Periderm

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Introduction

On herbaceous plants, the epidermis is the outer protective covering of all portions of the plant—roots, shoots, and flowers (▶ Chap. 9). Thus, the epidermis is of primary origin. In contrast, the periderm and bark are of secondary origin and are found on the stems and roots of woody eudicot plants, gymnosperms, and, in a different form, in some monocots. In this chapter we will identify the origin, components, development, and characteristics of periderm, consider the structure and function of lenticels, and describe the nature and composition of the rhytidome in its various forms.

16.1 Periderm Comprises a Large Component of Bark and Adds a Protective Layer to Plants

Of all plant anatomical structures, the **periderm** seems to have the most, and the most difficult to master, terminology. With this in mind, ◘ Table 16.1 and ◘ Fig. 16.1a, b may help better define the

◘ **Table 16.1** Layers of the epidermis, periderm, and rhytidome, starting from the outside of a stem or root and moving inwards

Technical terminology	
Phellem (cork)	2° growth produced by the phellogen to the exterior; usually multiple cell layers
Phelloid cell	Phellem cells that do not contain suberin; scattered throughout the phellem; may be sclereids in some species
Phellogen	aka cork cambium; the 2° meristem that gives rise to phellem and phelloid cells to the exterior and phelloderm to the interior
Phelloderm	2° growth produced by the phellogen to the interior; usually one to a few cell layer
Periderm	Sum of the phellem, phelloid cells, phellogen, and phelloderm
Polyderm	A specialized, multilayered tissue found in some roots and rhizomes; dead outer layers, but with non-suberized inner layers of storage cells; found in a select group of plant families
Rhytidome	A (sometimes) thick accumulation of dead tissue found on mature stems and roots, mostly outer layers containing periderm (produced by the phellogen) and secondary phloem (produced by the vascular cambium); everything to the outside of the most recent phellogen; roughly equivalent to bark
Nontechnical terminology	
Bark	All of the tissues to the exterior of the secondary xylem or wood
Inner bark	Living tissues of the vascular cambium and phloem and periderm
Outer bark	All dead tissues to the exterior of the inner bark

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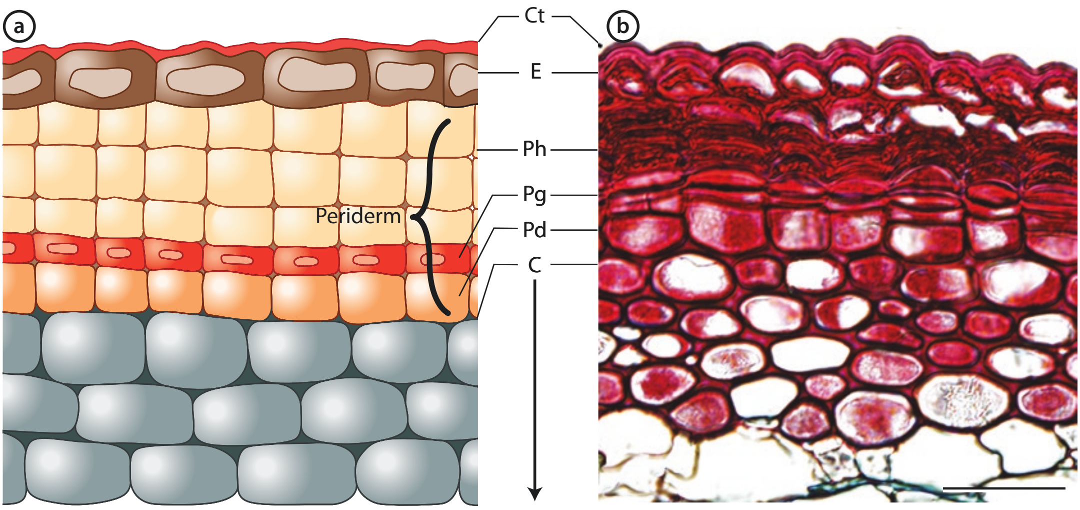


Fig. 16.1 **a** Drawing of epidermis, periderm, and cortical layers in a young stem. **b** A cross-section of a 1-year-old American basswood (*Tilia americana*) stem at the outer surface. The cuticle (Ct) and epidermis (E) have not been shed yet but will when the periderm has fully developed. The phellem (Ph) is composed of heavily suberized and partially collapsed cork cells. The phellogen (Pg) is meristematic and shows periclinal divisions, producing phellem to the exterior and phelloderm to the interior. The phelloderm (Pd) is a single layer of large cells that align in a radial direction with the phellogen. The cells in the outer layer of the cortex (C) do not align with the phelloderm/phellogen but are becoming suberized. The large, innermost cortical cells are parenchymatous. Phelloid cells, located in the phellem when found, are not shown in either **a** or **b**. Scale bar in **b** = 25 µm (**a**, **b** RR Wise)

tissues and layers that make up the periderm and associated tissues. The structure and function of the individual layers will be discussed in detail in the following sections of this chapter.

All woody plants begin with primary growth and have an exterior covering at the initial stage of the **epidermis** (▶ Chap. 9) and, perhaps, a **hypodermis** (refer to ▶ Sect. 11.5). Upon the initiation of secondary growth, cells in the epidermis, cortex or secondary phloem of the stem (depending on the species and organ), or the pericycle of the root become meristematic and differentiate into a cambial zone called the **phellogen** (or **cork cambium**). The phellogen gives rise to **phellem** tissue (also called "cork") to the outside and **phelloderm** tissue to the inside (◘ Fig. 16.1b). The periderm proper is thus the sum of the phellem, phellogen, and (if present) phellogen (which is dead at maturity). **Bark** is a nontechnical term used for all tissues to the exterior of the xylem, regardless of their origin. This includes the periderm, cortex (if present), active phloem conducting elements of the current growing season, as well as previous season's crushed conducting elements and phloem fibers. Therefore, even though the phloem tissues are not generated by the phellogen, it is common to call all of the living tissues between the xylem and the phellogen the "inner bark" and the dead tissues to the exterior of the phellogen the "outer bark" (◘ Fig. 16.1b).

The periderm does not always form a continuous ring around a root or stem. Certain zones of the phellogen in the burning bush (aka winged wahoo) become extremely active and generate large extensions of cork off of the stem (◘ Fig. 16.1c, d). While the function of such extensions is unknown, from their appearance alone, it has been postulated that it may function as browse deterrents.

Fig. 16.1 **c**, **d** These photographs demonstrate corky "wings" of the burning bush (*Euonymus alatus*), a native of China that is widely used as a landscape plant. The wings result from localized activity of the phellogen along the longitudinal axis of the stem. Scale bars = 2 cm in **a** and 0.5 cm in **b** (**c**, **d** RR Wise)

Box 16.1 High-Tech Potato Periderm Assessment

Potato (*Solanum tuberosum*) is one of those most important and widely grown crops in the world, with over 420 million tons of the starchy, tuberous rhizome produced each year. The potato tuber has a thin, corky periderm which has multiple variations—smooth, rough (russeted), brown, red, purple, or yellow—and has been the subject of intensive study for over a century. Growth, harvesting, and subsequent handling can damage the tuber periderm and degrade the quality, storage, and marketability of the crop. Therefore, potatoes are subject to postharvest grading and sorting, processes that benefit from sophisticated automated inspection based on image capture and computer-assisted evaluation. Riza et al. (2017) have moved beyond simple video-based inspection methods and conducted research on validating the use of measuring diffuse light reflectance across the range of ultraviolet (UV) to visible light (vis) to near infrared (NIR). Their goal was to develop a technology capable of simultaneously detecting multiple periderm flaws such as the presence of soil clods on the tuber surface, mechanical damage, greening, and three forms of common scab lesion (CSL), clear CSL, superficial CSL, and deep

CSL. They found the most accurate results were obtained using detection at six different wavelengths and processing those images using a machine learning process (specifically, subspace discriminant classifier) to separate the periderm defects into different classes. The use of diffusive reflectance measurements at specific wavelengths, and the processing of those signals through a statistically based classification system, can identify each of the periderm defect types and may contribute to the development of automated systems for multiple defect discrimination.
Reference: Riza et al. (2017).

16.2 Phellogens Originate De Novo by Dedifferentiation of Existing Cells in the Epidermis, Cortex, Phloem, or Pericycle

Similar to the secondary vascular cambium (▶ Chap. 14), the phellogen is a lateral, cylindrical, meristematic tissue. However, it is different in that it is a temporary meristem and a new phellogen must differentiate each growing season. In contrast, the vascular cambium persists for the life of the plant. The phellogen is typically just one cell layer thick and usually bifacial in stems (producing new tissues to both the inside and outside—phellem and phelloderm) and unifacial in roots (producing new tissues only to the outside—phelloderm).

The stem phellogen originates when mature parenchyma cells in the epidermis, cortex, or phloem parenchyma dedifferentiate, i.e., revert to a meristematic state. Periclinal divisions are necessary to produce phellem to the exterior and phelloderm to the interior. When the phellogen is situated at or near the surface, it is called a **superficial phellogen**. Superficial phellogens may arise in the epidermis, as seen in pear fruit (◘ Fig. 16.2a), or in cortical cells just interior to the epidermis (◘ Fig. 16.2b). **Deep-seated** phellogens originate to the interior of the stem when phloem parenchyma cells dedifferentiate and become meristematic (◘ Fig. 16.2c, d). As the periderm develops, it will cut off the supply of water and nutrients to the cortex, fiber caps, and the external periderm, which will be shed (◘ Fig. 16.2e). Multiple phellogens may arise in a single growing season from epidermal, cortical, or phloem cells, and few survive until the next growing season. Woody perennials start with a superficial phellogen in their first year or two of growth (as in the sycamore seen in ◘ Fig. 16.2b) and then transition to developing deep-seated phellogens as layers of periderm encircle the stem and the original epidermis and cortex are shed.

In roots, the deep-seated periderm always arises in the pericycle through the process of dedifferentiation and redifferentiation of parenchymatous meristematic cells. As the phellogen produces phellem (◘ Fig. 16.2f), the endodermis, cortex, and rhizodermis that were the

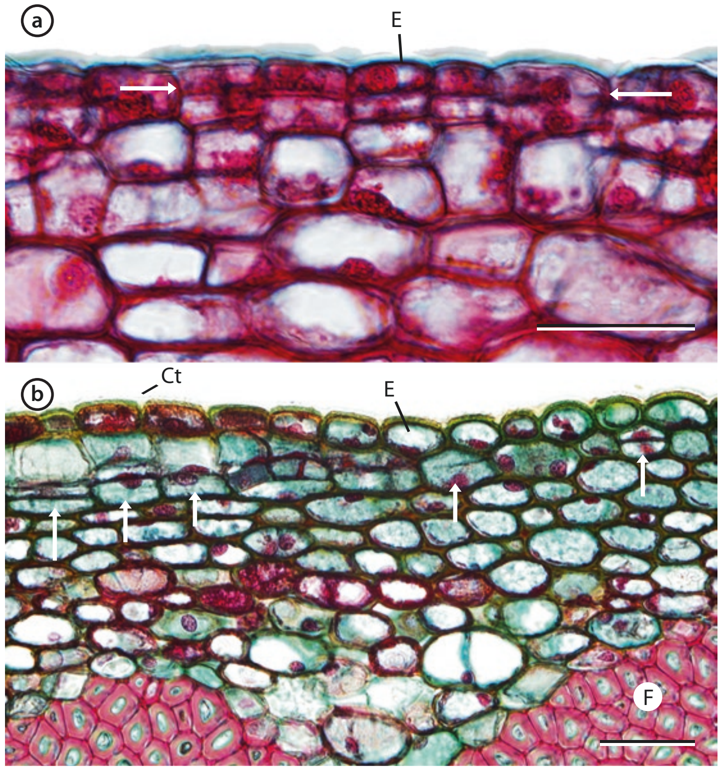


Fig. 16.2 **a**, **b** Superficial origin of the phellogen. **a** The phellogen of pear (*Pyrus communis*) fruit originates as periclinal divisions of the epidermal cells (E). Five pairs of epidermal/phellogen cells are shown between the two white arrows. **b** This 1-year-old sycamore (*Platanus occidentalis*) stem shows the phellogen originating as periclinal division of cells in the subepidermal cortex (white arrows). The cuticle (Ct) and epidermis (E) are still intact. The parenchymatous cortex lies between the phellogen and the large fibers (F) that cap the phloem (not shown). Scale bars = 20 µm in **a** and 25 µm in **b** (**a**, **b** RR Wise)

result of primary growth are shed (Figs. 10.9c and 16.2g). The development is primarily unifacial in cell production, and the derived cells typically lack intercellular spaces. Typically, the pericycle will develop a new phellogen every growing season, and the periderm will accumulate to seal off the root from the soil.

Box 16.2 Defense Components Found in the Periderm
Periderm replaces the epidermis early in tuber development, as in potato, and becomes the skin. In order to identify proteome factors (sets of proteins expressed by an organism) that may play a role in skin development and its defensive characteristics, proteins with high potentials were isolated and tested against biotic and abiotic stresses. High levels of patatin proteins (glycoproteins for storage and able to cleave fatty acids) were found in the young skins which exhibited antifungal resistance. It is believed that the skin may contain different isoforms of the proteins. The phelloderm (inner cell layers of the

periderm) contains high levels of glycoalkaloids which are toxic secondary metabolites active against a number of insect pests as well as pathogens. Periderm development is common among stems and roots of many seed plants and serves as a battery of defensive elements as the tissue increases in thickness by secondary growth as well as in lenticels and following wounding. Thus, the potato tuber skin may have functional implications for other periderm systems.
Reference: Barel and Ginzberg (2008).

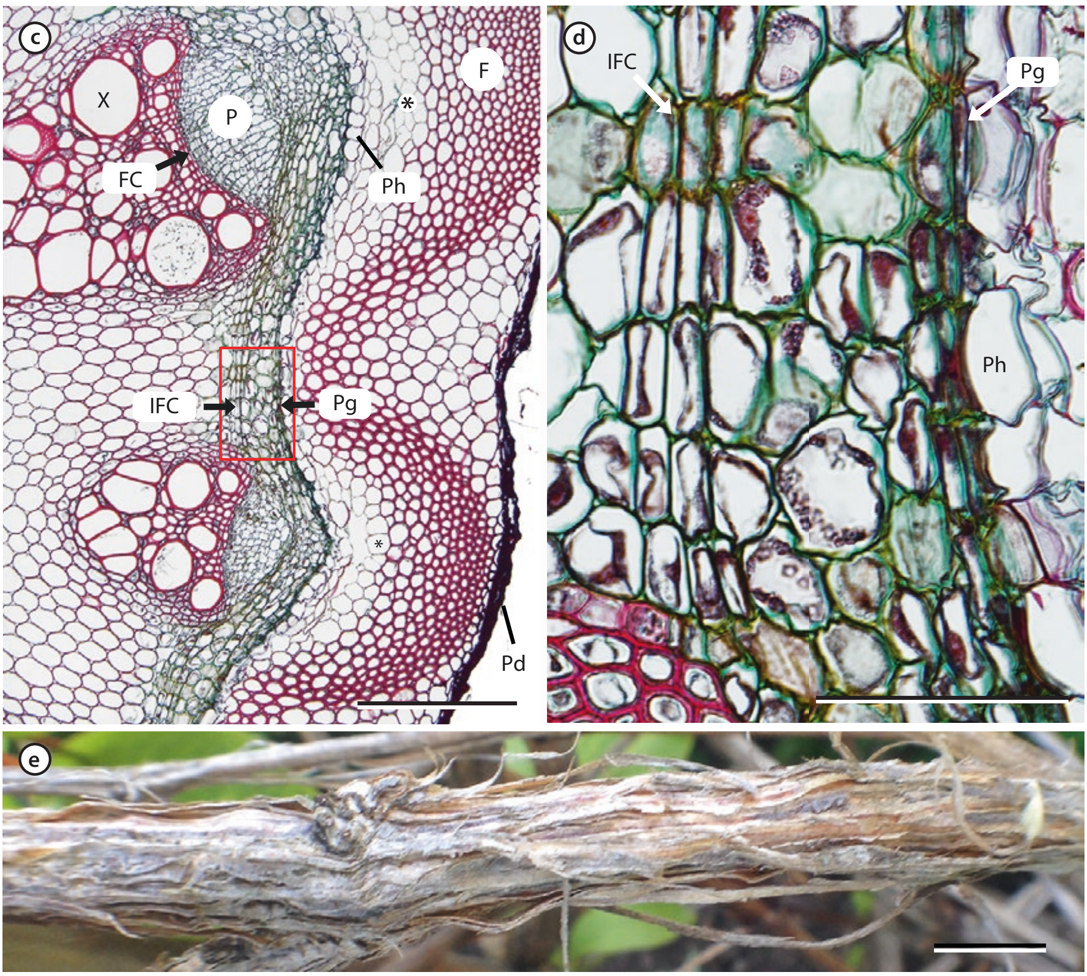
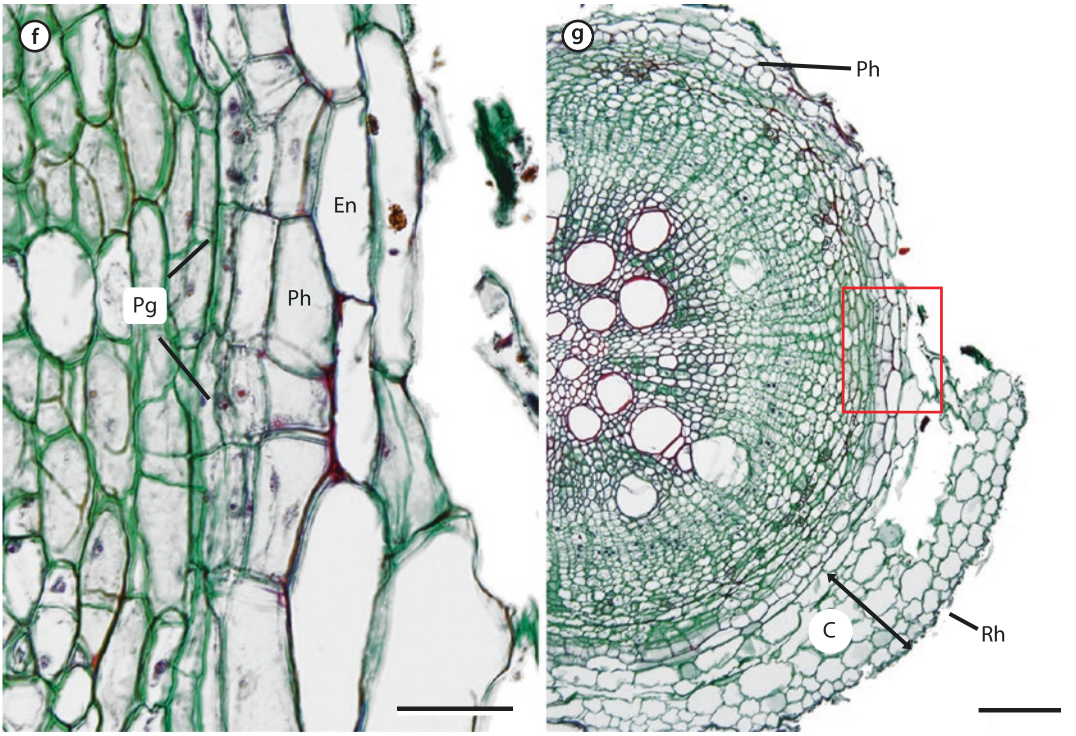


Fig. 16.2 **c–e** Deep-seated origin of the phellogen in a clematis (*Clematis* sp.) stem. **c** This low magnification view shows two vascular bundles containing xylem (X) and phloem (P) separated by a fascicular cambium (FC). Each bundle is capped by a group of fibers (F). An interfascicular cambium (IFC) has developed between the two bundles, and a phellogen (Pg) encircles the entire stem. Large phellem cells (Ph) are visible between the phloem and fibers toward the top of the image. Note how the parenchyma cells just interior to the fiber caps (labeled with *) show tearing. The original periderm (Pd) will be lost as the tissues to the exterior of the deep-seated phellogen mature. The red box indicates the area of **d**. **d** At a higher magnification, the early stage of development of the interfascicular cambium (IFC) and phellogen (Pg) can be seen. The IFC derivatives are still parenchymatous, not yet having matured into xylem (to the inside) or phloem (to the outside). The phellogen has produced a single layer of developing phellem (Ph) cells to the exterior. **e** Strips of periderm can be seen shedding off this 4-year-old *Clematis* stem. Scale bars = 100 µm in **c**, 50 µm in **d**, and 1 cm in **e** (**c**–**e** RR Wise)



◘ **Fig. 16.2** **f**, **g** Root phellogen initiation. **f** High magnification view of a castor bean (*Ricinus communis*) root pericycle at the start of periderm formation. The phellogen (Pg) has generated a few phellem cells (Ph) to the exterior, adjacent to the endodermis (En). **g** At a lower magnification, it can be seen that while portions of the original rhizodermis (Rh) and cortex (C) remain on this specimen, some has been shed. Short radial files of phellem cells (Ph) are evident in areas. Red rectangle indicates the area of ◘ Fig. 16.2f. Scale bars = 25 µm in **f** and 100 µm in **g** (**f**, **g** RR Wise)

16.3 Phellem Cells Are Suberized, Dead, and Generated to the Exterior of the Phellogen

Characteristically, phellem (cork) cells produced to the exterior of the phellogen have the same shape as their initials and are aligned in radial brick-like columns with no intercellular spaces (◘ Fig. 16.3a, b). The cell wall of cork cells contains suberin, a waxy protective substance that causes the cell to be impervious to water and gases. Upon functional maturity, cell death occurs accompanied by blockage of the plasmodesmata and emptying of the contents of cell lumens which are then filled with air, tannins, or resins. The elderberry phellem cells shown in ◘ Fig. 16.3a are mostly filled with tannins, while those of geranium (◘ Fig. 16.3b) are collapsed and air-filled.

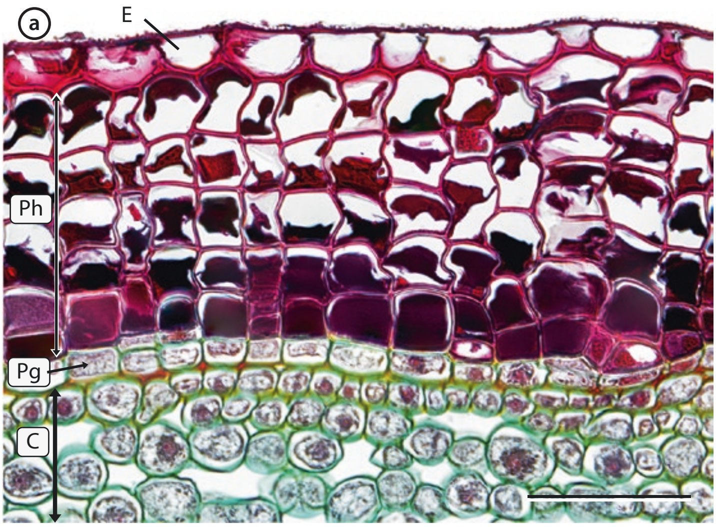


Fig. 16.3 **a** The periderm on this elderberry (*Sambucus* sp.) stem has one layer of epidermis (E), five to six layers of phellem (Ph) produced by the phellogen (Pg), and no phelloderm. Note the extensive suberization of the cell walls in both the epidermis and the periderm and lack of intercellular air space. Most of the phellem cells have extensive tannin deposits. Scale bar = 50 µm (RR Wise)

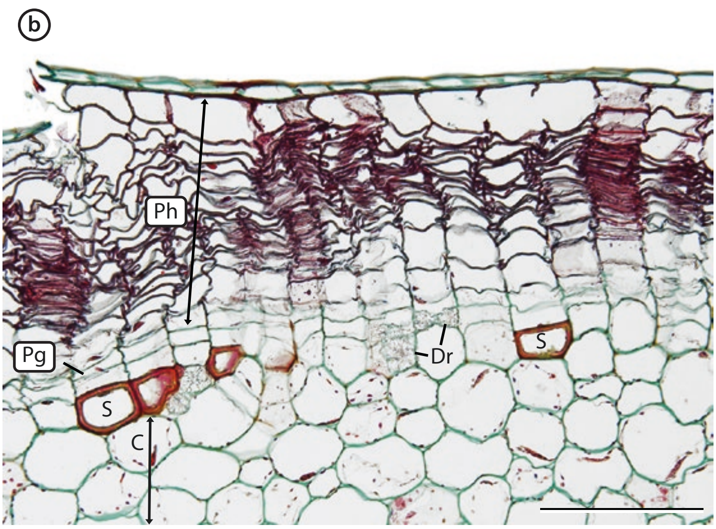
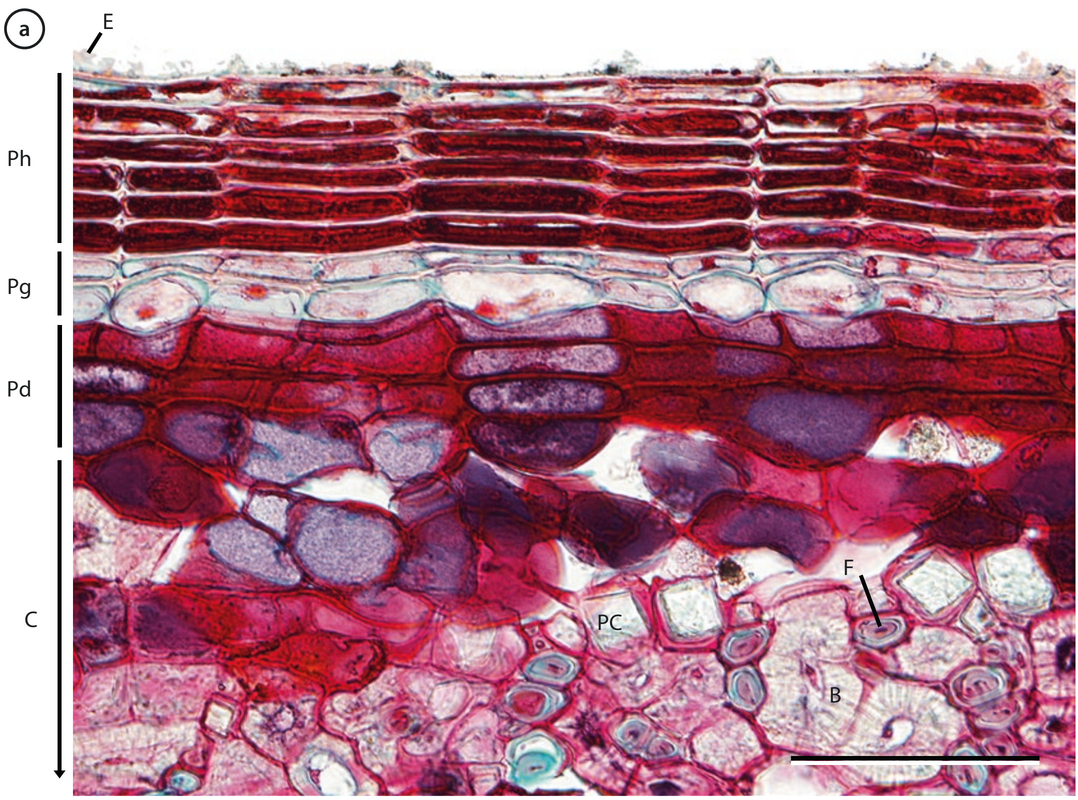


Fig. 16.3 **b** Phellem development in a geranium (*Pelargonium* sp.) stem. The phellogen (Pg) is loosely organized and not easily distinguished from the other layers. The phellem (Ph) cells are dead with the outer cells being crushed by the growth of the stem. Note that some of the phelloderm cells have developed in to sclereids (S), while others are filled with druse crystals (Dr). C cortex. Scale bar = 100 µm (RR Wise)

16.4 Phelloderm Cells Are Living and Generated to the Interior of the Phellogen

The phelloderm is a layer of parenchyma cells in the periderm generated by the phellogen toward the interior, opposite the phellem cell, and to the exterior of the cortex (◘ Fig. 16.4a). Not all species generate a phelloderm. The phelloderm is sometimes called a "secondary cortex" which reflects the overlap in function.

Phelloderm cells are shaped and arranged like phellogen cells but are larger and tend to be aligned in radial files that reflect their origin from the phellogen. They are parenchymatous, living cells at maturity and often are the sites of starch storage. Usually, the phellogen generates more phellem cells than phelloderm cells resulting in only one (refer back to ◘ Fig. 16.1b) to two or three layers of phelloderm (◘ Fig. 16.4a). However at sites where the phellogen is particularly active, such as where it underlies a lenticel, multiple layers of phelloderm may be produced (◘ Fig. 16.4b). Because they are living, phelloderm cells can undergo further development. Some mature into sclereids, while others may store starch or produce druse crystals (refer to ◘ Fig. 16.3b).



◘ **Fig. 16.4** **a** The phellogen (Pg) activity is directed primarily toward phellem (Ph) production to the exterior with smaller amounts of phelloderm (Pd) to the interior, as illustrated here for a 2-year-old tamarack (*Larix laricina*) stem. There are six layers of phellem and two to three layers of phelloderm. Remnants of the epidermis (E) can be seen at the stem surface. Note also the prismatic crystals (PC), fibers (F), and brachysclereids (B) in the cortex. Scale bar = 50 µm (RR Wise)

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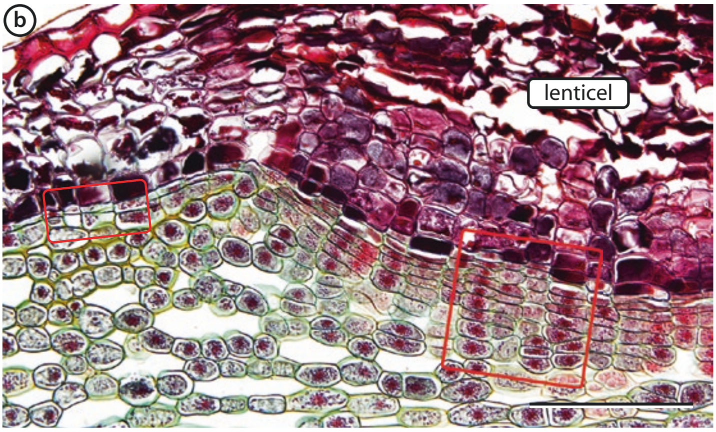

◘ Fig. 16.4 **b** In this elderberry (*Sambucus canadensis*) stem, the phelloderm is only one layer thick where there is no lenticel (*red box to left*) but up to six layers thick where it underlies a lenticel (*red box to right*). Scale bar = 100 µm (RR Wise)

16.5 The Polyderm Is an Internal Protective Tissue Composed of Alternating Rows of Suberized and Lignified Cells

A **polyderm** is, as its name implies, a multilayered cylinder of cells that serves as a bounding layer in or around stems and roots, being more common in the latter. It is composed of alternating layers of suberized and non-suberized cells (often, but not always, lignified). The polyderm is generated by the pericycle in roots, which explains its position to the interior of the endodermis in young roots of the wax apple (*Syzygium samarangense*, Myrtaceae) tree (◘ Fig. 16.5). A polyderm may have up to 20 layers, and, upon maturation of the root or stem, and loss of the cortex, it assumes the role of a periderm (Esau 1953). A polyderm may also develop in immature buds and serve as a barrier to fungal infection (Williamson 1984).

16.6 Lenticels Are Formed in Areas Where the Periderm Has Ruptured due to the Buildup of Filling Tissue, Facilitating Gas Exchange

Lenticels are interruptions within the periderm that extend through the phellem and allow for gas exchange between stems, roots, and fruits and the atmosphere (◘ Fig. 16.6a, b). Given that the periderm phellem cells are nearly impermeable to gasses and water, lenticels provide a means for gas exchange by providing openings in the periderm for carbon dioxide produced via cellular respiration to exit and for oxygen needed for mitochondrial respiration to enter.

Lenticels form in areas where the epidermis has ruptured (◘ Fig. 16.6c, d). The cork cambium beneath lenticels is more active, producing loosely arranged cells called **filling tissue** (◘ Fig. 16.6e–h). The area on stems containing the filling tissue often gives way to the

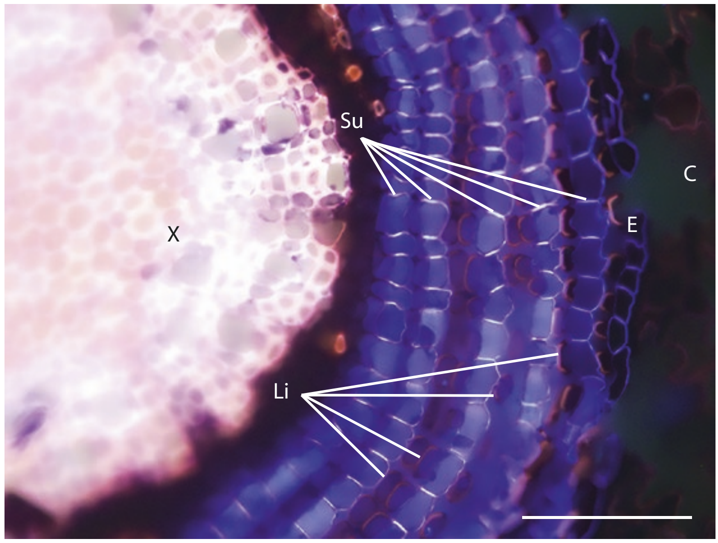

Fig. 16.5 A multilayered polyderm (P) developed in this young wax apple (*Syzygium samarangense*) root between the xylem (X) to the interior and the endodermis (E) to the exterior. The five suberized (Su) layers alternate with four lignified (Li) layers. The section was treated with a stain that fluoresces white in the presence of suberin and red in the presence of lignin. Scale bar = 100 µm. (A Tuladhar, Meijo University, Nagoya, Japan)

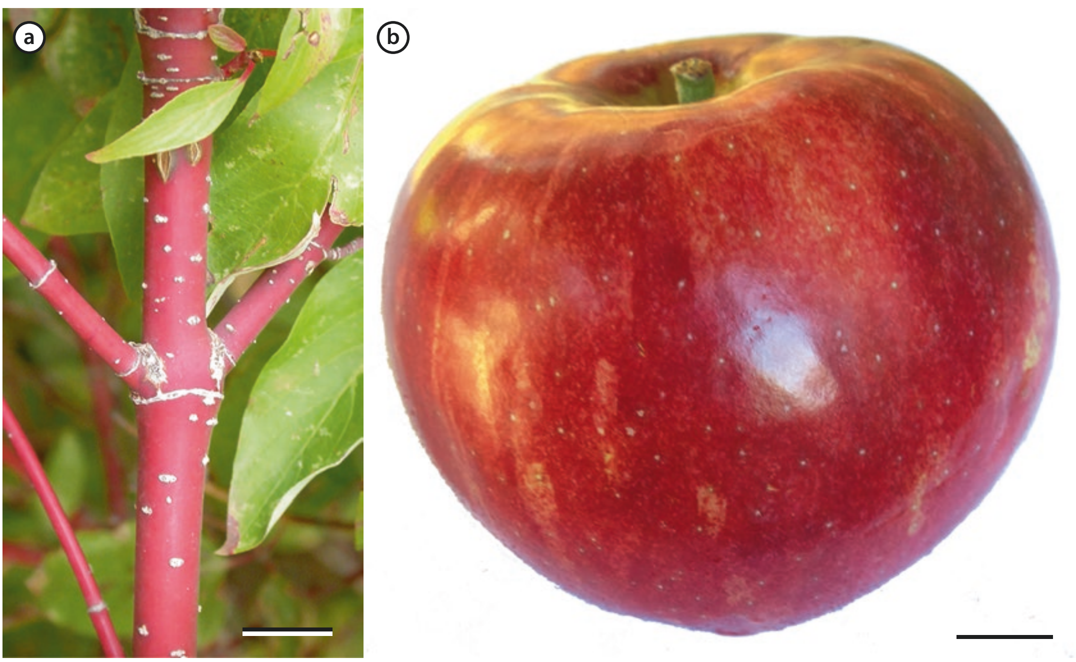

Fig. 16.6 **a** The outer morphology of lenticels is shown here in red osier dogwood (*Cornus sericea*). The lenticels are small and light colored. Their filling tissue is composed of very loosely arranged colorless cells with non-suberized cell walls. **b** Apples (fruit of *Malus domestica*) have extensive numbers of small, dot-like lenticels on the periderm surface. Scale bars = 1 cm (**a** Matt Lavin from Bozeman, Montana, USA, CC BY-SA 2.0; **b** S Lyons-Sobaski)

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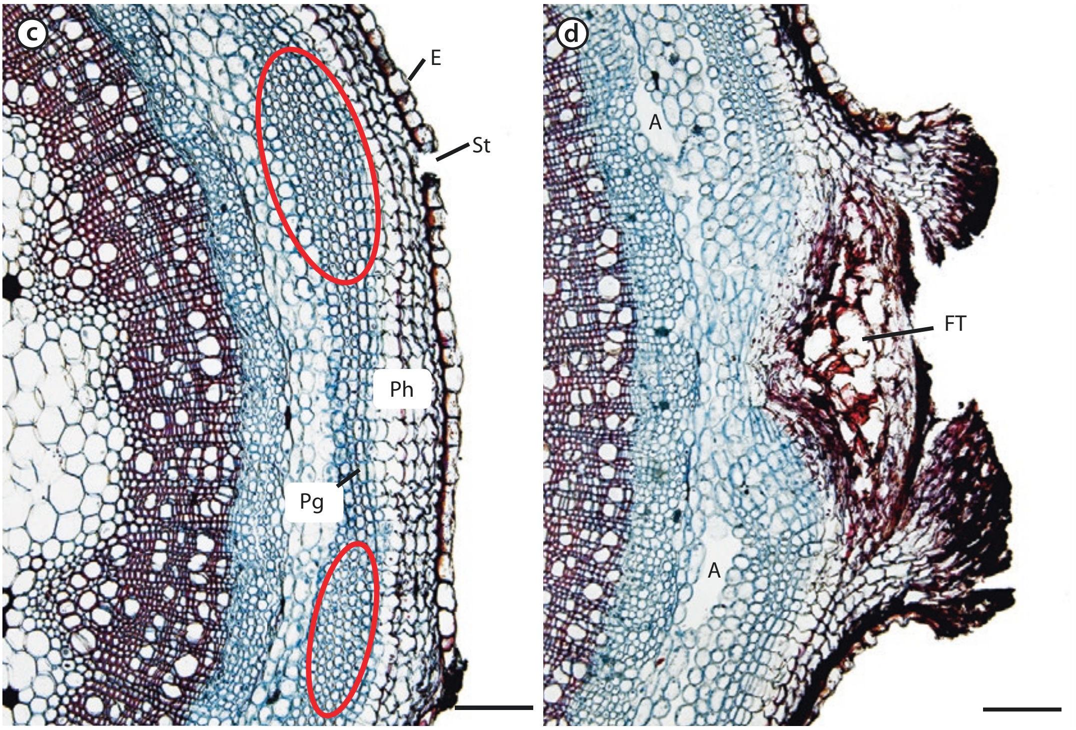


◘ **Fig. 16.6** Lenticel structure and development in elderberry (*Sambucus canadensis*) stem periderm. **c** Two lenticels are shown at an early stage of development. The lenticel toward the top of the image is apparent by the degradation of the stoma (St) and the proliferation of small parenchyma cells in the cortex (red ellipse). The lenticel to the bottom of the image is lightly more advanced. The phellem has started to push against the epidermis (E) and create a bump on the stem surface. Cortical parenchyma has proliferated (red ellipse). **d**. A mature lenticel has ruptured the stem surface and is composed of dead cells of the filling tissue. Air spaces (A) have developed in the cortex. Scale bars = 100 µm (**c**, **d** RR Wise)

pressure, and thus, the outer tissue ruptures forming the lenticel. It is common to see that lenticels have formed underneath stomata.

Lenticels get their name from the Latin term, "lens," due to the lens-like shape of these structures (Esau 1953). They are often used in species identification which may be especially helpful during winter months (◘ Fig. 16.6i, j). Lenticels are found in the periderm as long as it continues to grow; new lenticels will replace old ones. As the rhytidome is formed (see ► Sect. 16.7), lenticels become less active and usually blend into the corky tissue.

16.7 The Rhytidome Is a Multiyear, Multilayered Accumulation of Dead Tissues

The rhytidome is commonly called bark, although the two terms are not exactly synonymous. Bark is a nontechnical term for the thick, corky tissues on the outside of a plant, extending from the surface of the xylem (wood) to the surface of the stem or root. From an anatomical standpoint, there are multiple and different layers in bark. If you recall from earlier in the chapter, bark is made of both inner and outer bark. Inner bark extends from the cells immediately

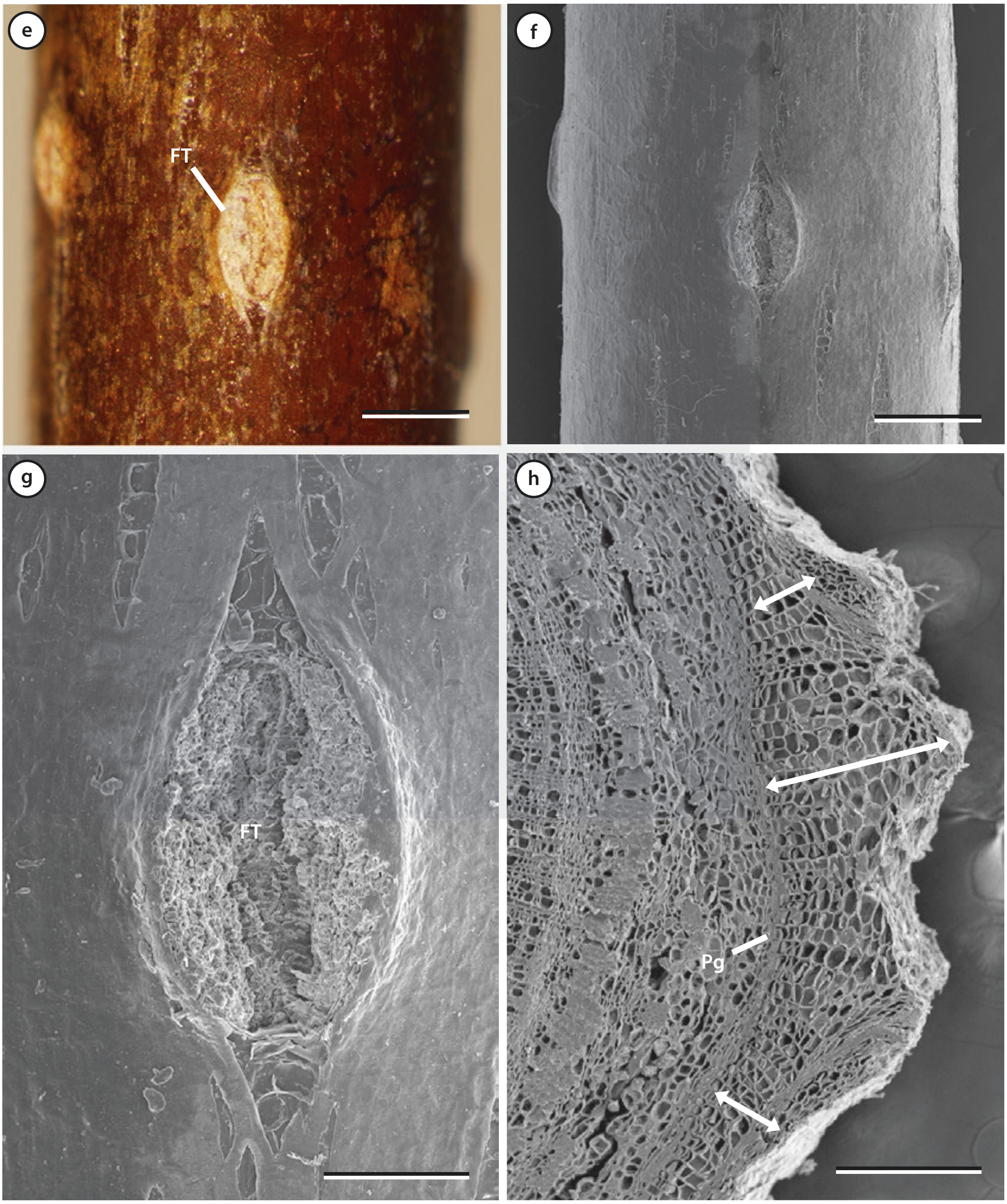


Fig. 16.6 **e**–**h** Four different views of lenticels on a young stem of a katsura tree (*Cercidiphyllum japonicum*). **e** Light macrograph showing the light color of the filling tissue (FT), as compared to the reddish bark. **f.** SEM of three lenticels, one in face view and two in side view. **g** SEM of filling tissue and the rupture in the epidermis and periderm caused by growth of the lenticel. Several smaller splits can be seen in the epidermis. **h** Cross-section SEM of a lenticel. The phellem of the filling tissue (*double-headed arrows*) extends from the phellogen (Pg) to the stem surface. Scale bars = 500 µm in **e** and **d** and 250 µm in **g** and **h** (**e**–**h** RR Wise)

Fig. 16.6 **i**, **j** Lenticels found in the surface of **i** white poplar (*Populus alba*) and **j** sweet cherry (*Prunus avium*). Scale bars = 2 cm (**i, j** RR Wise)

outside of the vascular cambium to the innermost cork cambium; thus, the inner bark extends from one secondary cambium to another secondary cambium (Fig. 16.7a). The rhytidome (rhytis = Greek for "wrinkle") is the outer bark; it is not wood because it is not made of secondary xylem tissue. It is composed of dead cells immediately external from the cork cambium to the outside of the stem or root. It includes the present year's phellem and any secondary phloem, crushed primary phloem, crushed cortex, prior periderms, and crushed epidermis from previous years. Given enough time, the rhytidome can become quite thick.

Figure 16.1a, b and most of the text in this chapter have described the development of a periderm during a single growing season in which a phellogen becomes active, produces phellem and (sometimes) phelloderm, and then dies. Superficial phellogens produce a periderm at the surface of the stem. Conversely, deep-seated phellogens in the stem and phellogens in the root produce a periderm inside the organ and to the exterior of the phloem (refer to Fig. 16.2c–g). Therefore, the periderm layers generated by those phellogens will cut off the supply of water and nutrients to any tissues to the exterior and they will die. Each growing season a new deep-seated phellogen arises and pushes the previous year's growth further outward. The accumulation of multiple years of periderms and the tissues they cut off (crushed phloem conducting elements and fibers) constitutes the rhytidome. Examples of the exterior and internal structure of the rhytidomes of several common tree species are given in Fig. 16.7b–i.

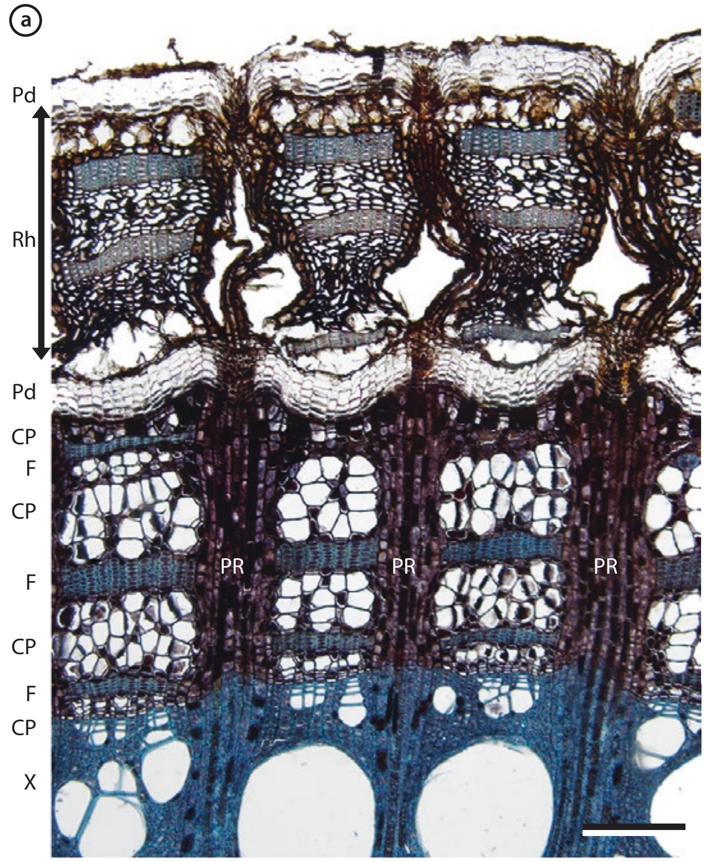


Fig. 16.7 **a** A cross-section of grape (*Vitis* sp.) rhytidome. Xylem (X) lies to the interior of the stem. Moving outward there are four layers of conducting phloem (CP) interspersed with three layers of phloem fibers (F). Those seven layers represent the phloem generated in the most recent year's growth. The vascular cambium (not shown) lies between the xylem and the first layer of conducting phloem. The periderm (Pd) appears in the form of colorless arches interrupted by narrow dark zones in which cork cells have pigmented contents. In the white zones, the phellogen was initiated in the secondary phloem axial parenchyma, while in the darker areas it originated in phloem rays (PR). The periderms are composed mostly of phellem cells. The zone of dead cells lying outside the innermost periderm is the rhytidome (Rh). This grape specimen only has one layer in its rhytidome. Scale bar = 100 µm (RR Wise)

16.8 Cork Is a Commercially Important Rhytidome

Cork is a portion of the bark from the cork oak tree (*Quercus suber*) indigenous to southern Spain, Portugal, and parts of northern Africa. The outer bark from the cork oak is sustainably harvested about every 9 years, leaving the inner bark intact, and thus, the trees may live to about 250 years old (Fig. 16.8a). From the cork, a number of commercial products are derived including bottle cork and stoppers, bulletin boards, dart board backers, flooring, fishing floats, insulation wall tiles, insulating hot pads and coasters, shoe wedges, and cork flooring among other products.

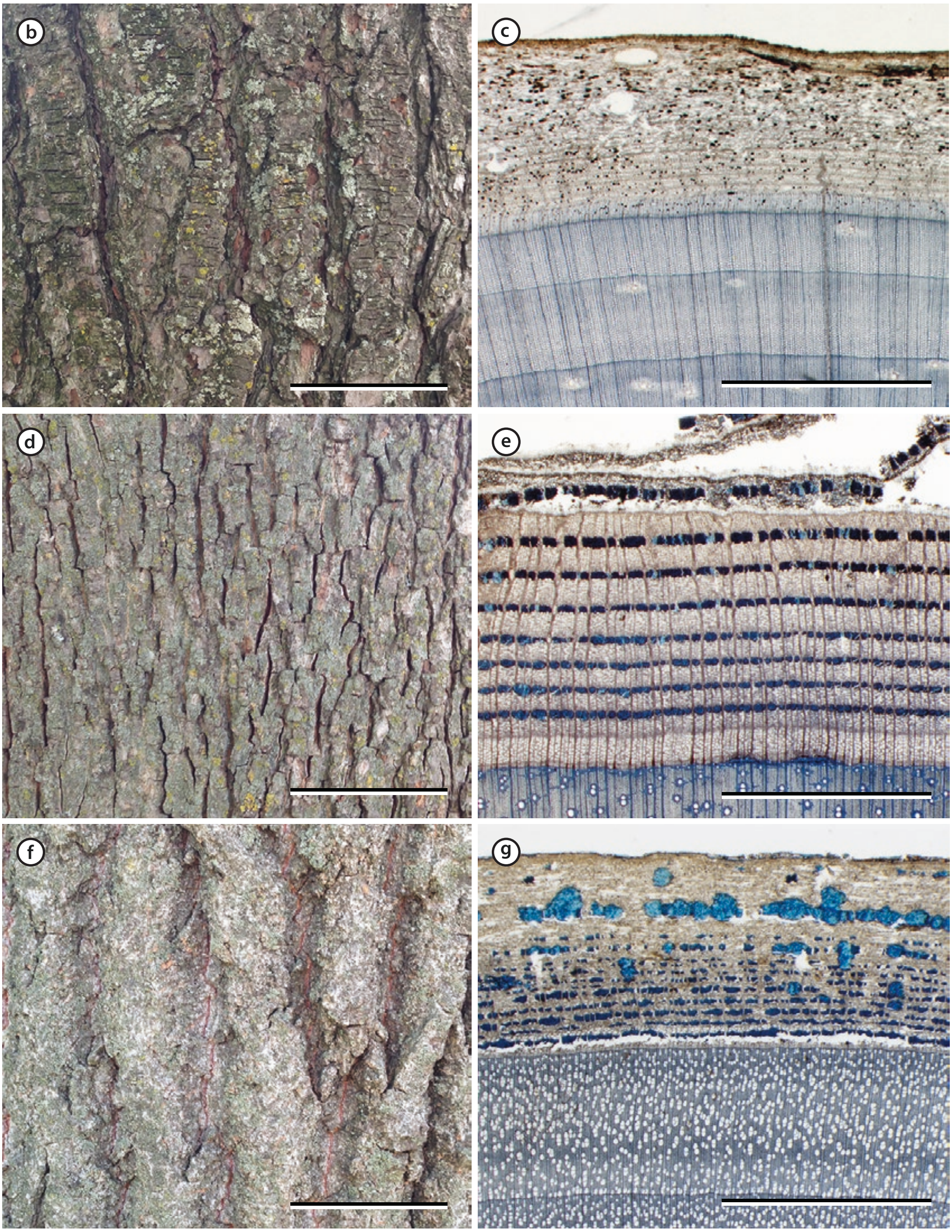


Fig. 16.7 **b**, **c** White pine (*Pinus strobus*), **d**, **e** green ash (*Fraxinus pennsylvanica*), **f**, **g** big-tooth aspen (*Populus grandidentata*), **h**, **i** white oak (*Quercus alba*). Scale bars = 5 cm in all left panels and 100 µm in all right panels (**b**–**i** RR Wise)

Cork cells are derived from phellogen initials and are developed in the radial direction. The tangential growth of the phellogen mother cell is reflected in the daughter cells. A highly suberized

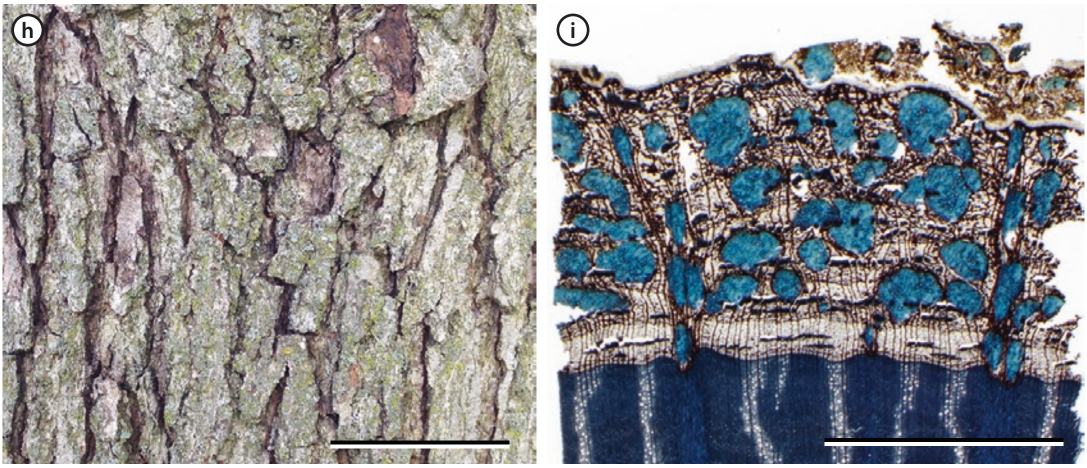


Fig. 16.7 (continued)

Fig. 16.8 **a** It requires manual skill, strength, and care to harvest the cork layer from the *Quercus suber* tree. With care, the cells grow back into new layers for harvesting about every 9 years. **b**. Individual layer of cork tissue showing the vertical extent of lenticel development as dark lines penetrating the homogeneous cork cells. (**a** Juan Carlos Cazalla Monijano, CC BY-SA 3.0; **b** Sallyofmayflower, CC BY-SA 3.0)

secondary wall is formed, and the cell contents are virtually devoid of cytoplasm and water, leaving only an air-filled lumen. The phellogen is functional during the growth months of the year and, in temperate zones, is not active during winter seasons. Thousands of cork cells can be found in a thin section of cork when viewed under the light microscope, and it was Robert Hook's famed observations of the compartmentalization of cork that gave rise to the name of "cells" as a unit of biological structure (refer to ► Chap. 2).

Cork has annual rings, although they may be difficult to always identify. While cork tissue is typically homogeneous in terms of cell types, lenticels interrupt the cork with cracks and irregular spaces brought about by the exchange passageways for air and other gasses (◘ Fig. 16.8b). The cells formed during the most active growth seasons are elongated in the radial axis with thin cell walls, while those formed in the end of the growth period are flattened radially with thicker walls. Cork development is promoted by periods of increased rainfall and higher temperatures.

16.9 Chapter Review

■ Concept Review

16.1 *Periderm comprises a large component of bark and adds a protective layer to plants.* The periderm is composed of a meristematic tissue called the phellogen that generates phellem cells to the exterior and phelloderm cells to the interior. The periderm is of secondary origin, and a new layer is generated each growing season.

16.2 *Phellogens originate de novo by dedifferentiation of existing cells in the epidermis, cortex, phloem, or pericycle.* The phellogen is a unique meristem—it does not persist from year to year and must arise anew via cellular dedifferentiation each growing season. Stem phellogens may arise in the epidermis or cortex (in younger stems; called superficial phellogens) or in the phloem (in older stems; called deep-seated phellogens). Root phellogens always arise in the pericycle.

16.3 *Phellem cells are suberized and dead at maturity.* Phellem cells are dead and their walls are heavily suberized. Therefore, they are impervious to water and gases. The cells themselves also contain air, tannins, or resins.

16.4 *Phelloderm cells are living cells generated to the interior of the phellogen.* Phelloderm cells are cork parenchyma. In contrast to the phellem, these cells are living and function in starch storage, contain calcium oxalate crystals, or develop into sclereids.

16.5 *The polyderm is an internal protective tissue composed of alternating rows of suberized and lignified cells.* This tissue type is not commonly found in many plants, but it plays a protective role in preventing fungal infections. It is usually restricted to the roots where it originates in the pericycle, interior to the endodermis.

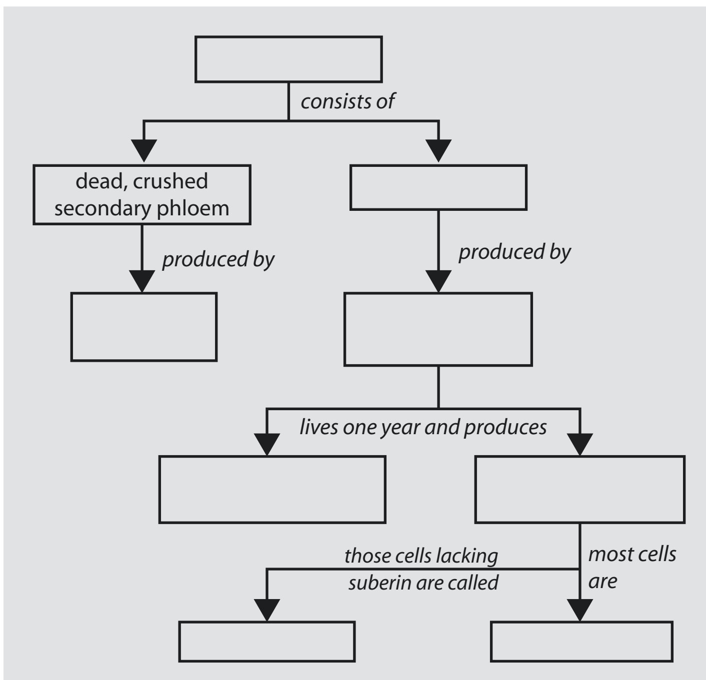
16.6 *Lenticels are formed in areas where the periderm has ruptured due to the buildup of filling tissue, facilitating gas exchange.* The periderm is impervious to gases and water. However, the living cells of the inner bark need oxygen to support respiration. Therefore, in certain localized areas, the phellogen will produce a large mass of phellem and phelloderm that pushes out and ruptures the surface of the stem or root, producing a structure called a lenticel. The lenticel is filled with loosely pack phellem cells that allow for the diffusion of O_2 into the stem or root and diffusion of CO_2 outward.

16.7 *The rhytidome is the outer bark and consists of dead cells.* Woody perennials generate a series of deep-seated phellogens over the course of their growth. The phellem and phelloderm produced by each successive phellogen cut off the living and dead tissues to the exterior. Over time, a multiyear, multilayered accumulation of dead periderms and phloem fibers accumulates at the stem or root surface. This is the rhytidome.

16.8 *Cork is a commercially important rhytidome.* Cork as an economic commodity is sustainably harvested from the cork oak tree (*Quercus suber*). Cork has a variety of applied uses as bottle stoppers, flooring, bulletin boards, and fishing floats to name a few.

Concept Connections

1. Use the following terms to complete the concept map below: cork cambium (phellogen), periderm, phelloderm to the inside (adaxial), phellem to the outside (abaxial), phelloid cells, rhytidome, suberized, vascular cambium.



Concept Assessment

2. From the perspective of a plant anatomist, the terms bark and periderm are synonyms.
   a. true; they refer to identical structures.

b. false; bark is made up of both living and nonliving components in contrast to periderm that is made up of only nonliving cells.
c. false; periderm is composed of the phellogen, secondary phloem, and vascular cambium only.
d. false; periderm contains the living cells of the cork cambium and nonliving cells of the cork; bark is more inclusive and also contains secondary phloem from the vascular cambium.
e. false; the periderm includes the vascular cambium and all the structures external from it whereas the bark does not include the vascular cambium.

? 3. Generally speaking, cork cells are impermeable to gasses and water because of
a. the presence of suberin.
b. air-filled cells in the lumen of the periderm.
c. the cork cambium.
d. the presence of sclereids in the cork tissue.
e. the presence of lenticels.

? 4. In stems, the development of periderm often starts
a. with the pericycle.
b. as a branching of the vascular cambium.
c. with the parenchyma cells differentiating into the cork cambium.
d. as epidermal cells that morph directly into cells of the outer bark.
e. both a and c.

? 5. Which of the following analogies is most appropriate?
a. periderm : phellogen :: phellem : phelloid cell.
b. phelloid cells : phellogen :: vascular cambium : cork cambium.
c. rhytidome : phloem :: phellem : phellogen.
d. phelloid cells : xylem :: polyderm: phellogen.
e. phellogen : phellem :: vascular cambium : phloem.

? 6. Where does the periderm begin development in root systems?
a. vascular cambium.
b. phellogen.
c. pericycle.
d. xylem.
e. phloem.

? 7. In the potato tuber, the periderm of the underground stem originates from the
a. pericycle.
b. epidermis.

c. starch-filled parenchyma cells.
d. vascular cambium.
e. secondary phloem.

8. The primary function of lenticels is to
   a. produce cork cells within the phellem.
   b. regulate the production of oxygen in the periderm.
   c. produce suberin and prevent oxygen from exiting the plant.
   d. allow for the exchange of gasses through an otherwise impermeable cell layers.
   e. form the rhytidome.

9. The cork that is harvested for cork products such as bottle stoppers, bulletin boards, and flooring is harvested from which plant species:
   a. *Robinia pseudoacacia.*
   b. *Betula pendula.*
   c. *Quercus alba.*
   d. *Tilia americana.*
   e. *Quercus suber.*

10. Why can cork be used as fishing bobbers/floats?
   a. because cork contains air-filled cells that allow the tissue to be buoyant in water.
   b. because the suberin present within the cells is less dense than water.
   c. because the suberin contained within the cells doesn't allow for water to enter cells.
   d. both a and c.
   e. all of the above.

11. Why are spaces and cracks found within cork?
   a. the spaces were caused by insects boring into the periderm.
   b. the spaces are lenticels and allow for gas exchange within the periderm.
   c. the spaces are caused by drought conditions causing disruptions in the periderm during the growing season.
   d. nutrient deficiency as the bark develops leads holes within the periderm.
   e. the spaces are the result of viral infections that occur commonly among many plant species.

16

Concept Applications

12. Explain why harvesting cork from cork oak trees is sustainable and doesn't lead to premature death of the tree. What if cork from a cork oak tree was overharvested? What would happen if the inner bark was removed? What if the secondary phloem was removed? Finally, explain what would happen if the vascular cambium was removed? What would be the fate of this tree following the three different scenarios and why? Explain.

13. Compare the role, and longevity, of the vascular cambium to the cork cambium (phellogen) in terms of their contributions to the rhytidome.

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