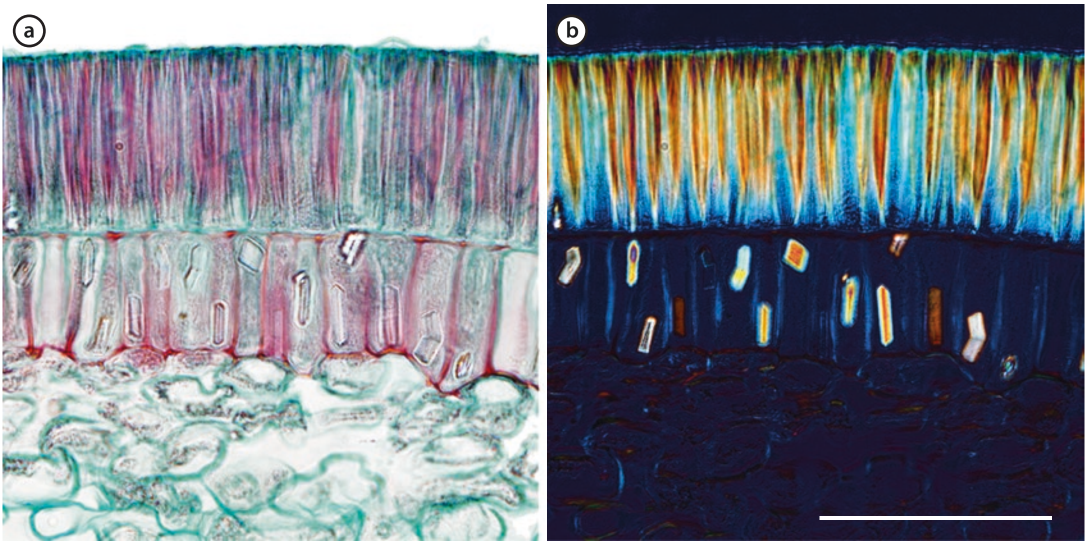
(ovular) origin. Although all angiosperms produce an endosperm, that tissue may not persist to the mature seed stage. In seeds with **non-endospermic storage**, the food reserves are synthesized within the endosperm but are soon transported into the cotyledons of the embryo (a.k.a. an **exalbuminous seed**). This can be seen in the eudicot seed shown in ◘ Fig. 19.6b in which little endosperm remains and the cotyledons are enlarged. But in most flowering plants, the endosperm tends to remain; such seeds are said to have endospermic storage (◘ Fig. 19.6c). The ratio of volumes occupied by the embryo and endosperm in the mature seed varies greatly among different plants.

In monocotyledons, the large, single cotyledon is termed the scutellum (◘ Fig. 19.6c; refer also to ◘ Fig. 19.3c). The scutellum is an absorptive organ. As food monomers are liberated from the stored reserves in the endosperm, they are loaded into the scutellum which has a direct vascular connection (mostly phloem) to the developing shoot and root on the embryonic axis. The immature leaves of the plumule are protected by a **coleoptile** that will grow in length and protect the juvenile leaves as they push through the soil. In a similar fashion, the **coleorhiza** will protect the young root tip until a proper root cap matures. In the **aleurone layer** (refer to ◘ Fig. 19.3c), the cell walls are thickened due to the deposition of hemicellulose reserves. During germination, cells of the aleurone layer secrete starch-degrading enzymes that are released into the endosperm. There, the enzymes break down the starch reserves and mobilize simple sugars for absorption by the scutellum. The scutellum then delivers the sugars to the germinating embryo.

19.7 The Seed Coat Surrounds the Embryo and Storage Tissues

The seed coat (or testa) is derived from the integument(s) of the ovule. It is the sole protective layer for the embryo in seeds released from dehiscent fruit but may be lost from or heavily modified on seeds in indehiscent dry fruits or in fleshy fruits. The frequent brown or black color of seeds is due to pigments accumulated in the cells of the seed coat. In single-seeded, indehiscent fruits where the embryo is protected by the pericarp, the seed coat is often obliterated or appears as a very thin, structureless membrane between the embryo and the pericarp, as in the sunflower seeds shown in ◘ Fig. 19.3b.

Most commonly, the seed coat in mature seeds is dry and usually consists of dead cells. The withering away of different layers of the seed coat occurs asynchronously in a developing seed. One or several cell layers may become nonliving when the cell walls are thin and the seed is still enlarging. Such layer or layers become crushed and may eventually disappear. But other layers remain alive and grow in pace with the seed expansion. Their cells may undergo sclerification and lignification after the cessation of seed growth. The pattern of secondary thickenings in the sclereids and the shape



■ **Fig. 19.7** **a**, **b** Bean (*Phaseolus vulgaris*) seed coat. **a** The seed coat is composed of an outer layer of columnar macrosclereids and an inner layer of osteosclereids. **b** Polarized light reveals the lignin of the outer layer and prismatic calcium oxalate crystals within the cells of the inner layer. Scale bar = 50 µm. (**a**, **b** RR Wise)

of sclereids themselves in the supporting layers of the seed coat vary greatly and are taxon-specific. In different plants, the transformation of the integumentary parenchyma into seed coat sclerenchyma may occur in different cell layers. The presence of one or more layers of calcium oxalate crystal-containing cells is also a frequent phenomenon (■ Fig. 19.7a, b).

One of the roles for the seed coat is to keep water out and prevent premature germination. But it must be able to allow the seed to dry down upon maturity and enter the desiccated, dormant stage. Thus, water must have a path to exit the seed and not reenter. The **hilum** serves that function in legumes. The hilum is the scar left by the attachment of the seed to the **funiculus**, the strand of vasculature that supplies the seed with water and food reserves for storage. It is typically dark colored and is represented by the "eye" of black-eyed peas. In legumes, the hilum is also a one-way valve that opens in dry air and shuts in the presence of water thus letting the seed dry down when conditions allow, but not reabsorb water upon hydration. When the seed is exposed to dry air, the thick-walled cells of the hilum shrink and open the pore of the hilum (■ Fig. 19.7c). Water within the seed collects in patch of vasculature just underneath the hilum pore (■ Fig. 19.7d) and exits the seed. If the air is humid, the thick-walled cells swell and close the pore so that no water can enter. Thus, water is lost from the seed in dry air, but no water can enter the seed in humid air. Constant exposure to water, such as in wet spring soils, combined with overwintering breakdown of the seed coat in other areas allows water to enter the seed and initiate germination.

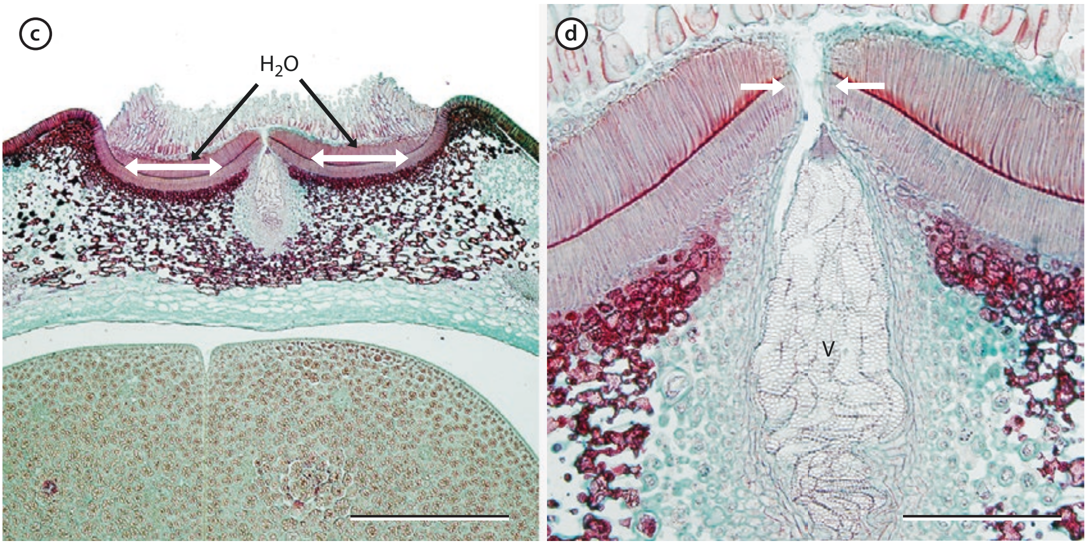


Fig. 19.7 **c**, **d** The bean (*Phaseolus vulgaris*) hilum is composed of a ring of thick-walled cells with an underlying patch of conducting vessel elements. **c** Upon exposure to water or high humidity, the cells of the ring swell and expand in the lateral direction (double-headed white arrows). This expansion closes the pore in the hilum and water cannot enter the seed. **d** Water from the seed collects in the vasculature (V) just inside the hilum pore and readily escapes when the pore is open. Scale bars = 500 µm in **c** and 100 µm in **d**. (**c**, **d** RR Wise)

In some species, the cells of the outer layer of the seed coat may become heavily modified in other ways. The seed coat of lily secretes a conspicuous amount of slime at the terminal stage of seed development. When moistened, the slime becomes sticky and adheres to the soil. It may also facilitate seed dispersal by protecting the embryo as the seed passes through the gut of animals. The mucilaginous seed coat of mistletoe, a hemiparasitic plant, serves two purposes. It protects the seed during passage through a bird digestive system, and it adheres the seed to a tree branch when it is passed by the bird. The seed can then germinate directly on a potential host. The seed coat of cotton (*Gossypium* sp.) is covered with long trichomes composed of almost pure cellulose, a valuable fiber used for textiles for over 8000 years. Other seed coats may have hooks or grapples to attach to animal dispersers.

During desiccation of seeds at the final stage of their ripening, the seed surface relief, or micromorphology, acquires a characteristic pattern that is stable and taxon-specific (Fig. 19.5e–j). Therefore, scanning electron microscope studies of seed surface have proved to be of great importance in solving taxonomic problems. Among the characters that may determine taxon-specific seed surface patterns are the cellular arrangement, the shape of cells, the outline (straight, lobed, or irregularly curved) of their anticlinal walls, the surface relief of their outer periclinal walls, the sculptures of the cuticle and epicuticular waxes, etc.

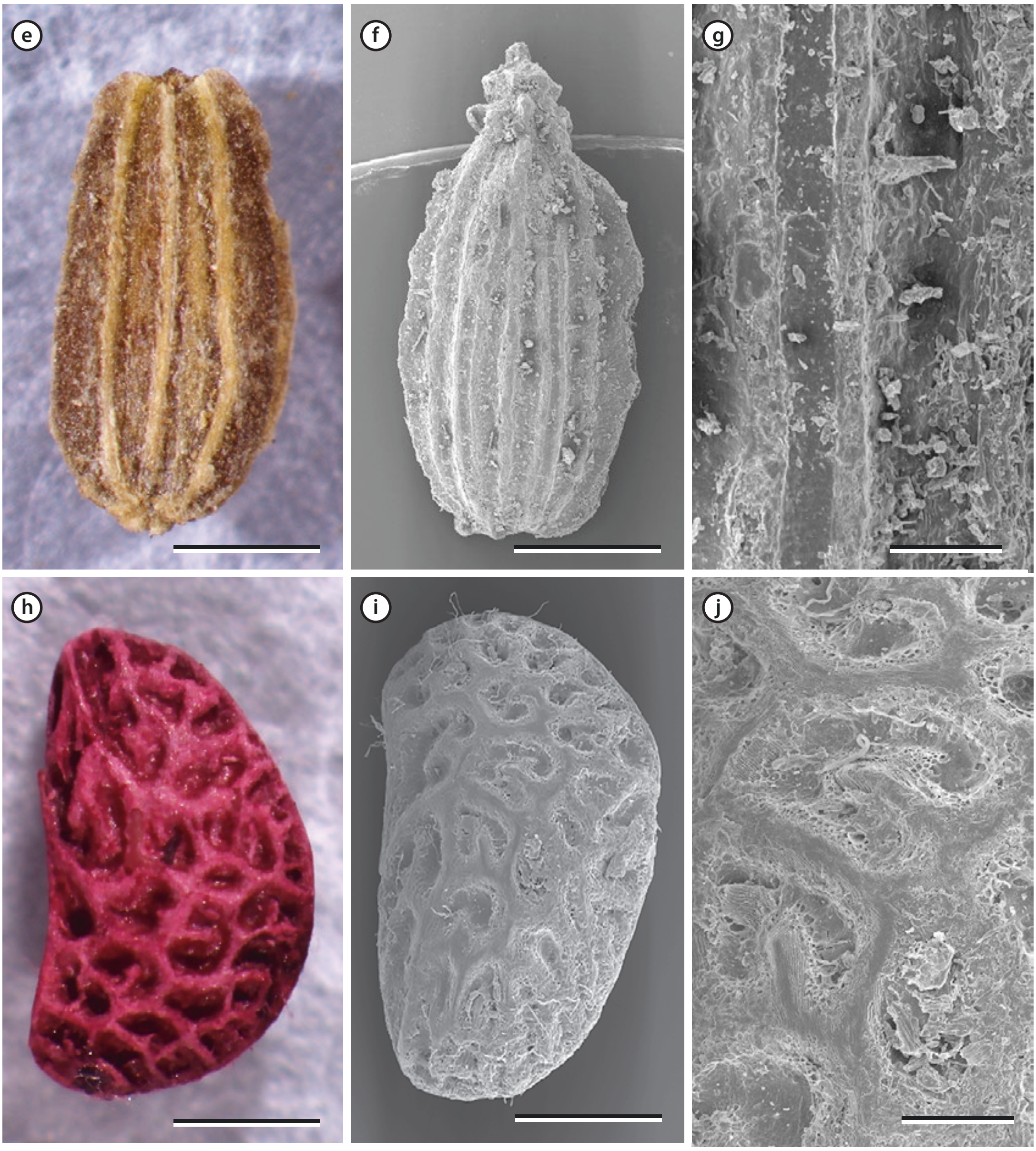


Fig. 19.7 **e**–**j** Mature seeds of carrot (*Daucus carota*—top row) and black raspberry (*Rubus occidentalis*, bottom row). Scale bars = 1 mm in **e**, **f**, **h**, and **i** and 250 μm in **g** and **j**. (**e**–**j** RR Wise)

Box 19.1 Insights from Nature—Adhesive Fruits and Hook and Loop Fasteners

Plants have inspired technological advances in some surprising ways. Perhaps the one that impacts most of us is "hook and loop" or Velcro-like fasteners that were invented in 1941. These fasteners are used in clothing, shoes, and hanging pictures, just to name a few. The inspiration for these fasteners is linked with burdock, an angiosperm with adhesive fruits (Saunders 2015). The hooklike structures on fruits assist in seed dispersal, to move the embryo away from conspecifics to limit competition and disease transmission, but also tend to get caught on clothing when walking through the woods and other habitats.

The physical structure of adhesive fruits can vary in terms of density of hooks as well as in physical characteristics such as length and width of hooks, leading to differences in the behavior of hooks. The force needed to remove fruits with hooks varies with sizes and shapes (Gorb and Gorb 2002). Further research reinforced the earlier discovery that the small hooks of *Galium aparine* had a larger load at contact separation than a larger hooked species, *Circaea lutetiana*. Thus, *G. aparine* could hold more force before separation from a substrate than *C. lutetiana*. Additional tests of hook behavior among several species showed that longer hook length and hook spans yielded more displacement of the hook from its initial position. These data may provide insight into new designs of hook and loop fasteners than what we currently use today (Chen et al. 2013).

References: Chen et al. (2013), Gorb and Gorb (2002), Saunders (2015)

19.8 Germination of the Seed Occurs when Environmental Conditions Are Appropriate and Marks the "Birth" of the Individual Plant

After the exposure of a desiccated dormant seed to favorable conditions, e.g., appropriate soil moisture, temperature, and aeration, it usually germinates. Germination is preceded by the absorption of large amounts of water. The imbibition of seeds is, as a rule, accompanied by the rupture of the seed coat usually at the micropylar end of the seed. The mobilization of food reserves coincides with water absorption. Water-soluble products of hydrolysis are transported to the activated apical meristems. First, the radicle elongates; the root appears out of the micropyle and starts its downward growth into the soil. The root develops root hairs and, frequently, lateral roots. Only after this do the other organs of the embryo start to emerge. The absorptional activity of the emerging root helps to assure the young seedling has an adequate supply of water and mineral nutrients when the shoot breaks through the surface of the soil.

During germination in some eudicots, the cotyledons, together with the incipient shoot apex, emerge above ground due to the intercalary growth of the hypocotyl, which pushes the first internode (to which the cotyledons are attached) above the soil surface. In such **epigeal** (above ground) germination, the cotyledons unfold, turn green, and become the first photosynthesizing organs of the seedling (◘ Fig. 19.8a). In other eudicots, the cotyledons, which are thick and rich in food reserves, remain within the seed coat under-

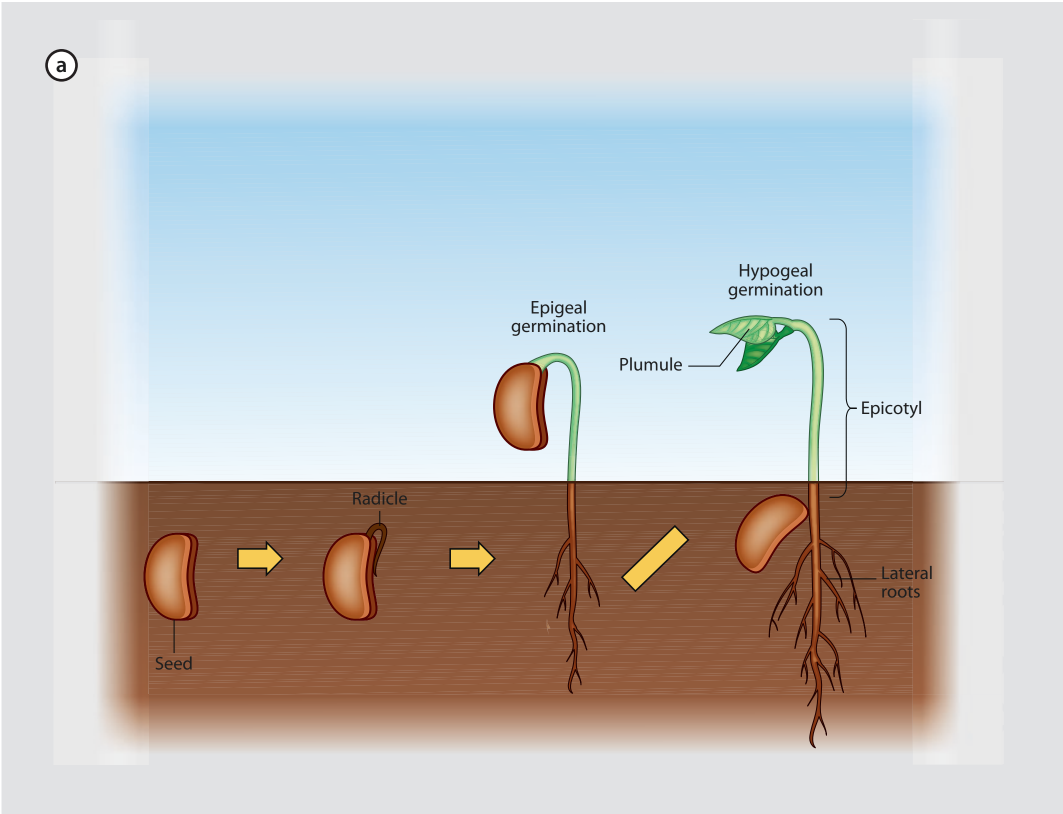


Fig. 19.8 **a** Epigeal and hypogeal germination. Both hypogeal and epigeal germination in eudicotyledons are shown in this figure. The first two images are the same for both processes. The embryo germinates and the radicle (immature root) emerges and grows downward. The third image shows epigeal germination in which the cotyledons are pushed out of the soil by growth of the hypocotyl. The fourth image shows hypogeal germination in which the cotyledons remain below the soil surface while growth of the epicotyl pushes the plumule out of the soil. (Redrawn from Begoon, CC BY-SA 3.0)

ground. In this **hypogeal** (below ground) germination, the shoot apical meristem is pushed through the soil surface by the elongating epicotyl (the internode between the cotyledons and the immature leaves) and the first photosynthesizing organs of the seedling are the leaves. This collection of immature leaves is called the plumule. As the leaves unfold, the stem portions between them elongate into internodes, new leaves emerge from each node, and, thus, the shoot system is established. The embryonic root develops into the primary root of the seedling. The primary root produces lateral (branch) roots that are called secondary roots. As a result, the root system is initiated, and the young sporophyte becomes established.

In contrast to eudicots, during epigeal germination in some monocots such as onion, the hypocotyl is not involved in breaking the seedling out of the soil. In onion, for example, this process occurs due to intercalary growth of the single cotyledon. The cotyledon expands unevenly and bends, forming a so-called hook that facilitates penetration through the soil surface. The apical portion of the cotyledon inside the seed coat does not grow, but the aboveground portion turns green and continues to elongate. This creates a force that causes the

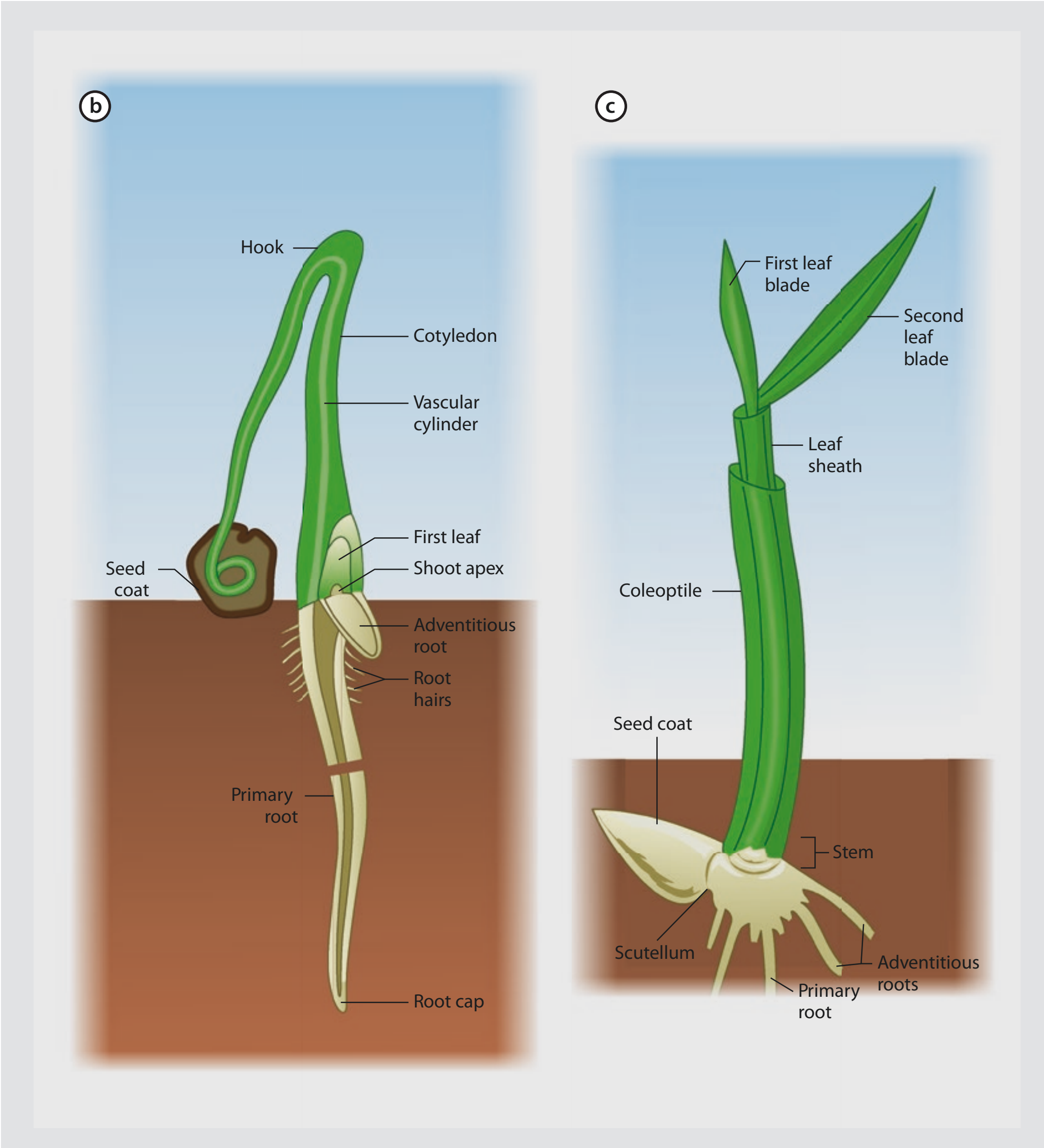


Fig. 19.8 **b**, **c** Epigeal germination and seedling structure in onion (*Allium cepa*), a monocot. Note that the seed will be above soil level as germination progresses. **c** Hypogeal germination in a typical grass. Note that the grain (seed) remains in the soil during germination. (Redrawn from Crang and Vassilyev 2003)

seed coat to be pulled out of the soil (Fig. 19.8b). In other monocots, such as grasses, germination is hypogeal since the grain with the enclosed cotyledon (scutellum) remains in the soil (Fig. 19.8c). At the onset of germination, the root and coleoptile elongate and break out of the grain. Intercalary growth pushes the coleoptile out from the soil and it subsequently becomes green. Adventitious roots then begin to emerge from the primary root. The first and subsequent leaves of the incipient shoot grow inside the coleoptile, and sheaths of the preceding leaves emerge into the light from the seedling by a type of telescopic intercalary growth.

Box 19.2 Trigger for Seed Germination in *Arabidopsis*

It is generally recognized that seeds need an appropriate temperature in order to germinate. However, breaking dormancy is not quite as simple as providing the proper temperature alone as has been documented by Topham et al. (2017). Studies at the University of Birmingham, UK, and the University of Toronto, Canada, reveal that in *Arabidopsis thaliana* seeds, plant growth regulators abscisic acid (ABA) and gibberellin (GA) together create a bistable developmental switch required to process temperature inputs to break dormancy. Of particular interest has been the fact that both ABA and GA were found to occur within distinct cell types. While alternating signals of temperature and light are recognized triggers to break dormancy, the sites of plant growth regulators appear to trigger phytochrome B to accept temperature induction for seed germination. Thus, the co-functioning of temperature and light may have ecological and adaptive consequences in seed plants.

Reference: Topham et al. (2017)

19.9 Chapter Review

Concept Review

19.1 *Fruits are highly modified ovaries***.** The fruit is a specialized tissue found only in angiosperms. It is an expansion of the ovary wall called the pericarp. The fruit/pericarp has three layers—exocarp on the outside, mesocarp in the middle, and endocarp to the interior.

19.2 *Fruit classification is based on characters, not necessarily species relatedness***.** Fruits are classified on the basis of pericarp texture, dry vs. fleshy, whether or not seeds are released upon maturation of the fruit (dehiscent vs. indehiscent), the number of carpels per fruit, and the nature of the individual pericarp layers (papery, hard, fleshy, stringy).

19.3 *Dry fruits are often hard, containing fused pericarp layers and dead cells***.** Dry fruits have a hard or papery pericarp. Indehiscent fruits do not release seeds and include the achene, caryopsis, samara, and nut. Dehiscent fruits release seeds when mature. They include the follicle, legume, and capsule.

19.4 *Fleshy fruits are characterized by an enlarged, juicy pericarp***.** Fleshy fruits have an enlarged, mostly parenchymatous pericarp used for photosynthesis or storage. Drupes have a papery exocarp, a fleshy or stringy mesocarp, and a thick, hard endocarp (peach, coconut). Berries are similar except that the endocarp is fleshy (grape, banana). Pepos are like berries (fleshy meso- and endocarp), except the exocarp is a hard, thick rind (cucumber, pumpkin). A hesperidium (typical of citrus) has an oily exocarp or rind, a spongy air-filled mesocarp, and a papery endocarp. The locules are full of juice sacs. The flesh of a pome (apple, pear) is composed mostly of an expanded and tasty hypanthium (floral tube).

19.5 *Fruit structure can include aggregations of flowers into one fruit or many small fruits within a larger assembly***.** Aggregate fruits are a collection of individual fruits from a single, multi-carpel flower. The fruit may be achenes (as in strawberry), follicles (some magnolias), or drupes (blackberry). A multiple fruit is one in which the individual fruits of multiple flowers are fused together. Pineapple is a good example.

19.6 *The seed is an individual plant containing nutrition for the embryo***.** The seed contains an embryo, food reserves, and a seed coat. Food reserves in gymnosperm seeds are derived from gametophytic tissue. Eudicots store reserves either in the endosperm or in the two cotyledons. Monocots store food in the endosperm and absorb the mobilized reserves through the single cotyledon (scutellum).

19.7 *The seed coat surrounds the embryo and storage tissues***.** The seed coat is derived from the integument of the ovule. Its main functions are to allow desiccation of the developing seed yet prevent water uptake until the time is right for germination. The seed coat typically is composed of one to several layers of sclereids and is impregnated with tannins or calcium oxalate crystals.

19.8 *Germination of the seed occurs when environmental conditions are appropriate and marks the "birth" of the individual plant***.** Upon germination, the seed imbibes water, and the embryo "wakes up," begins breaking down the food reserves, and begins growth of the radicle. In hypogeal germination, the cotyledons remain below ground, and only the primary leaves emerge from the soil. In epigeal germination, the cotyledons are pushed above the soil surface, expand, and become green and photosynthetic.

■ Concept Connections

1. In the picture below, identify
   - a–d. the seedling organs.
   - e. the type of germination.
   - f. whether it is a monocot or a eudicot.

■ **Concept Assessment**

2. A pericarp is derived from
   a. integuments.
   b. endosperm.
   c. ovule wall.
   d. ovary wall.
   e. placenta.

3. What kind of plant would most likely have a hesperidium?
   a. oak.
   b. lime.
   c. maple.
   d. watermelon.
   e. strawberry.

4. In the classification of fruit, the primary division is based upon
   a. dry vs. fleshy.
   b. dehiscent vs. non-dehiscent.
   c. superior vs. inferior ovary.
   d. one carpel vs. multiple carpels.
   e. one seed vs. multiple seeds.

5. Which is true of hypogeal germination?
   a. a hypocotyl arch is formed.
   b. the cotyledons remain below the soil.
   c. a cotyledon arch is formed.

d. the primary shoot tip is first to emerge from soil.
e. it is characteristic of eudicots.

6. In a pome, a large part of the fruit is derived from the floral tube or hypanthium.
   a. true.
   b. false.

7. An example of a dry, dehiscent fruit is
   a. pome.
   b. nut.
   c. samara.
   d. berry.
   e. legume.

8. In monocots, the embryonic root is covered by a(n)
   a. hypodermis.
   b. scutellum.
   c. coleorhiza.
   d. endosperm.
   e. foliage leaf.

9. The fruit of a cucumber is termed a(n)
   a. hesperidium.
   b. drupe.
   c. achene.
   d. pepo.
   e. caryopsis.

10. In the formation of a fruit, the style, perianth, and androecium generally
    a. become the seed coat.
    b. are parts of the floral tube for fruit development.
    c. represent the pedicel.
    d. dry up and abscise.
    e. become part of the pericarp.

11. The "wing" of a maple seed is an outgrowth of the pericarp.
    a. true.
    b. false.

Concept Applications

12. Tomatoes (fruit type = berries) have a *very* interesting history. Research and write a minute paper on one of the following topics:
    a. In 1893, the US Supreme Court (Nix vs. Hedden) issued the decision that tomatoes are vegetables, in spite of the fact they are clearly fruits. What was the rationale behind this SCOTUS decision?
    b. Tomatoes were once considered by Europeans to be poisonous. Why?

   c. For almost 200 years, the Latin binomial for the tomato was *Lycopersicon esculentum*. Recently, that name was changed to *Solanum lycopersicum*. Research and explain why the change was made.

13. Compare and contrast the following terms:
   a. Aggregate vs. multiple fruits
   b. Drupes vs. achenes
   c. Epigeal vs. hypogeal germination

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