6. Primary, secondary and tertiary meristems

Definitions

Meristems initiate longitudinal growth on tips of shoots and roots of plant bodies. Meristematic tissues consist of living cells, which produce new cells.

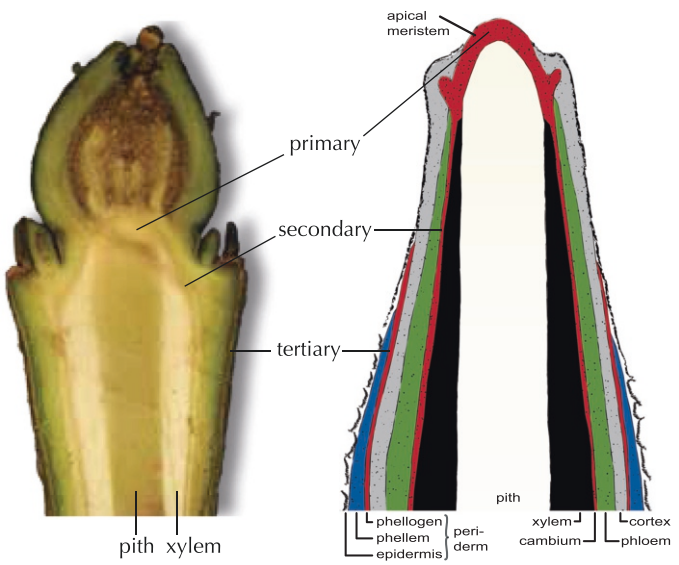
Primary meristems on shoot tips (apical meristems) are embryonic tissues, which originate from seeds. They produce the epidermis, the cortex, the leaves and the pith.

Secondary meristems originate from primary meristems and produce the xylem and phloem. The whole conducting system is called stele. The arrangement of vascular bundles within the central strand defines the type of stele. Protostele: one vascular bundle (mosses); plectostele, polystele: several vascular bundles in the center (lycopods); eustele: concentrically arranged isolated or laterally connected vascular bundles in a ring (most dicotyledons). The term stele is used here only as an anatomical characteristic, not in relation to evolutionary stages.

Tertiary meristems originate from parenchymatic tissues, which are located within xylem, phloem and cortex.

Structural variation in meristematic products will be discussed in the following chapters.

Location of meristems



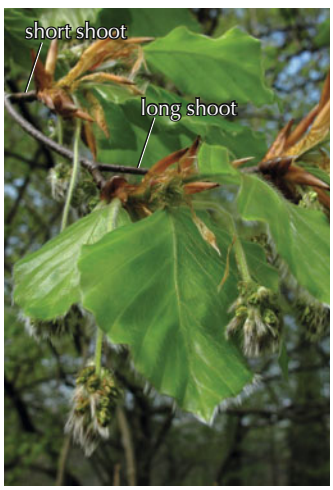
6.1 Left: Primary, secondary and tertiary meristems in a twig of *Fraxinus excelsior*. Right: Schematic representation of primary, secondary and tertiary meristems. Reprinted from Schweingruber *et al.* 2008.

Production rates

Production rates and proportions between shoot length, diameters and number of cells within the pith, xylem, phloem, cortex and phellem vary greatly. Most obvious are differences in the xylem (product of the cambium) and the product of the primary and secondary meristems (cortex, phloem, phellem).

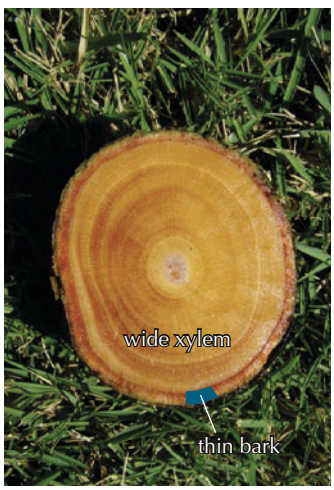
Long and short shoots

6.2 Short shoots on a long shoot of the conifer *Larix decidua*.



6.3 Short and long shoots in *Fagus sylvatica*.

Proportions of xylem, phloem, cortex and phellem

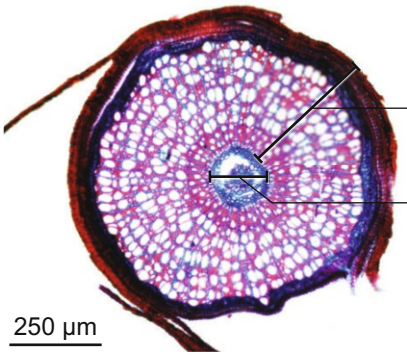


6.4 Xylem to bark proportion of 10:1 in the mangrove *Rhizophora mangle*.

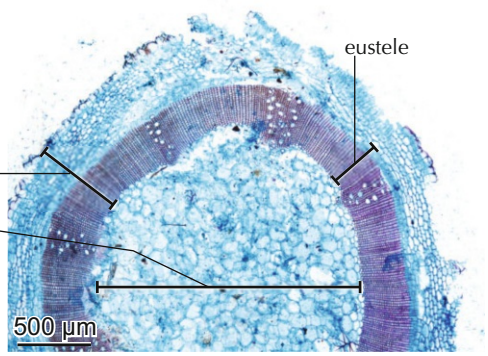
6.5 Xylem to bark proportion of 2:1 in a young stem of *Quercus suber* (cork oak).

F. H. Schweingruber, A. Börner, *The Plant Stem*, https://doi.org/10.1007/978-3-319-73524-5_6

Small and large pith

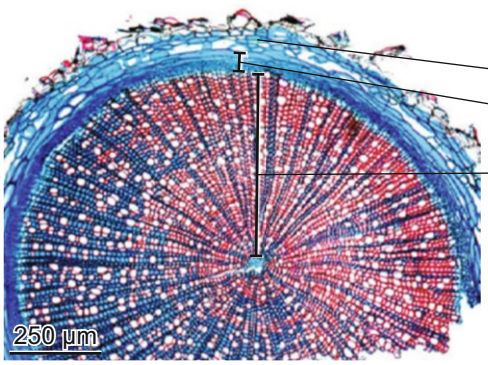


6.6 Herb with a small pith. Pith to xylem and bark proportion of 1:6 in *Schistophyllidium bifurcum*.

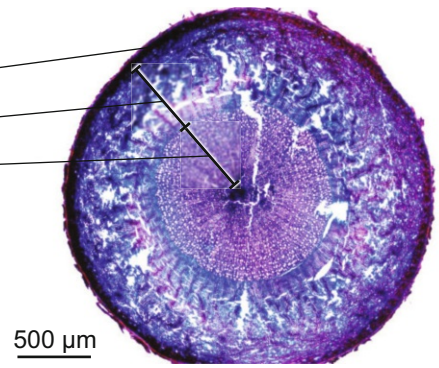


6.7 Herb with a large pith. Pith to xylem and bark proportion of 1:0.3 in *Impatiens macroptera*.

Small and large phloem

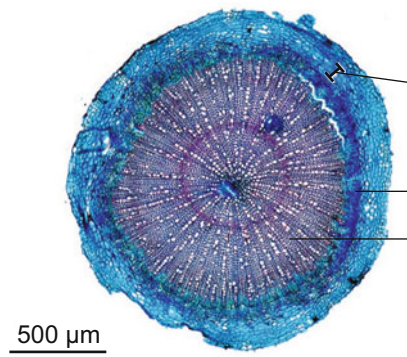


6.8 Herb with a small phloem. Phloem to xylem proportion of 1:10 in *Linum bienne*.

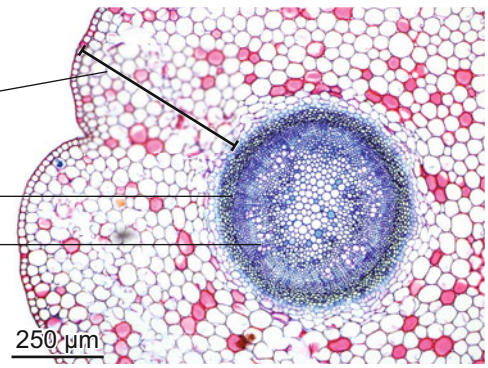


6.9 Herb with a large phloem. Phloem to xylem proportion of 1:1 in *Draba cachartena*.

Small and large cortex

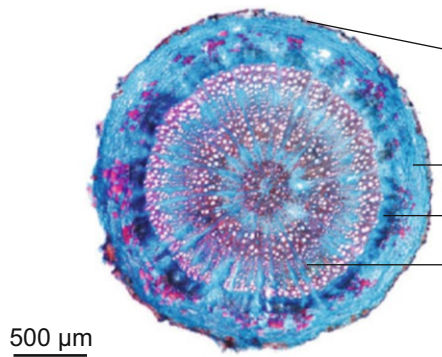


6.10 Herb with a small cortex. Cortex to phloem proportion of 1:1 in *Bupleurum bladensis*.

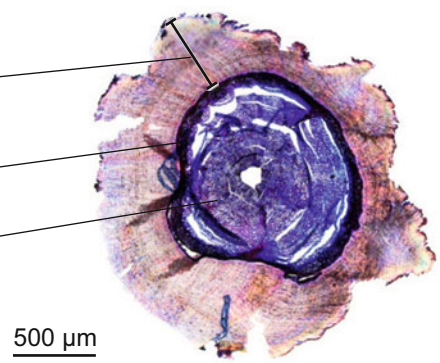


6.11 Herb with a large cortex. Cortex to phloem proportion of 8:1 in *Honkenia peploides*.

Small and large phellem



6.12 Herb with a small phellem. Phellem to phloem and cortex proportion of 1:5 in *Thesium arvense*.



6.13 Herb with a large phellem. Phellem to phloem and cortex proportion of 4:1 in *Saxifraga oppositifolia*.

6.1 Primary meristems in apical zones – Initials of longitudinal and radial growth

6.1.1 Macroscopic aspect of primary meristems in apical shoots and roots – Grow higher, grow deeper

The origin of primary meristems is in the seed and all meristematic derivates in apical zones are also primary meristems. As soon as the seed germinates, the germs divide into a root and a shoot. Apical meristems occur on roots and shoots, on the primary as well as on all adventitious shoots and roots. In dormant as well as in active periods apical meristems in roots are not protected by buds but often wrapped in a mantel of hyphae (mycorrhiza).

Apical meristems occur in mosses and in all vascular annual and perennial plants.

Apical meristems in shoots first form stems with leaves. These meristems often change their mode and also form flowers and fruits (see also Chapter 10, Fig. 10.1).

Apical meristems on shoots and roots

6.14 *Castanea sativa* seedling with a primary shoot and primary root.

6.15 *Carpinus betulus* seedling with primary apical meristems.

6.16 *Lonicera xylosteum* sapling with apical meristems on shoots and roots.

6.17 Adult grass *Festuca rupestris* with apical meristems in the root zone.

6.18 Moss *Polytrichum commune* with apical meristems on shoots. Rhizoides are covered by mycorrhiza.

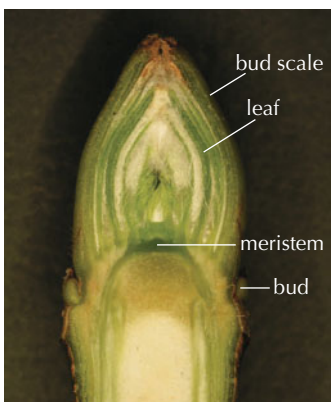
Apical meristems on adventitious shoots

6.19 Injured stem of *Taxus baccata* with adventitious shoots, which contain apical meristems.

6.20 Adventitious shoot on a *Fagus sylvatica* stem.

Apical meristems in buds

6.21 Terminal shoot of *Acer pseudoplatanus* with a terminal bud and two adventitious buds.



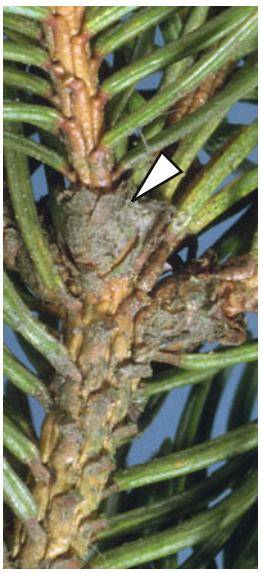
6.22 Terminal shoot of *Acer pseudoplatanus* with an apical meristem wrapped in undeveloped leaves and bud scales.

6.1.2 Apical shoot dynamics – Long and short shoots – Grow fast, grow slow

The aspect of plants is determined by the position of buds, the formation of long and short shoots, and the growth and death dynamic of apical meristems in shoots. The past activity of apical meristems on shoots can be determined by ***bud scale scars***. They are overgrown wounds of deleted bud scales after leaf flushing. The terms short and long shoot are vaguely defined.

Internodes between bud scale scars indicate an extreme ***variability of longitudinal growth***. The long distances between bud scale scars, e.g. in long shoots, make it easy to ***determine the age*** of twigs. Short distances, or indiscernible bud scale scars at the outside of shoots (e.g. short shoots) hinder macroscopic age determination of shoots. However, microscopic age determination is possible with remaining ***pith bridges*** in the position of bud scale scars. ***Ring counting*** in short shoots is normally not reliable.

Macroscopic aspect of bud scale scars and short shoots



6.23 Bud scales in *Picea abies*.

6.24 Short shoots in *Pinus mugo*.

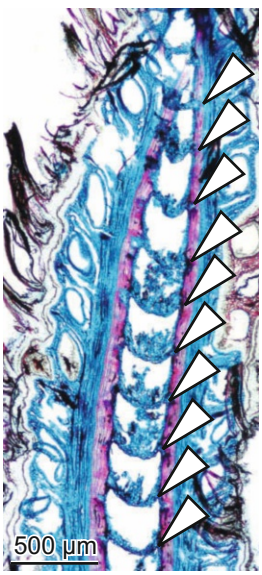
6.25 Bud scale scars in *Pinus mugo*.

6.26 Bud scale scar in *Quercus robur*.

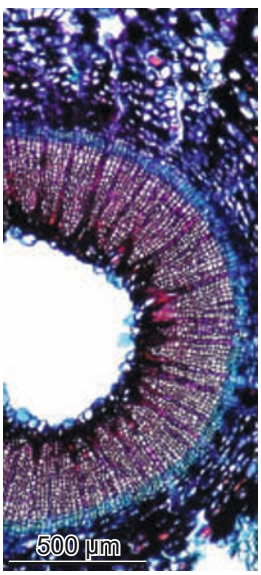
6.27 Rhizome with short shoots and shoot scars in *Polygonum officinale*.

External and internal delimitations of short shoots

6.28 Short shoots in *Larix decidua*.

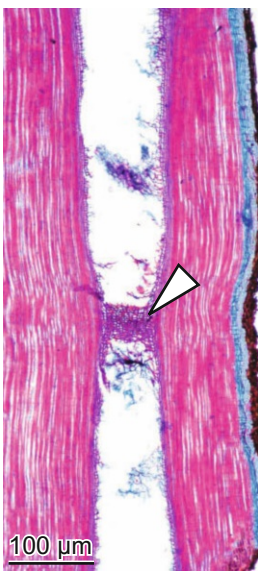


6.29 Longitudinal section of a short shoot with annual bridges in the pith of *Larix decidua*.



6.30 Cross section of *Larix decidua* short shoot. Annual rings are absent.

6.31 Shoots of the arctic dwarf shrub *Cassiope tetragona*.



6.32 Annual latewood bridge in the latewood of a shoot of *Cassiope tetragona*.

6.1.3 Shoot death and metamorphosis – The end of longitudinal growth: Twigs must die

Normal shoot formation happens in a period of two to four weeks (e.g. in *Quercus*) or lasts for the whole vegetation period (e.g. in *Populus*). However, the life span of shoots varies between one and more than 1,000 years.

Very soon after the formation of twigs, the ***self pruning*** process starts. The majority of twigs die and drop after a few years. Only a few dominating shoots remain on the plant for the whole lifetime on the individual. The survivors develop into branches and stems and form the crowns of trees, shrubs and herbs. The crown form is a result of selective death of twigs and branches. The principal stem is the winner of an extensive programmed dying process.

Twig shedding, also called twig abscission or cladaptosis, occurs principally in three forms:

a) Twigs dry out, get affected by fungi and drop even due to slight mechanical disturbances. This is the most common type of twig shedding.
b) The shedding zone is not anatomically visible, but the strength is reduced near the base of the twig in *Salix*. The twig drops before it dries out.
c) The shedding zones are anatomically predetermined in *Quercus* and *Populus*. This shedding mechanism is expressed by dramatic anatomical change between the remaining and discarded part and the breaking zone.

The most common shoot transformation (metamorphosis) is the change from the vegetative to the generative form; from shoot to flower formation.

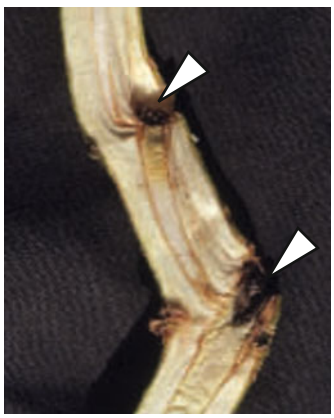
Very common is the transformation of shoots into thorns. In this case the apical meristem loses its replication capacity and changes its mode to an extensive growth of secondary walls.

Twigs die and drop

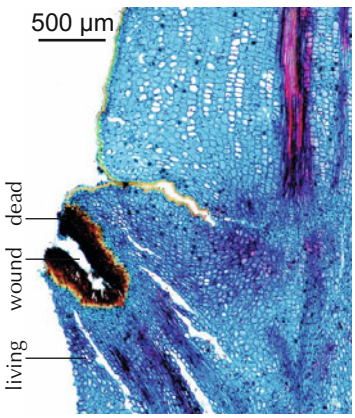
6.33 Twigs lose their vitality, die, get affected by fungi and break off. *Corylus avellana*.

6.34 Twigs break near the base at a predetermined mechanical weak zone in *Salix alba*.

Breaking zones compartmentalize

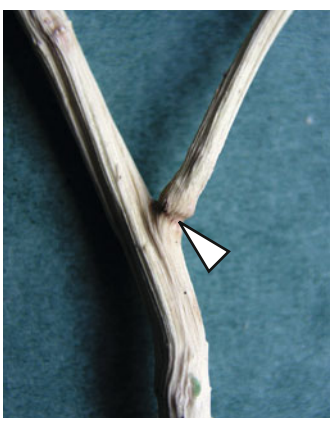


6.35 Compartmentalized wounds of broken twigs in *Fraxinus excelsior*.



6.36 Compartmentalized wound in *Viscum album*.

Macroscopic aspect of breaking zones



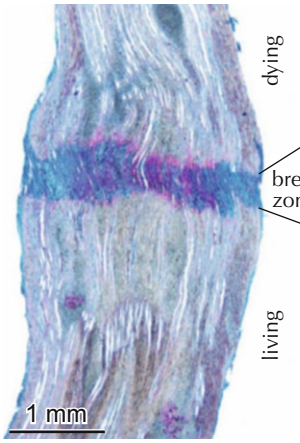
6.37 Predetermined breaking zone on a debarked twig of *Quercus robur*.

6.38 Scar of a broken twig in *Quercus robur*.

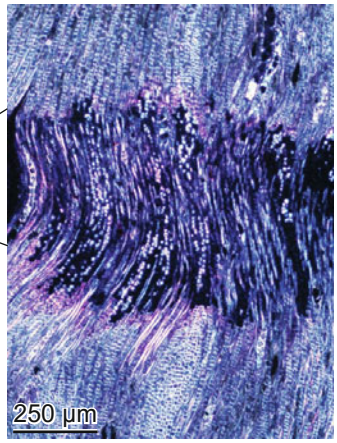
6.39 Shed twigs of *Quercus robur*.

6.40 Shed twig of *Gnetum gnemon*.

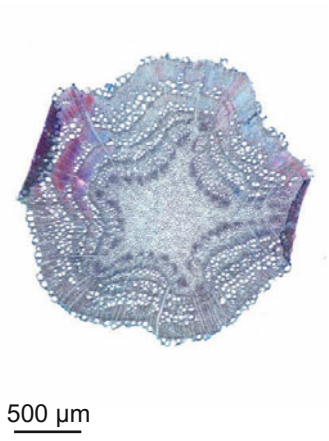
Microscopic aspect of breaking zones in Quercus robur



6.41 Longitudinal section through a breaking zone. It is characterized by a poor lignification (blue zone).



6.42 Breaking zone with numerous crystals, polarized light.



6.43 Anatomical structure below the breaking zone. This structure is typical for oak wood.

6.44 Anatomical structure of the breaking zone. This structure is very different from the basal twig and characterized by the absence of fibrous latewood and small vessels.

Transformations of apical meristem to flowers, fruits and thorns

Flowers on long shoots

6.45 *Carduus macrocephalus*

6.46 *Sempervivum wulfenii*

6.47 *Gentiana utricularia*

Flowers on long shoots, needles on short shoots

6.48 *Pinus mugo*

Flowers and fruits on short shoots

6.49 *Alnus viridis*

6.50 *Buxus sempervirens*

Thorns on long shoots

6.51 *Crataegus monogyna*

6.52 *Crataegus monogyna*

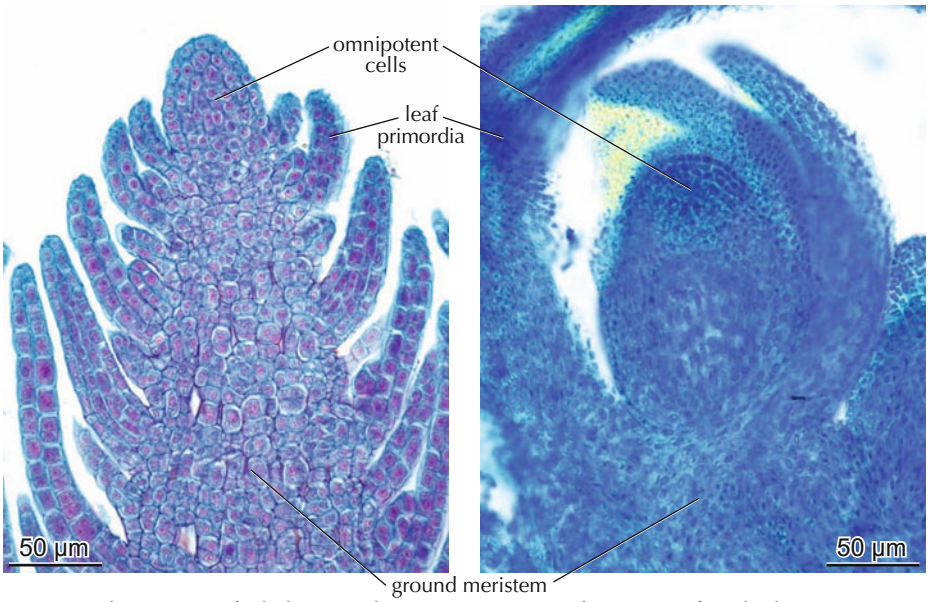
6.1.4 Microscopic aspect of apical meristems of shoots and roots – Towards heaven and earth

The principal differences between apical root and shoot growth are shown below. Differences and similarities between apical meristems in roots and shoots are obvious in microscopic sections. This is here demonstrated on some dicotyledonous and monocotyledonous species.

Omnipotent cells in the center of the shoot are common for the apex of roots and shoots. Bipolarity is also common, which means meristematic cells produce cells towards two axial directions: geocentric and heliocentric. Central cells of the roots produce the root cup, which determines the trajectory and protect the inner central cells. Root cup cells get sloughed off by abrasive soil particles. Central shoot cells primarily produce leafs, but also all parts of flowers.

The major difference between the two types is in the zone behind the tip. Soon after the first cell differentiation, the dicotyledonous plant produces a cambial zone which separates the cortex with the initial leaves (leaf primordial) from the central cylinder.

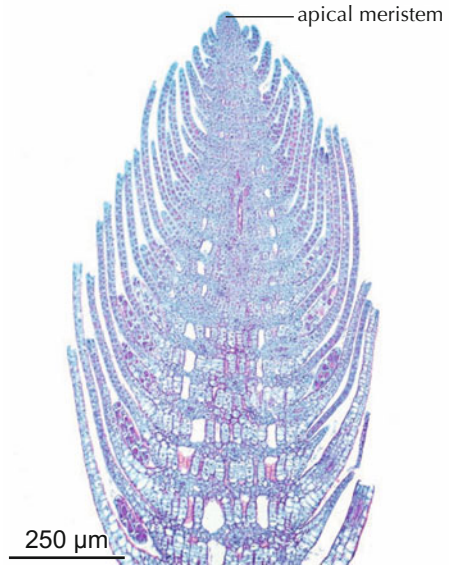
Apical shoot meristems



6.53 Apical meristem of *Elodea canadensis*, a monocotyledonous water plant. Slide: J. Lieder.

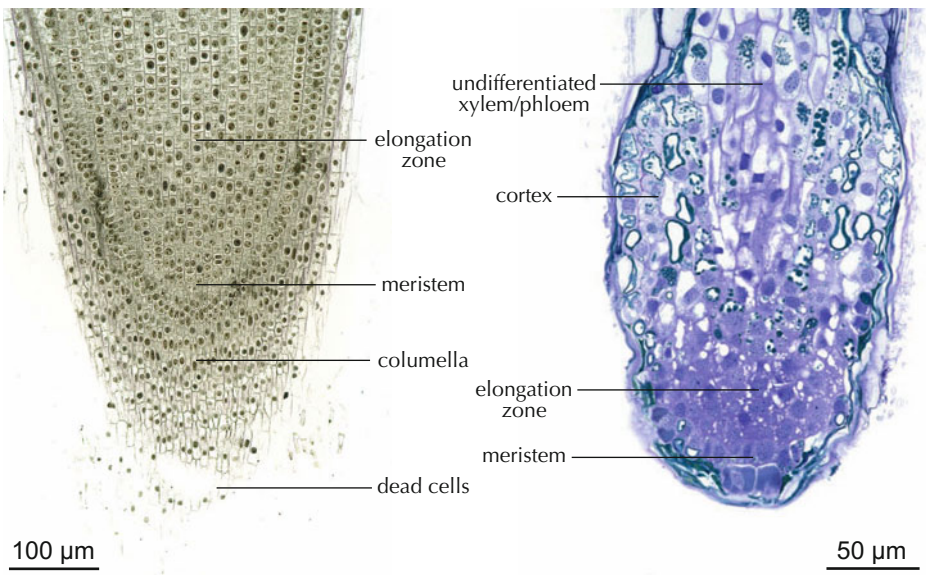
6.54 Apical meristem of *Euphorbia cyparissias*, a dicotyledonous terrestrial plant.

Development behind the initial zone



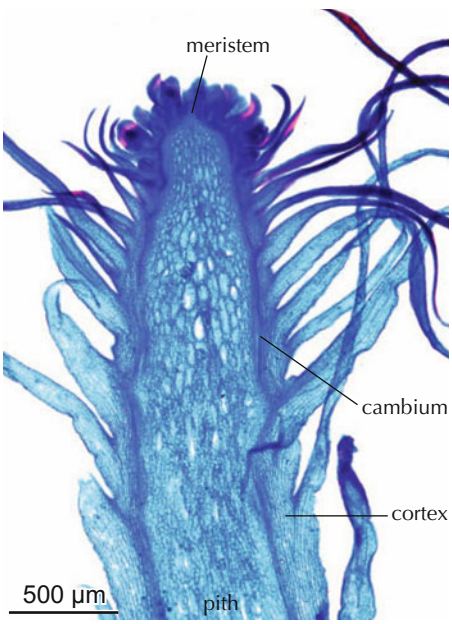
6.55 No cambium in the monocotyledonous water plant *Elodea canadensis*. Slide: J. Lieder.

Apical root meristems



6.56 Apical root meristems in the monocotyledonous plant *Allium ursinum*.

6.57 Apical root meristems of an unidentified dicotyledonous species. Slide: S. Egli.



6.58 Cambium present in the dicotyledonous *Euphorbia cyparissias*.

6.1.5 From primary apical meristem to secondary lateral meristems in *shoots* – From longitudinal to radial growth

The transformation from primary to secondary meristems occurs in apical zones of roots and shoots of dicotyledonous plants. Initial apical meristems in herbs are mostly unprotected, while in trees they are mostly protected by bud scales.

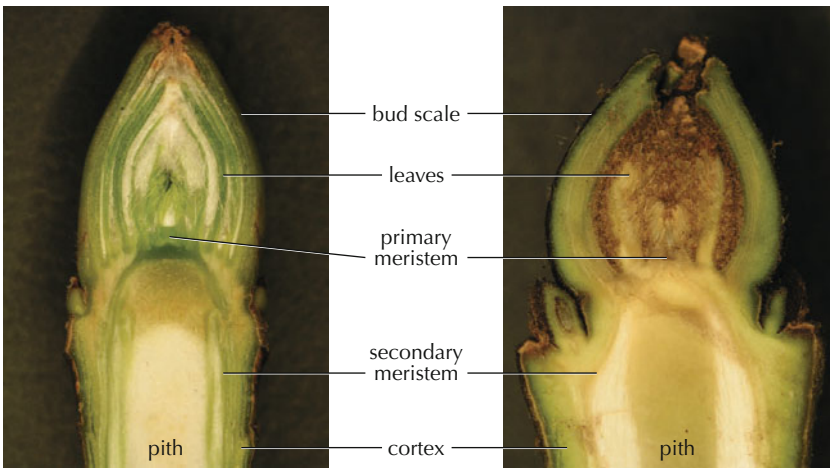
The principles of secondary meristem formation are similar in all shoots of plants, however, in the detail there are many differences. The herb *Euphorbia chamaecyparissias* and the trees *Acer pseudoplatanus* and *Fraxinus excelsior* are discussed here.

In shoots, the formation of leaves in the cortex and the central pith are common. In all examined species, xylem and phloem formation starts near the apex and lignification occurs later. In detail: Cells of the central part of shoots of dicotyledonous plants remain in a parenchymatic, undifferentiated state (the pith). Around the primary meristem a ring of collateral vascular bundles is formed, which consists of protoxylem and protophloem. Lignification occurs in *Euphorbia* 10 mm and in *Acer* and *Fraxinus* 2 mm behind the apex. Vessels of the protoxylem and metaxylem are characterized by annular and helical thickenings. Crystals of various forms are very frequent in *Acer* and *Fraxinus* but are almost absent in *Euphorbia*. Crystals play a role in cell wall formation.

Protected in leaf sheath of bud scales – macroscopic aspect

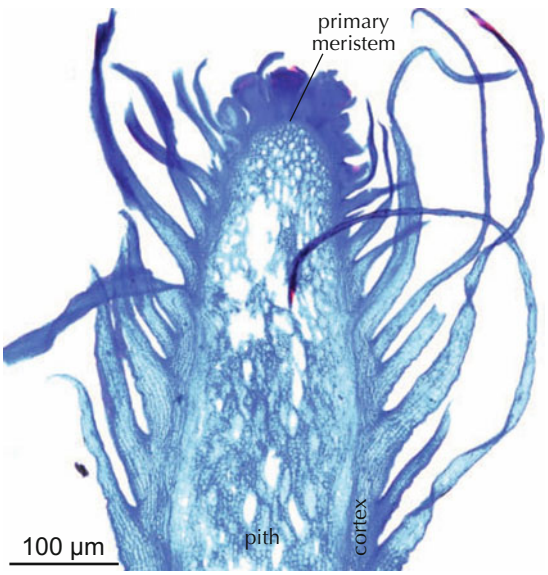
6.59 A mantel of poorly developed leaves wraps the meristematic apex in *Euphorbia cyparissias*.

6.60 Bud scales wrap the meristematic apex in *Acer pseudoplatanus*.

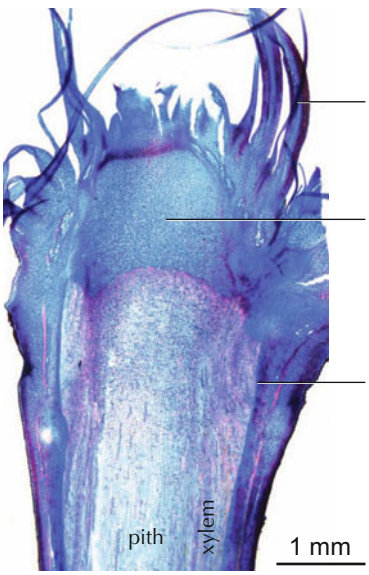


6.61 External bud scales and internal initial leaves protect the meristematic apex in *Acer pseudoplatanus* and *Fraxinus excelsior*.

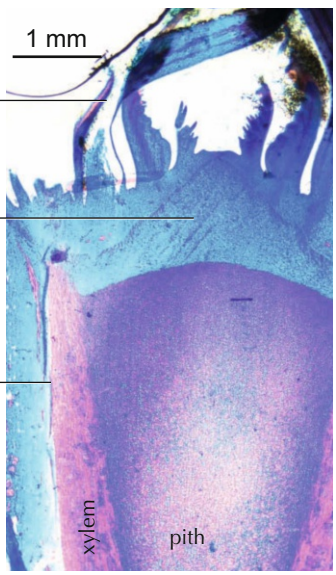
Pith and cortex with initial leaves – product of the primary meristem



6.62 Longitudinal section of *Euphorbia cyparissias*.

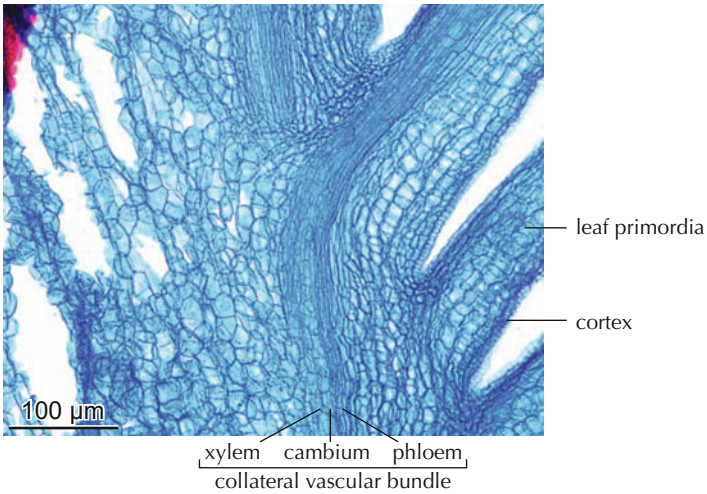


6.63 Longitudinal section of *Acer pseudoplatanus*.

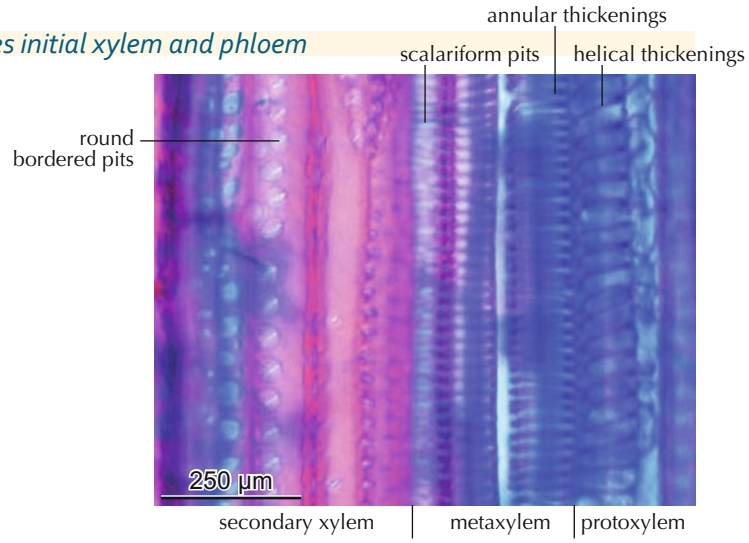


6.64 Longitudinal section of *Fraxinus excelsior*.

Secondary meristem creates initial xylem and phloem

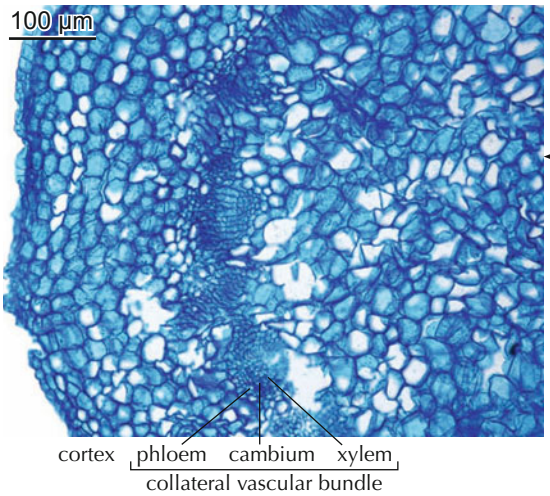


6.65 Longitudinal section of a vascular bundle in the tip of *Euphorbia cyparissias*.

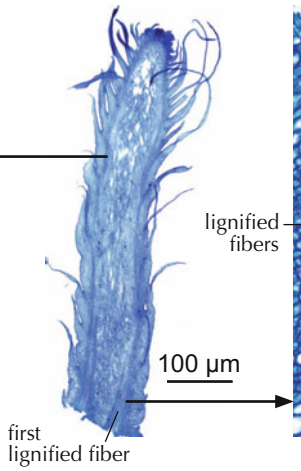


6.66 The vessel wall structure changes from helical thickenings in the protoxylem to round bordered pits in the secondary xylem of *Cycas revoluta*.

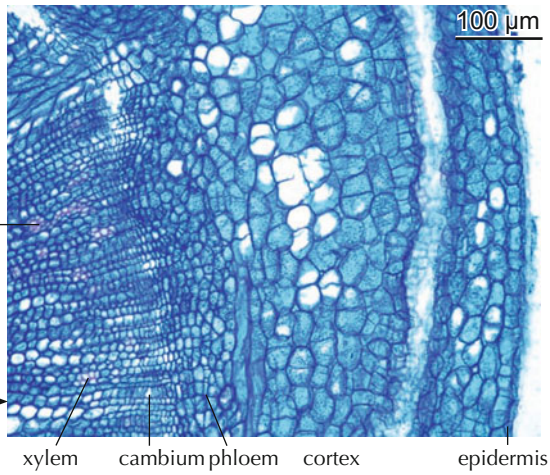
Delayed lignification



6.67 Cross section near the tip of a young shoot of *Acer pseudoplatanus*. First vascular bundles are formed but there is no lignification.



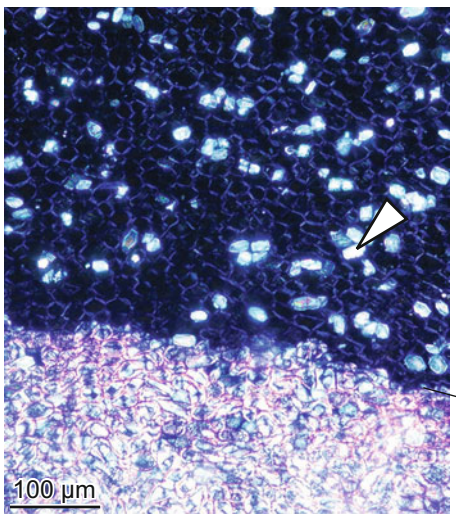
6.68 Longitudinal section of a young shoot of *Euphorbia cyparissias* with initial vascular bundles.



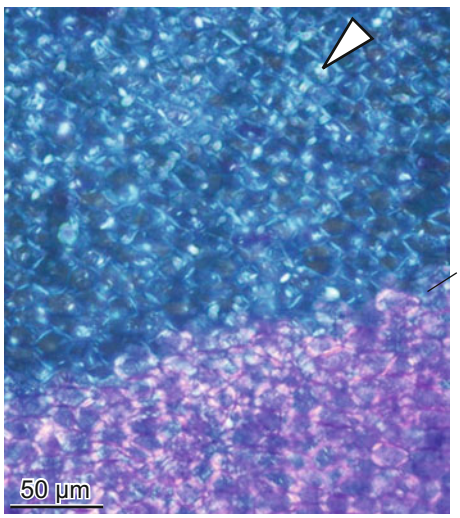
6.69 Cross section of *Euphorbia cyparissias* 10 mm behind the tip. The xylem of the vascular bundles already contains a few lignified fibers.

Cell-wall formation and calcium oxalate crystals

6.70 Vegetation point within a bud of *Acer pseudoplatanus*, polarized light.



6.71 Cambial zone of *Acer pseudoplatanus*, polarized light.



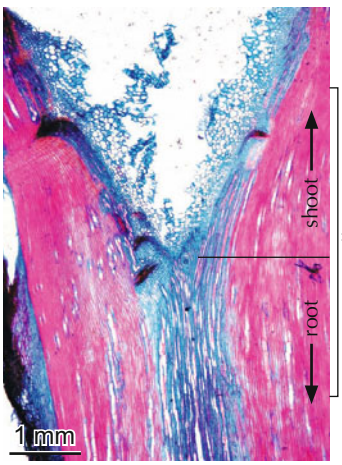
6.72 Cambial zone of *Fraxinus excelsior*, polarized light.

6.1.6 From primary apical meristem to secondary lateral meristems in *roots* – From longitudinal to radial growth

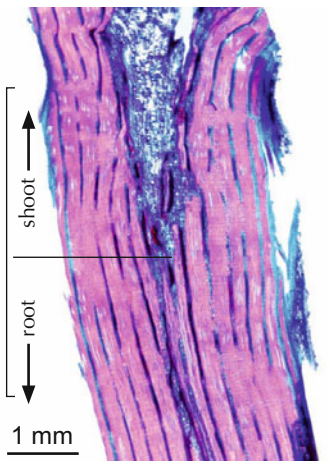
Differentiation between shoot and root takes place in the so-called root collar, the zone between the cotyledons and the root which can be found in herbs, shrubs and trees. Shoots are characterized by a pith, while roots have none.

In contrast to the shoot, apex cells of the root differentiate very soon after their formation, xylem towards the inside and phloem towards the outside. Root apex cells behave like a secondary meristem. Therefore the roots of dicotyledonous plants have no pith. However, the width of the transition zone between the pith-filled shoot and the pith-less root varies between 5 mm and 20 cm.

Root collar – transition zone between root and shoot

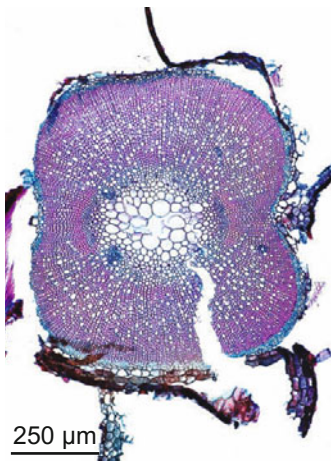


6.73 Root collar of *Tordylium apulum*.

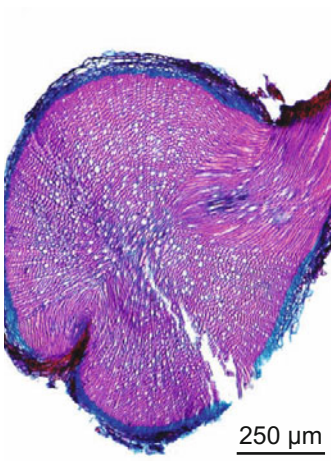


6.74 Root collar of *Chenopodium opulifolium*.

Shoot and root in an annual dicotyledonous herb



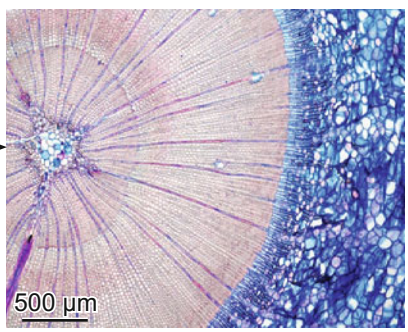
6.75 Shoot, with a pith, of *Euphrasia* sp.



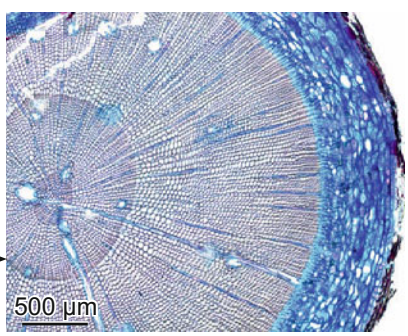
6.76 Root, without a pith, of *Euphrasia* sp.

Shoot and root in a conifer

6.77 Sapling of *Picea abies*.

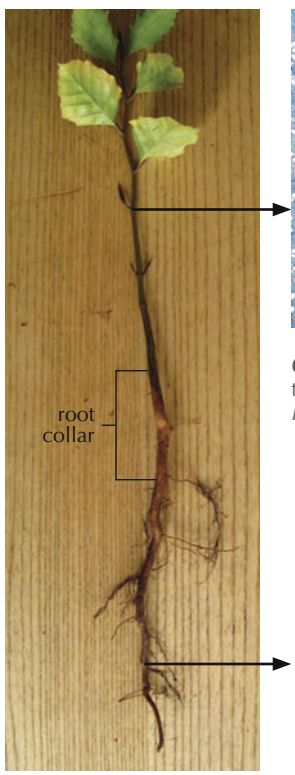


6.78 Cross section of a shoot of *Picea abies* with a pith.

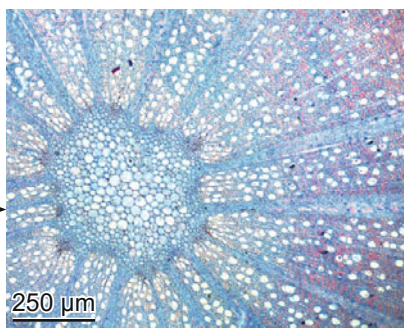


6.79 Cross section of a root, 10 cm below the ground, of *Picea abies* without a pith.

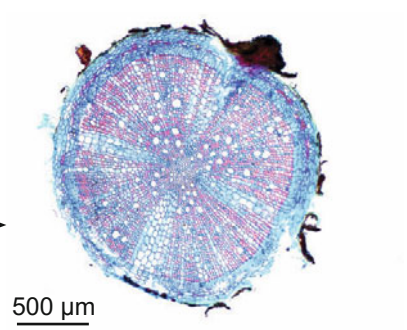
Shoot and root in a dicotyledonous tree



6.80 A 30 cm-tall sapling of *Fagus sylvatica*.



6.81 Cross section of a shoot with a pith, in the upper part of the germination stem of *Fagus sylvatica*.



6.82 Cross section of a root without a pith, 10 cm below the ground, of *Fagus sylvatica*.

6.1.7 From primary apical meristem in shoots to roots in plants without cambium (*monocotyledons*)

The taxonomic and morphological diversity is enormous within the monocotyledons, be it in shoots, rhizomes or roots. Dramatic anatomical changes occur along the stem axis. Each section is characterized by typical anatomical structures.

Cells of the apical meristem of shoots and rhizomes differentiate very soon after their formation into parenchyma and isolated closed vascular bundles (no cambium). The bundles in the flower stalk (culm) are collateral, those in the rhizome in general concentric. Cells of the apical meristem of roots form a central vascular cylinder and a cortex. The cylinder is surrounded by an endodermis and a pericycle. The pericycle occasionally initiates lateral roots. Vascular bundles are located in the central cylinder inside an endodermis.

This is shown here for a few species from different families. However, the anatomical diversity is much larger.

Macroscopic aspect of shoots, rhizomes and roots

6.83 Young apical meristem in *Asparagus officinalis*.

6.84 Rhizome of *Juncus conglomeratus*.

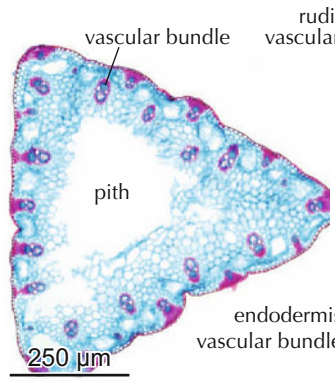
6.85 Rhizomes of *Hedychium gardnerarum*.

6.86 Polar root of *Plantago maritima*.

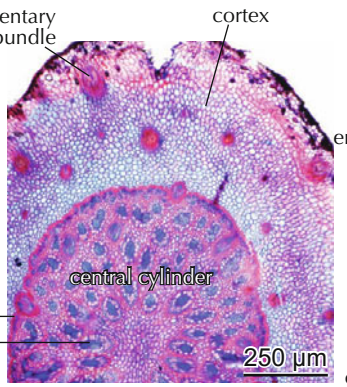
Morphological and anatomical stem structure of shoots, rhizomes and roots

Carex pendula, Cyperaceae

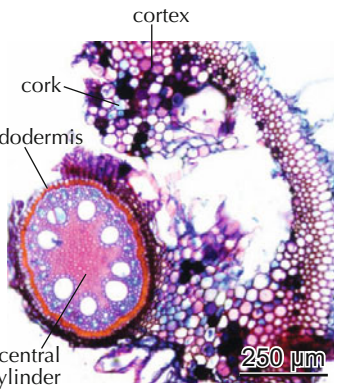
6.87 Flower stalk of *Carex pendula*.



6.88 Cross section of a triangular culm. Vascular bundles are located at the periphery.



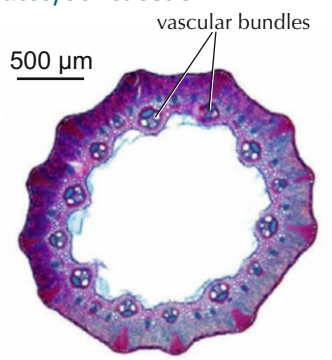
6.89 Cross section of a rhizome. Concentric vascular bundles are located in the central cylinder inside of a thick-walled endodermis.



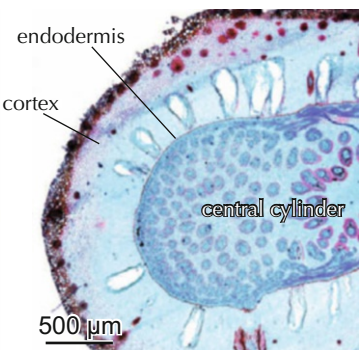
6.90 Cross section of a root. Vascular bundles are located around a thick-walled central fibrillose center.

Juncus inflexus and *conglomeratus*, Juncaceae

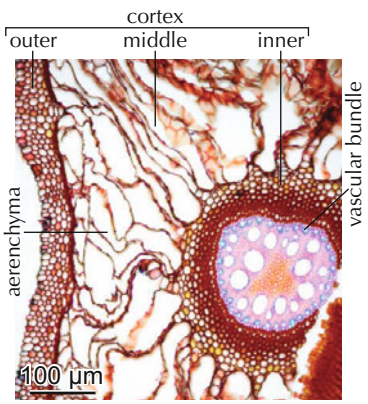
6.91 Culms of *Juncus inflexus*.



6.92 Cross section of a culm of *Juncus inflexus*. Large and small vascular bundles alternate at the periphery.



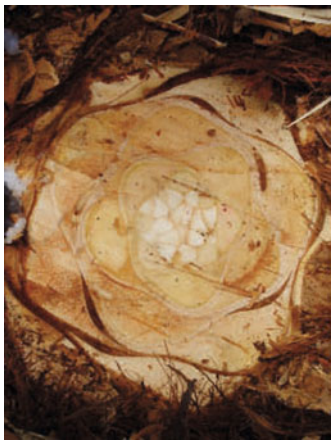
6.93 Cross section of a rhizome of *Juncus conglomeratus*. Vascular bundles are located in the central cylinder inside a thick-walled endodermis.



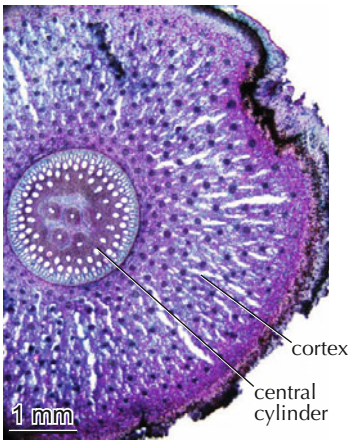
6.94 Cross section of a root of *Juncus conglomeratus*. Vascular bundles are located around a thick-walled central fibrillose center. The cortex contains large aerenchymatic tissue.

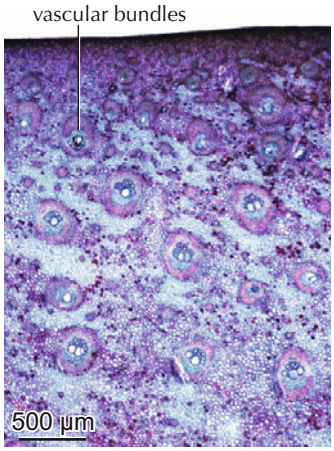
Phoenix canariensis, Palmaceae

6.95 *Phoenix canariensis*



6.96 Cross section of a vegetation point from where palm syrup is harvested.

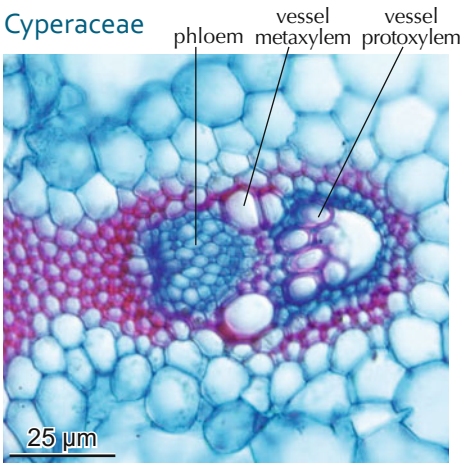




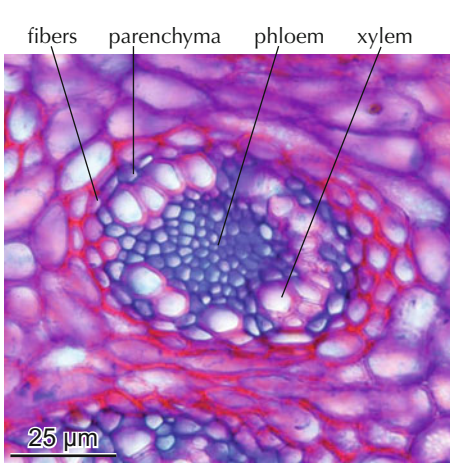
6.97 Cross section of a root. Vascular bundles are located around a thick-walled central fibrillose center.

Structure of vascular bundles in shoots, rhizomes and roots

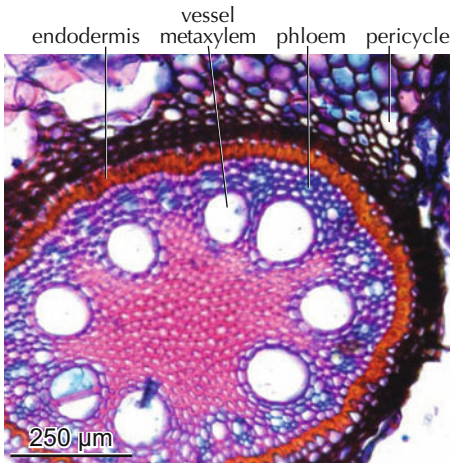
Cyperaceae



6.98 Closed collateral vascular bundle in a shoot of *Carex pilosa*. The xylem consists of a group of protoxylem and a few lateral metaxylem vessels. The phloem consists of sieve tubes and companion cells. The vessels are surrounded by a layer of fibers.

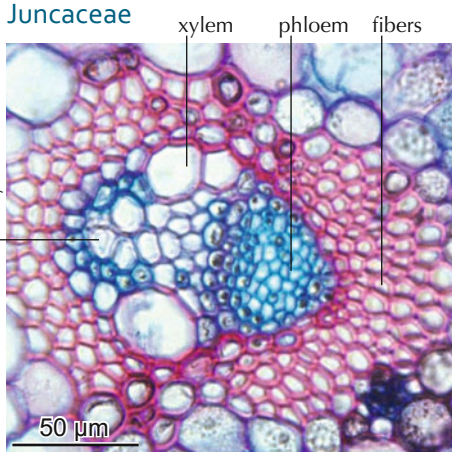


6.99 Concentric vascular bundle in a rhizome of *Carex pilosa*. Vessels surround a central group of sieve tubes. A small sheath of fibers surrounds the vascular bundle.

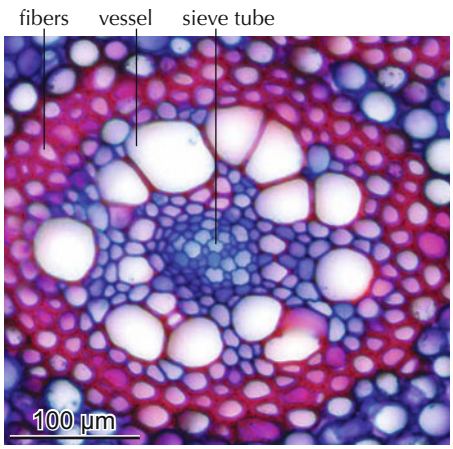


6.100 Closed collateral vascular bundles in a root of *Carex pendula*. The closed collateral vascular bundles are located inside of a thick-walled endodermis.

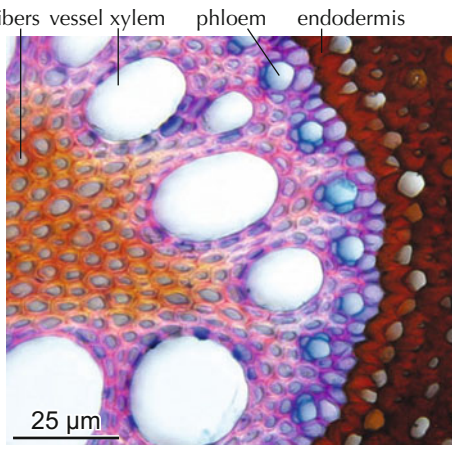
Juncaceae



6.101 Closed collateral vascular bundle in a shoot of *Juncus arcticus*. The xylem consists of a group of protoxylem and a few lateral metaxylem vessels.



6.102 Concentric vascular bundle of a rhizome of *Juncus arcticus*. Vessels surround a central group of sieve tubes and companion cells. A sheath of thick-walled fibers surrounds the vascular bundle.



6.103 Separated xylem and phloem inside a thick-walled endodermis in a root of *Juncus conglomeratus*.

6.1.8 From primary apical meristem in shoots to roots in vascular *spore plants*

There is a great taxonomic and morphologic variety within the vascular spore plants, e.g. the lycopods, spikemosses, horsetails and ferns. Little variation occurs in the first three units, however, it is tremendous within the ferns. Major vascular spore plants have no secondary growth but anatomical changes occur along the stem axis. Products of apical meristem in shoots are leaves, often with sporophytes, and rhizomes. The product of geotropic apical meristem is the root.

The plant size and morphological variability is rather small in spikemoss (*Selaginella*), clubmoss (*Lycopodium*) and in horsetails (*Equisetum*). All types form long shoots and rhizomes with thin roots. In contrast, size and morphological variability is extremely large in ferns. All plant parts have concentric vascular bundles with the xylem in the center. Their bundles are surrounded by a cortex. The form varies from round to long oval. The number of vessels is normally high in *Selaginalla*, clubmosses and ferns. It is reduced to a few vessels in horsetails. This section presents an overview. More details are shown in Chapter 7.

Macroscopic aspect of the whole plant

6.104 Perennial prostrate shoots of the spikemoss *Selaginella denticulata*.

6.105 Fertile annual shoots of the clubmoss *Lycopodium clavatum*.

6.106 Fertile annual shoots of the horsetail *Equisetum telmateia*.

6.107 Sterile annual shoots of the horsetail *Equisetum hiemale*.

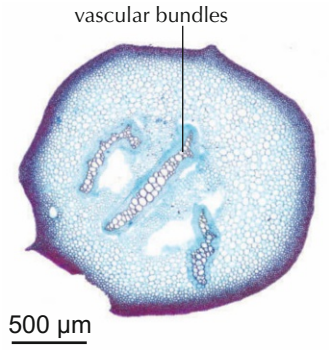
6.108 Tree fern *Cyathea cooperi*.

6.109 Climbing fern *Lygodium* sp.

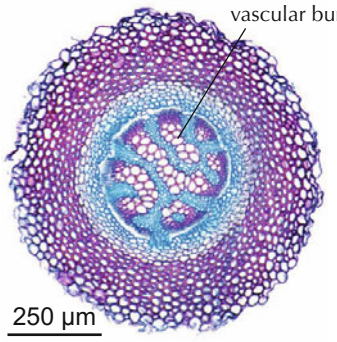
6.110 Hemicryptophytic fern *Blechnum spicant*.

6.111 Hydrophytic fern *Marsilea quadrifolia*.

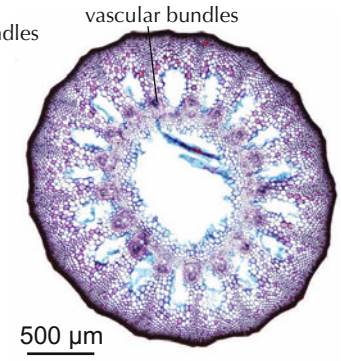
Anatomical structure of shoots, rhizomes and roots



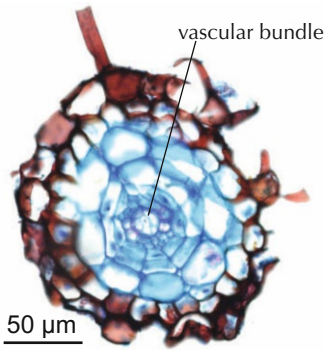
6.112 Shoot of *Selaginella* sp. with three vascular bundles.



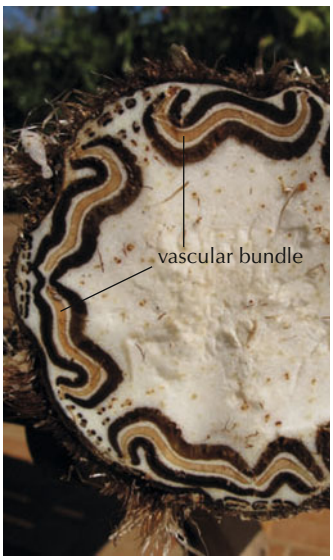
6.113 Shoot of *Lycopodium alpinum*. Irregularly distributed vascular bundles in a central cylinder (stele).



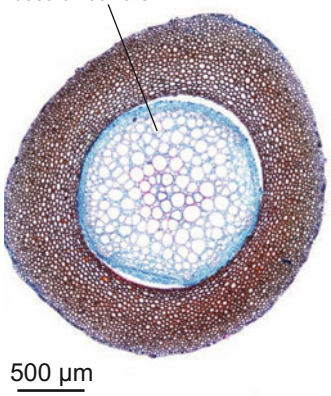
6.114 Shoot of *Equisetum hiemale*. Circular arranged, round vascular bundles.



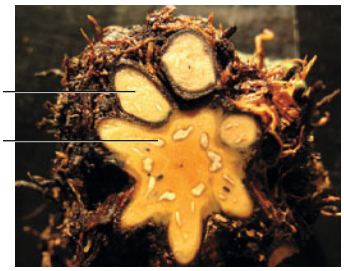
6.115 Root of *Equisetum arvense*. One concentric vascular bundle.

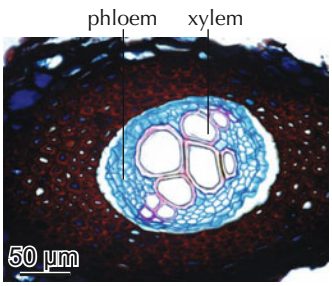


6.116 Stem cross section of the tree fern *Cyathea cooperi*.



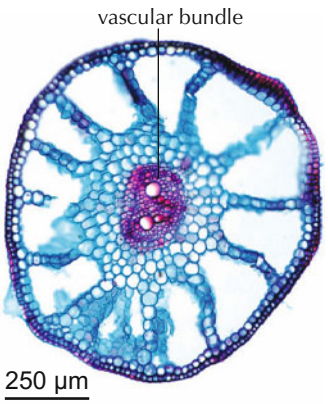
6.117 One central vascular bundle in the liana-like fern *Lygodium* sp.





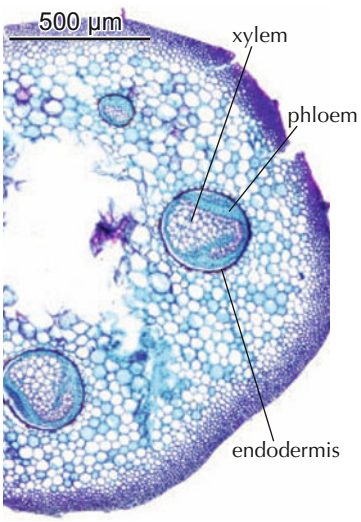
6.118 Fine root of the hemicryptic fern *Dryopteris filix-mas* with a single concentric vascular bundle.

◂ **6.119** Basal part of the hemicryptic fern *Polystichum lonchitis*. Irregularly formed vascular bundles are arranged around the pith.

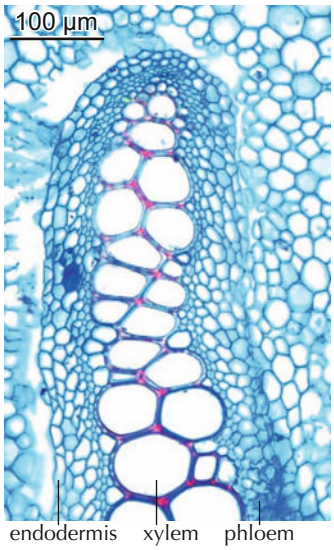


6.120 Microscopic cross section of a petiole of the hydrophytic fern *Marsilea quadrifolia* with collateral vascular bundles.

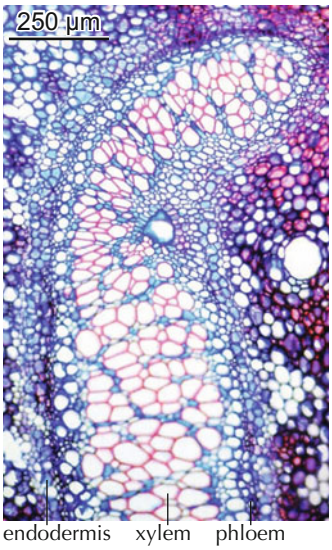
Structure of vascular bundles in shoots, rhizomes and roots



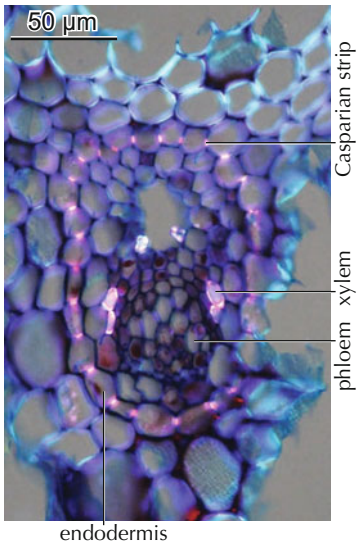
6.121 Round vascular bundle in a leaf of *Dryopteris filix-mas*.



6.122 Long oval vascular bundle in a shoot of *Selaginella* sp.



6.123 Long oval vascular bundle in a stem of the tree fern *Cyathea cooperi*.



6.124 Round vascular bundle with reduced xylem in the hemicryptophytic horsetail *Equisetum hiemale*, polarized light.

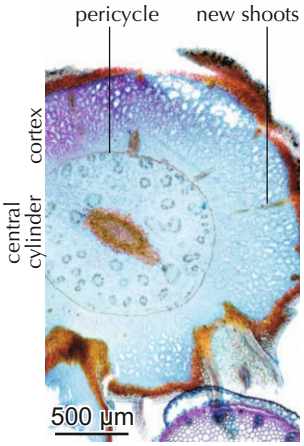
6.1.9 Pericycle and endodermis – Separation of central cylinder and cortex

Cortex and central cylinder (stele) in roots and rhizomes of monocotyledonous and dicotyledonous plants are separated by a pericycle and an endodermis. The pericycle is the outermost layer of the stele and the endodermis is the innermost cell layer of the cortex. The pericycle is a meristematic relict of the primary root meristem; it keeps its protoplast. Most of the time it is in a dormant state, but if it is in a meristematic mode it produces lateral roots. In young states it also initiates the cork cambium. The endodermis primarily regulates hydrological differences between the central cylinder and the cortex. It maintains the root pressure and protects the central vascular bundles from toxic substances, which occasionally occur in the cortex.

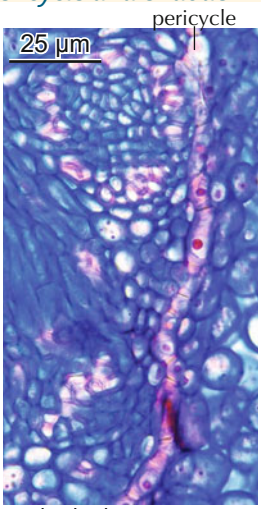
Only optimally developed endodermis and pericycle zones in a few roots are described in textbooks. In reality endodermis and pericycle are often unrecognizable or difficult to distinguish. Also, the anatomy of endodermis varies. Presented here are a few "unproblematic" examples.

In many monocotyledonous plants the cell walls are extremely thick-walled on the inner and lateral sides. Often described but rarely occurring is the endodermis with Casparian strips. The strips form a lignified band of radial and transverse walls.

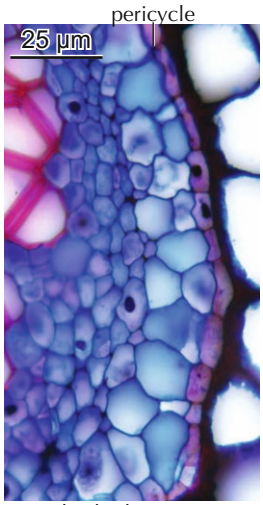
Pericycle and endodermis



6.125 Pericycle separates central cylinder and cortex and initiates new lateral shoots in the rhizome in *Triglochin palustris*.

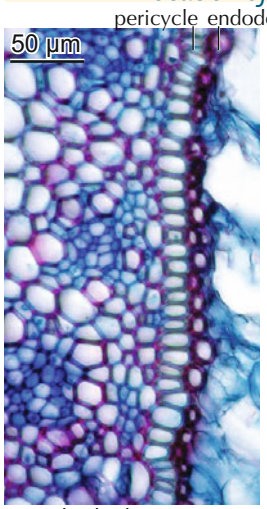


6.126 Pericycle cells with nuclei in *Triglochin palustris*.

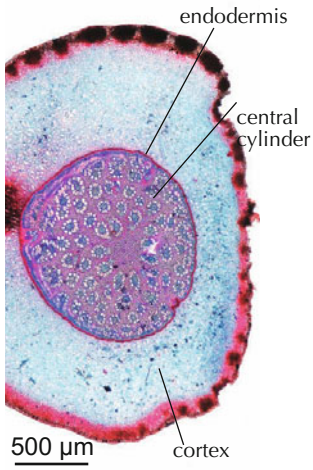


6.127 Pericycle with nuclei, surrounding a concentric vascular bundle in *Polypodium vulgare*.

Location of endodermis

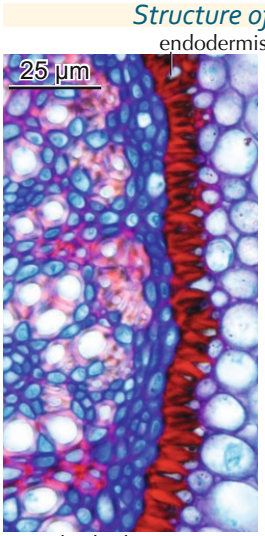


6.128 Distinct pericycle and endodermis in *Eleocharis palustre*.

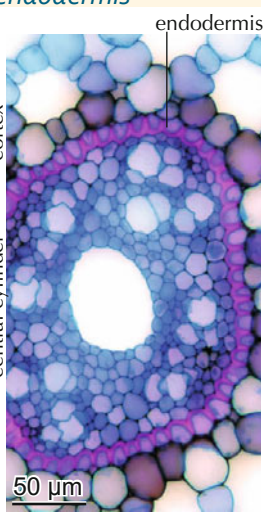


6.129 A thick-walled endodermis separates the cortex from the central cylinder in *Carex appropinquata*.

Structure of endodermis

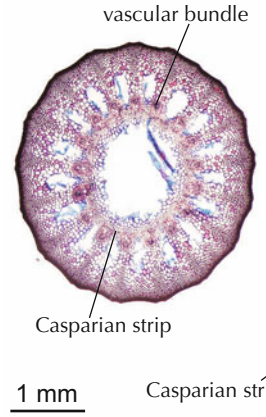


6.130 Thick-walled endodermis in the rhizome of *Juncus gerardii*.

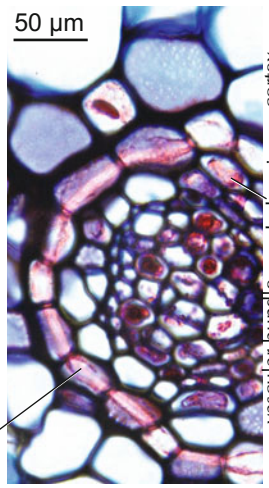


6.131 Thick-walled endodermis in the shoot of *Potamogeton gramineus*.

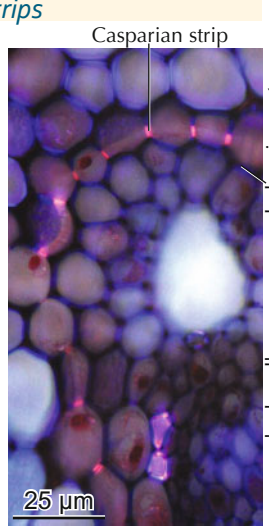
Endodermis with Casparian strips



6.132 Location of Casparian strips around vascular bundles in *Equisetum hiemale*.



6.133 Endodermis of *Equisetum hiemale* with Casparian strips around vascular bundles.



6.134 Endodermis of *Equisetum hiemale* with Casparian strips, polarized light.

6.2 Secondary and tertiary meristems and radial growth – Cambium and cork cambium

6.2.1 Macroscopic aspect of radial growth and xylem coloration – Stems get thicker

Stem thickening occurs through the lateral secondary meristem. This is the cambium, which is located between the xylem and phloem. In most conifers and dicotyledonous plants the cambium forms a mantle around the xylem. Plants with successive cambia (several active cambia) are a special case.

Years after wood formation, the inner part of the stem loses its conducting capacity. This is the moment when the stem differentiates into sapwood and heartwood. The peripheral sapwood conducts water and contains living parenchyma cells. In contrast, the heartwood does not conduct water and all cells are dead. Here, parenchyma cells often contain phenolic substances which play an important part in biological defense mechanisms. The width of the sapwood is generally proportional to the transpiring leaf area: the more leaves in the tree crown, the larger the sapwood.

A few groups of stem cross sections can be differentiated macroscopically.

Species with colored heartwood

- Species with high water content in the sapwood and low water content in the heartwood; e.g. in the genera *Pinus*, *Larix* and *Taxus*.
- Species without notable water content differences between sapwood and heartwood; e.g. in the genera *Quercus*, *Castanea*, *Robinia*, *Prunus* and *Juglans*.

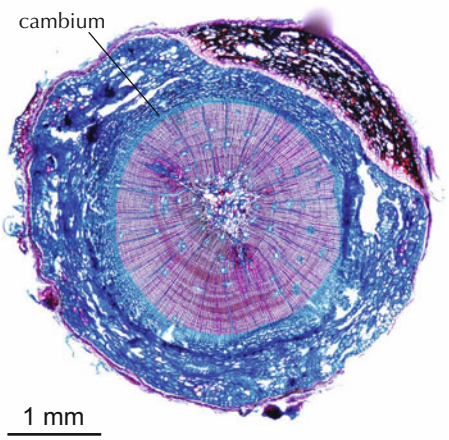
Species without colored heartwood

- Species with high water content in the sapwood and low water content in the heartwood; e.g. in the genera *Picea* and *Abies*.
- Species with high water content in the whole stem; e.g. in the genera *Fagus*, *Carpinus* and *Alnus*.
- Species with higher water content in the sapwood than in the heartwood; e.g. in the genera *Acer* and *Citrus*.

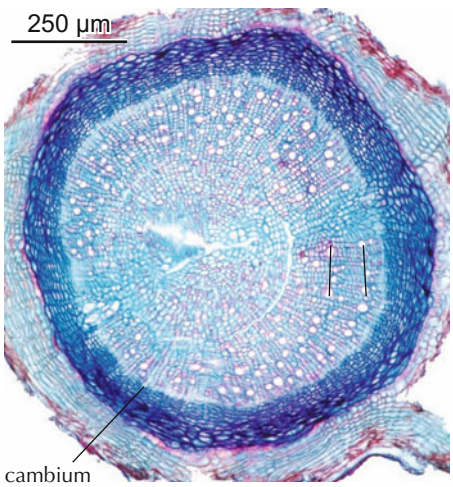
Irregularly shaped discolorations are related to biological attacks. Different colors, textures and brilliance of heartwood, as well as color differences between heart- and sapwood are basic features for macroscopic wood identification. This is perfectly presented in the old *Woodbook* by R.B. Hough, republished in 2002.

The outline of stems varies from round (most trees), to eccentric (leaning trees), to fluted (buttressed stem basis) and square. Multiple stems occur mainly in perennial herbs. The bark thickness (phloem, cortex, cork) in relation to the xylem is very variable. The texture in transverse and longitudinal sections is species-specific, or mainly related to the structure of annual rings and rays.

Location of the cambia



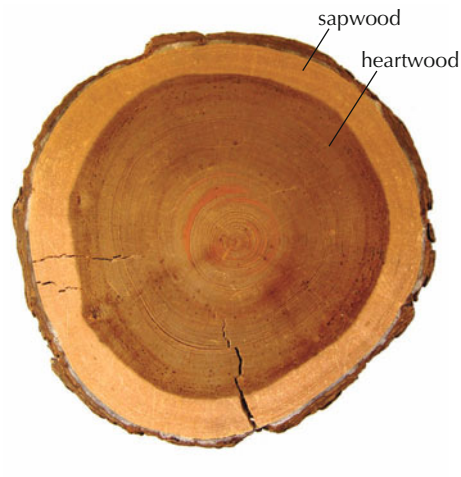
6.135 One cambium is located between the central xylem and the peripheral bark in an 11-year-old conifer twig of *Pinus sylvestris*.



6.136 One cambium is located between the central xylem and the peripheral bark of a four-year-old arctic herb, *Cerastium arcticum*.

6.137 Several peripheral cambia form several fiber and parenchyma bands during one year. This plant of *Haloxylon persicum* is approximately 10–12 years old.

Sapwood and heartwood



6.138 A belt of light sapwood surrounds the brown heartwood in the center of the conifer *Pinus sylvestris*.

6.139 A belt of light sapwood surrounds the dark brown heartwood in the center of the deciduous tree *Rhamnus cathartica*.

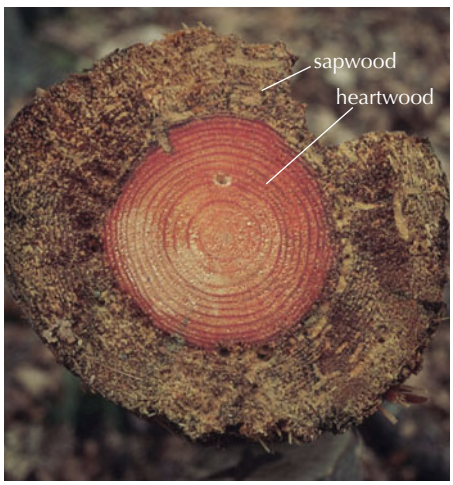
6.140 Heartwood and sapwood are not differentiated by color differences in the deciduous tree *Carpinus betulus*.

Discolorations are defense reactions

6.141 Living parts of stems react to injuries with the formation of dark-stained phenolic substances. Compartmentalized overgrown injury in *Acer pseudoplatanus*.

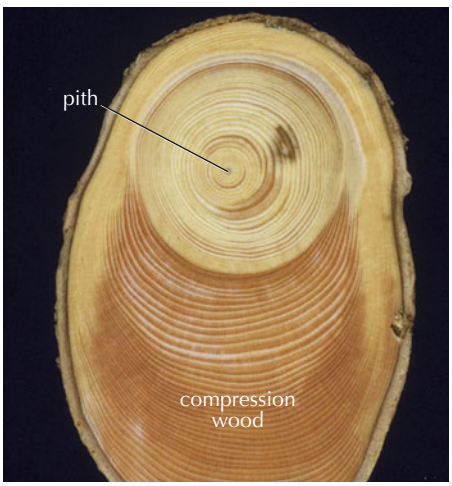
6.142 "Splash heartwood" (German "Spritzkern") in *Fagus sylvatica* is a sign of bacterial infections.

Biological resistance



6.143 Heartwood of *Pinus sylvestris* is more resistant against fungal infestations than sapwood.

Outline of stems

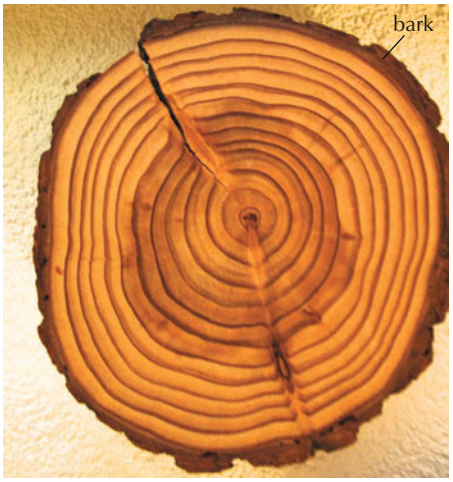


6.144 Eccentric stem due to compression wood formation in *Picea abies*.

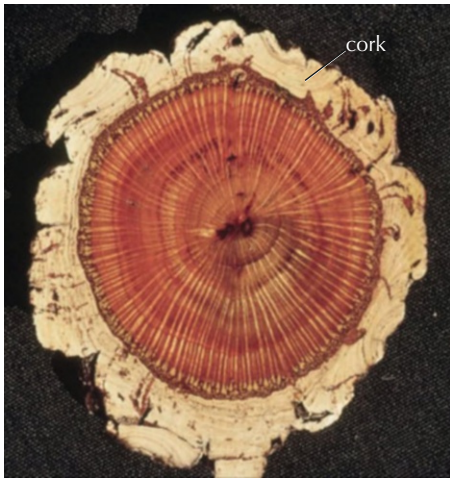
6.145 Fluted stem of the shrub *Crataegus* sp.

6.146 Square stem of the tree-like succulent *Euphorbia ingens*.

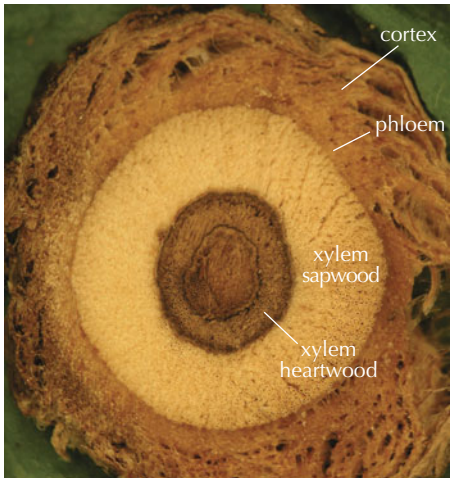
Bark thickness



6.147 Thin bark in relation to the xylem in *Pinus mugo*.



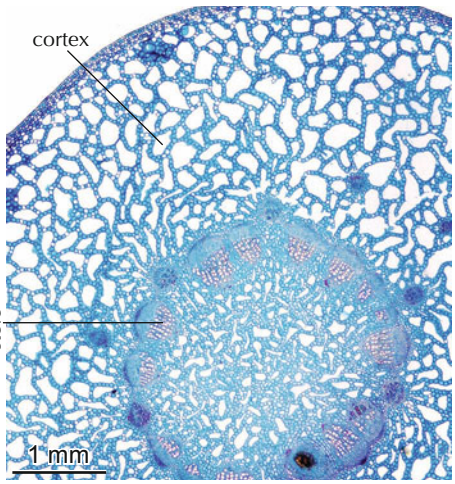
6.148 A large cork belt and a small phloem surround the xylem in *Quercus suber*.



6.149 A large cortex surrounds the xylem of the herb *Heracleum pinnatum*.

Bark thickness

6.150 An extremely large cortex surrounds a very small xylem in the giant cactus *Carnegia gigantea* (dry cross section).



6.151 An extremely large aerenchymatic cortex surrounds a very small stele in the water plant *Menyanthes trifoliata*.

Multiple stems

6.152 Stems of small cushion plants like *Saussurea glanduligera* in alpine zones are composed of many small individual stems.

Wood texture

6.153 The cutting direction of stems in parquet flooring highlights the annual ring structure of the wood of *Quercus* sp.

6.154 The radial cutting direction shows the structure of the rays in parquet flooring of *Quercus* sp.

6.155 The section through burls with sleeping buds shows the unusual wood structure in an antique chest, made of a deciduous tree species.

6.2.2 Microscopic aspect of radial growth (conifers, dicotyledonous plants and palm ferns) – An overview

Radial growth of conifers and dicotyledonous plants with one cambium

As soon as the cambium is active it forms secondary tissue: the secondary xylem and the secondary phloem. The xylem is different from the one that was formed by the primary meristem: Tracheids and vessels do not have any annular or thick annular or spiral thickenings. The cambium transfers the single vascular bundles into a continuous ring of xylem and phloem.

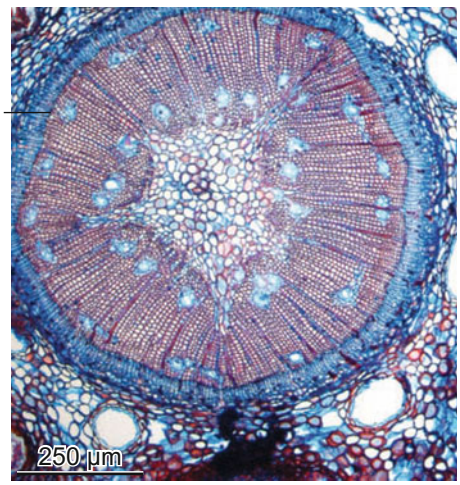
Radial growth of some dicotyledonous plants with several (successive) cambia

Numerous species, especially those in the families of Amaranthaceae and Caryophyllaceae, form and maintain several cambia. As soon as the first cambium is formed it produces a xylem and a phloem like in all other dicotyledonous plants. However, this stage lasts only for a short time. For growing in thickness, parenchyma cells outside of the phloem get reactivated and form a new cambium, which again produces a xylem and a phloem. This process repeats itself over many years. The lifetime of successive active cambia is limited but their effect is preserved in the anatomical structure of the stem.

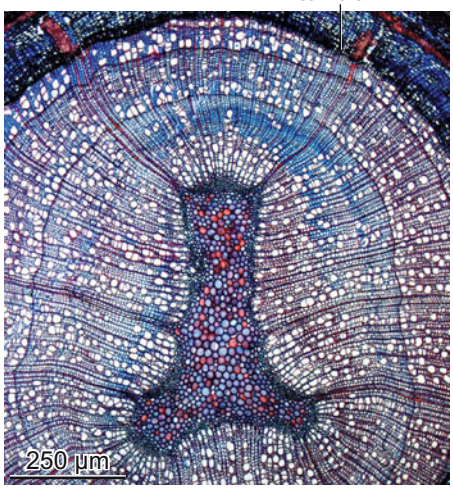
Radial growth of a few monocotyledonous plants

Secondary radial growth occurs in a few families of monocotyledonous plants, e.g. in *Dracaena* sp. and *Yucca* sp. As in the group with successive cambia, parenchyma cells in the primary bark (cortex) get reactivated and form—towards the center—a continuous belt of parenchyma cells around the stem. A few of them remain active and form vascular bundles.

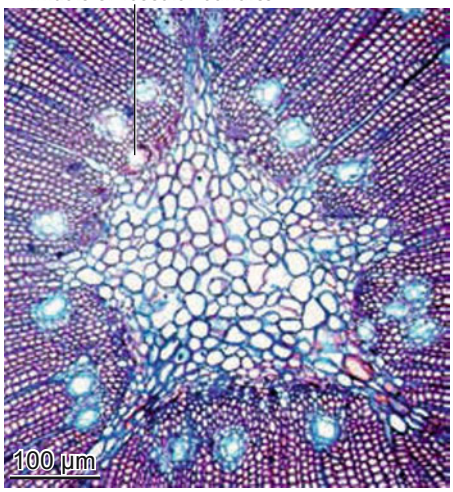
Radial growth with one cambium



6.156 One cambium produces the xylem and phloem. One-year-old shoot of the conifer *Pinus sylvestris*.



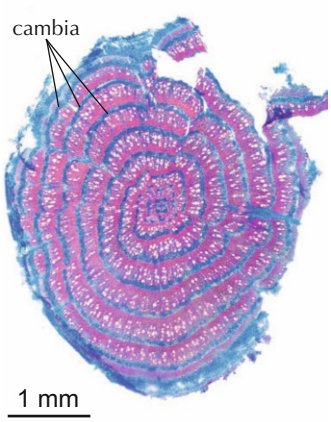
6.157 One cambium produces the xylem and phloem. Three-year-old shoot of the dicotyledonous tree *Alnus glutinosa*.



6.158 The secondary cambium merges the primary vascular bundles into a continuous belt in a twig of *Pinus sylvestris*.

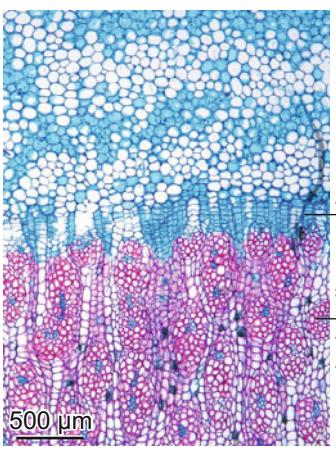
Radial growth with several cambia (successive cambia)

6.159 The annual dicotyledonous herb *Chenopodium botrys*, Amaranthaceae.



6.160 Cross section of the basal stem of the annual dicotyledonous herb *Chenopodium botrys*. Several cambia (blue rings) produce xylem and phloem simultaneously.

6.161 The monocotyledonous tree *Dracaena draco*, Asparagaceae.



6.162 Cross section of the peripheral part of the stem of *Dracaena draco*. The cambium produces vascular bundles and rays towards the inside and parenchyma cells towards the outside.

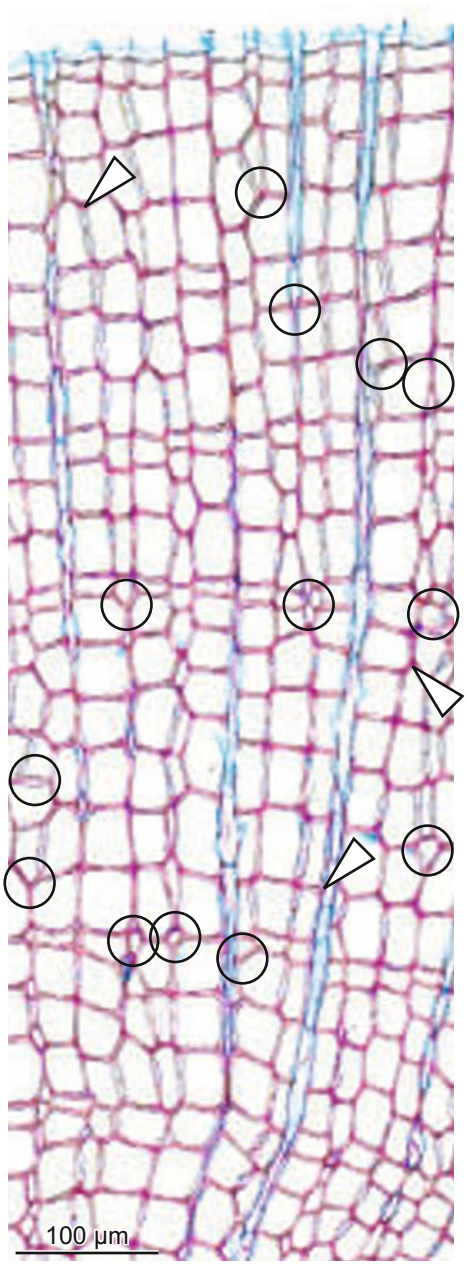
6.2.3 Production and enlargement of new cells in the xylem of a thickening stem – The need for more and larger cells

Stem thickening is related to an increase and enlargement of axial elements, like parenchyma cells, tracheids and fibers, and an increase and enlargement of rays. The number of cells at the periphery is lower in smaller than it is in thicker stems. Due to increased leaf area and plant weight, larger plants need more water-conducting and stabilizing cells than smaller plants.

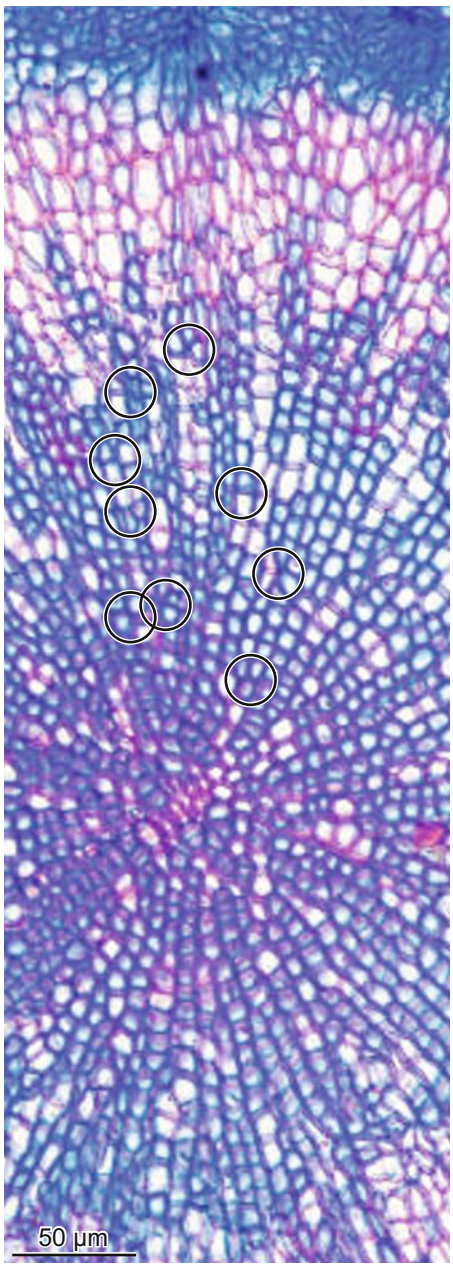
The process of stem thickening is anatomically expressed by axial cell initiations (tracheids, fibers, parenchyma cells and vessels), new ray initiations and dilating rays. This is underlined by Bailey 1923 who counted 794 tracheids in a one-year-old stem of *Pinus strobus* and 32,000 tracheids in a 60-year-old plant. The thickening process is also accompanied by cell death; cross sections of conifers show the disappearance of cell rows.

With the insertion of new ray cells and the enlargement of primary rays (ray dilatation), radial strength as well as storage capacity increases. The initial point for new cells is located in the cambial zone. New tracheids divide longitudinally. New rays are initiated in living tracheids, which change their mode; instead of longitudinal separation into tracheids, a small ray cell splits off laterally.

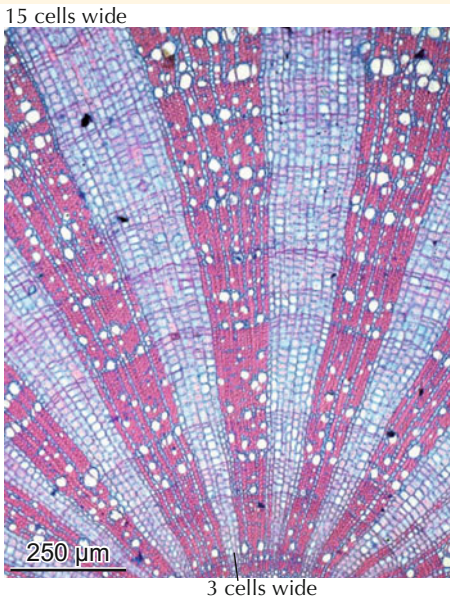
More cells and larger cells



6.163 Initiation (circles) and disappearance (arrows) of tracheids in the young root of a 20 m-tall *Pinus nigra* tree.

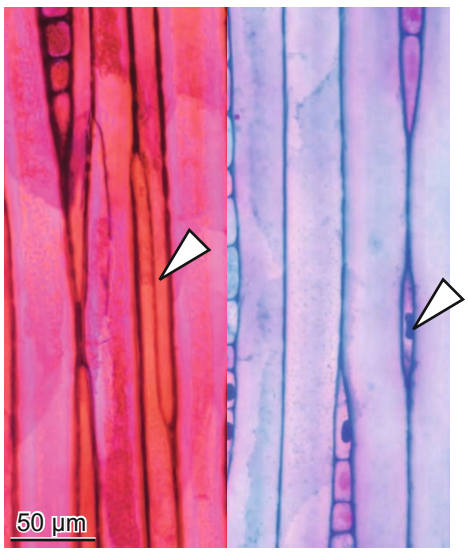


6.164 Initiation and enlargement of fibers in the stem of a 7 cm-tall annual herb *Erophila verna*.



6.165 Dilatation of large rays by insertion of new ray cells and enlargement of cells in *Rosa pendulina*.

Birth of cells



6.166 Dividing of tracheids in longitudinal direction (left) and separation of a single ray cell from a tracheid (right) in *Pinus sylvestris*.

6.2.4 Cell formation and differentiation in the *xylem* – The multifunctional stem center

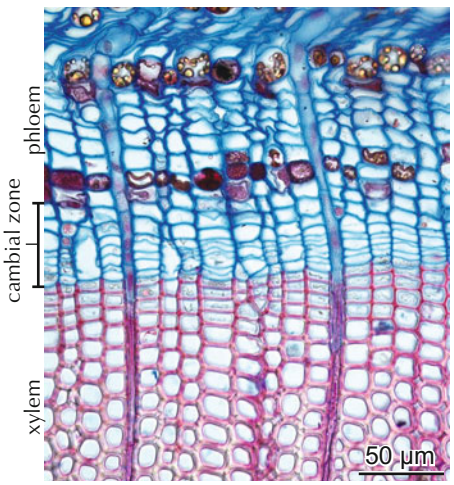
Genetic information, physiological needs and ecological triggers form the background for all anatomical structures. The anatomical expression of many biological and biochemical processes are presented in the following. Basic wood and bark formation processes already existed in late Devonian times (370 million years ago) in conifer-like stem structures. These ancient principles have been transferred to the phylogenetically young angiosperms (140 million years ago).

The following basic processes can be observed in conifers and angiosperms: cell-type differentiation, cell-wall differentiation, nuclei differentiation, cell-wall enlargement, cell-wall thickening and lignification. Genetic information determines the general arrangement and distribution of cell types.

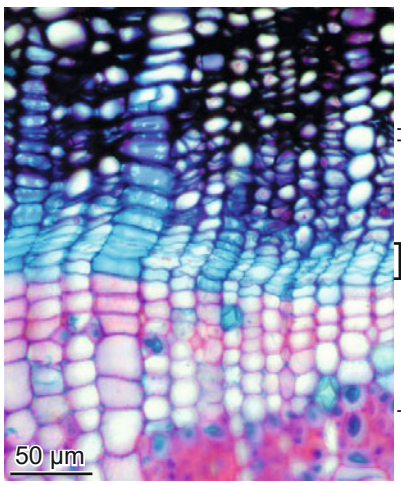
Cambium mother cells form anatomically undifferentiated phloem and xylem mother cells. These three cell types are anatomically combined in the cambial zone.

The first anatomical expression of ***cell differentiation*** appears within the cambial zone. Initial stages of conifers show tracheids, rays and resin ducts in the xylem and sieve cells and parenchyma cells in the phloem. In addition, angiosperms form vessels. In relation to space and physiological needs, some cell types have priority; resin ducts push aside tracheids and rays and, in angiosperms, vessels displace fibers and rays. The differentiation of the ***nucleus form*** takes place along with the cell-type differentiation.

Cambial zone

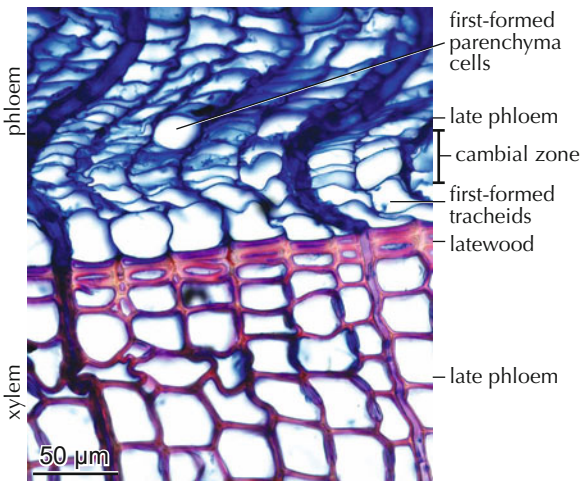


6.167 Cambial zone of the conifer *Picea abies* in the dormant state. Cambium initials, xylem mother cells and phloem mother cells are not anatomically differentiated.



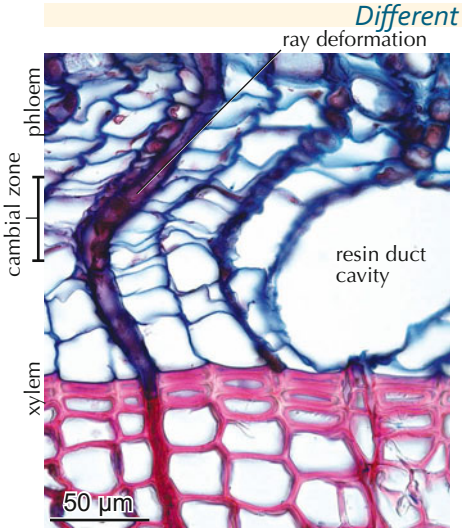
6.168 Cambial zone of the angiosperm *Ficus carica* in a dormant state. Cambium initials, xylem mother cells and phloem mother cells are not anatomically differentiated.

First-formed xylem cells

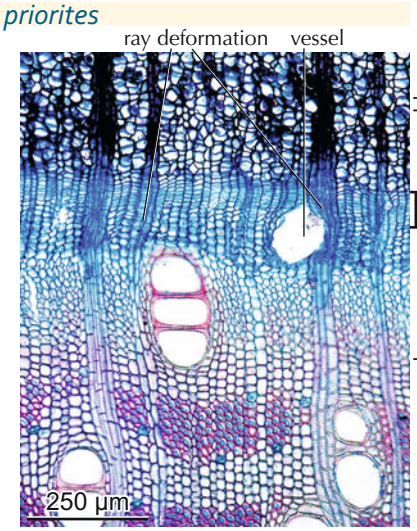


6.169 First-formed cells in the earlywood of a conifer. Tracheids and ray cells can be recognized on the xylem side and parenchyma cells on the phloem side.

Different priorites

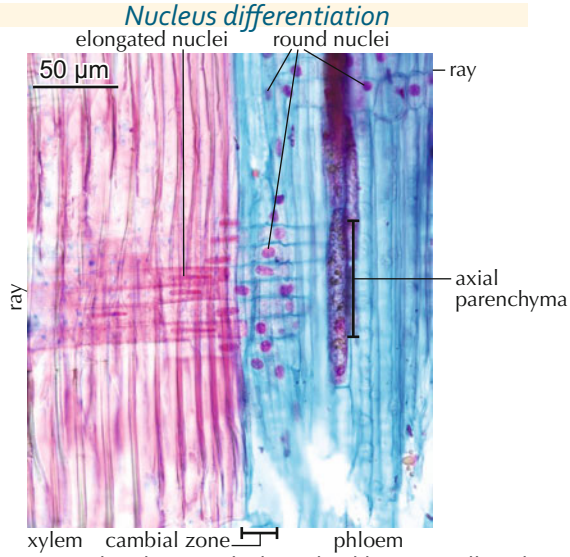


6.170 First-formed cells in the earlywood of the conifer *Larix decidua*. Formed are 2–3 rows of tracheids and a large cavity for a resin duct. The duct has the spatial priority.



6.171 First-formed cells in the earlywood of the angiosperm *Ficus carica*. Formed are 20 cells of fibers and a large vessel. The vessel has the spatial priority.

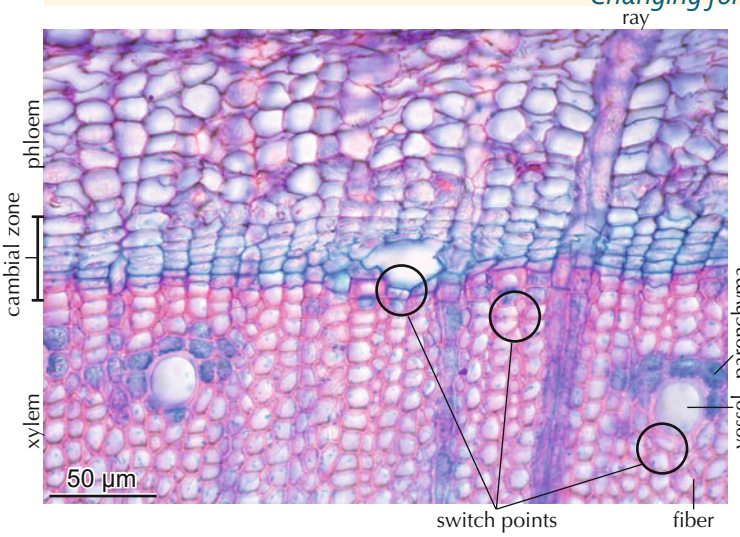
Nucleus differentiation



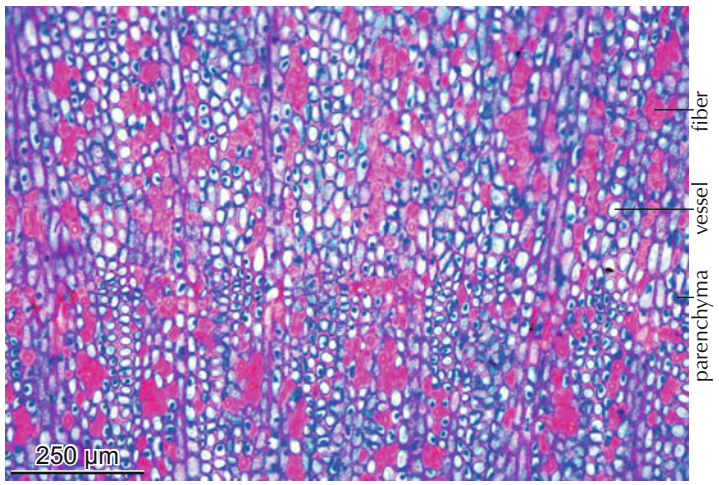
6.172 Round nuclei in cambial initials, phloem ray cells and axial phloem parenchyma cells; axially elongated nuclei in tracheids and phloem initials; radially elongated nuclei in xylem ray parenchyma cells in the conifer *Picea abies*.

The xylem and phloem mother cells already contain the information about their ***cellular pathway*** before their anatomical expression. The differentiation capacity of anatomically undifferentiated mother cells is very dynamic and changes within short time periods. This is very obvious in angiosperms. In one moment xylem mother cells divide into fibers and in the next into vessels, however, the change from fiber or vessel to ray cells is inexistent or rare.

Changing formation mode



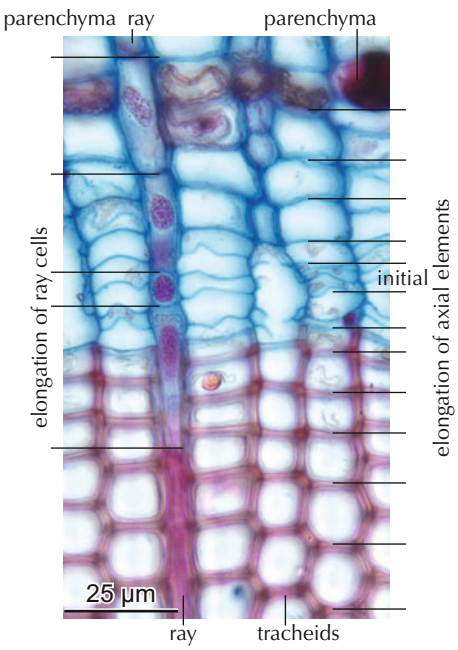
6.173 Cambial initials periodically determine which cell type has to be formed. Sometimes the initial differentiates into a fiber and sometimes into a vessel. *Fraxinus excelsior*.



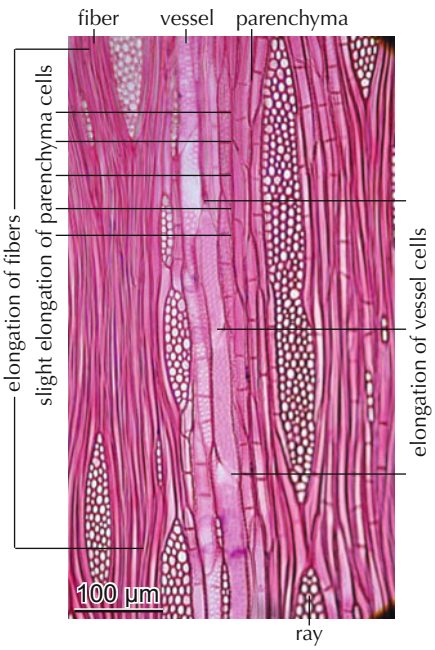
6.174 Cambial initials periodically determine which cell type has to be formed. The radial continuation of formed cell types (fibers, vessels and parenchyma cells) seems to be chaotic, however, the general pattern is typical for *Viscum album*.

The second phase of radial growth is radial and axial ***cell enlargement***. The process takes place in the stage of primary wall formation, however, each cell type has its own expanding characteristic. Radially, fibers expand poorly, but longitudinally, they do so extensively (up to nine times), at which the axial ends become wedged. Axial parenchyma cells radially also expand poorly, and longitudinally only slightly; they generally remain in the state of the initials. Ray cells radially expand extensively, while longitudinally hardly at all. Vessels expand in radial, tangential and longitudinal direction.

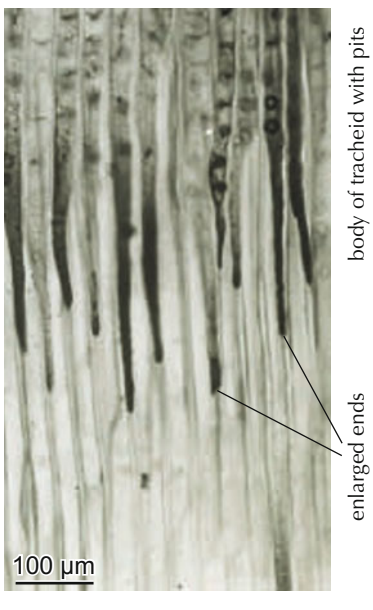
Cell enlargement



6.175 Derivates of xylem mother cells axially enlarge at different rates. Initial fiber and ray cells have the same radial dimension. Tracheids expand slightly; ray cells expand extensively. *Picea abies*.



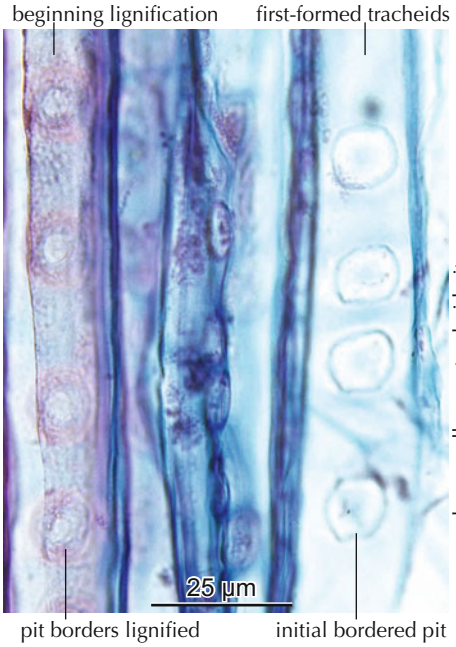
6.176 Derivates of xylem mother cells axially enlarge at different rates. Parenchyma cells stay more or less their initial length, however, fibers axially expand extensively. *Ulmus laevis*.



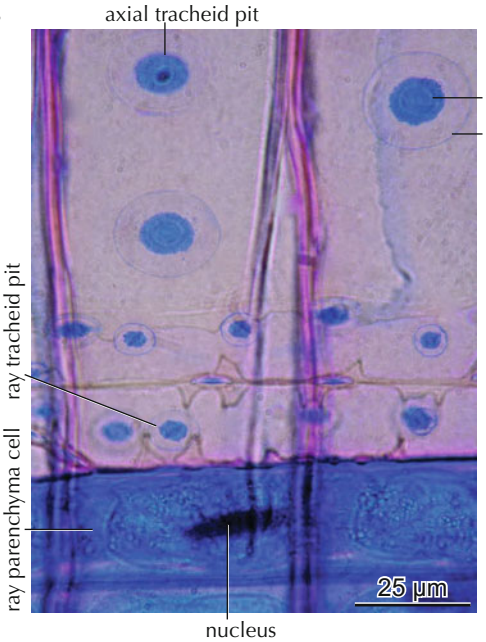
6.177 After elongation, the axially elongated tracheids in *Picea abies* become wedged.

Simultaneously with the wall expansion, ***cell-wall differentiation*** takes place. This is demonstrated here on bordered pits in conifers and dicotyledonous angiosperms. First, micro-fibrils form a submicrosopic comb-like pattern. Next, the outer border of the bordered pits in tracheids can be observed under a microscope. It indicates the final size of the tracheid wall. Differentiation of the pits takes place over the course of a few weeks into pits with lignified borders and unlignified tori. Tori of conifers lignify when they are no longer involved in the water-conducting process. This normally occurs at the sapwood-heartwood boundary.

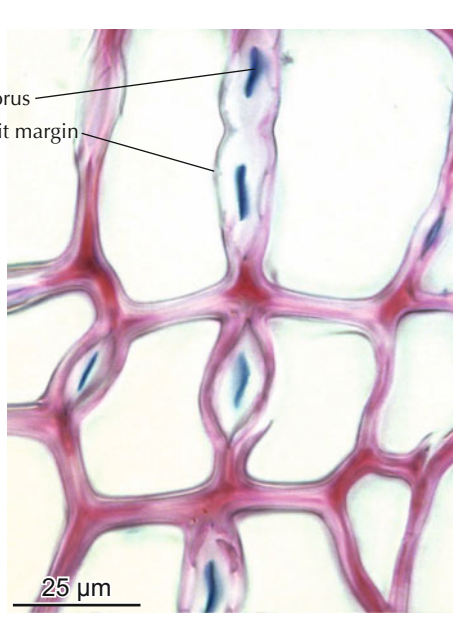
Cell wall differentiation and pit structure



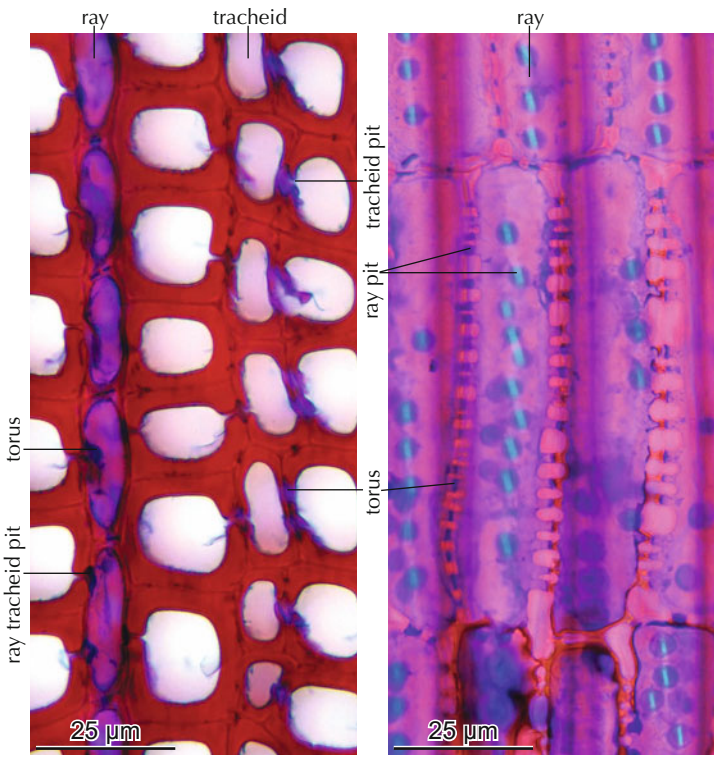
6.178 Formation of bordered pits in tracheids of the conifer *Picea abies*. First, unlignified, round, small pit borders appear. Development of the pit borders occurs simultaneously with lignification.



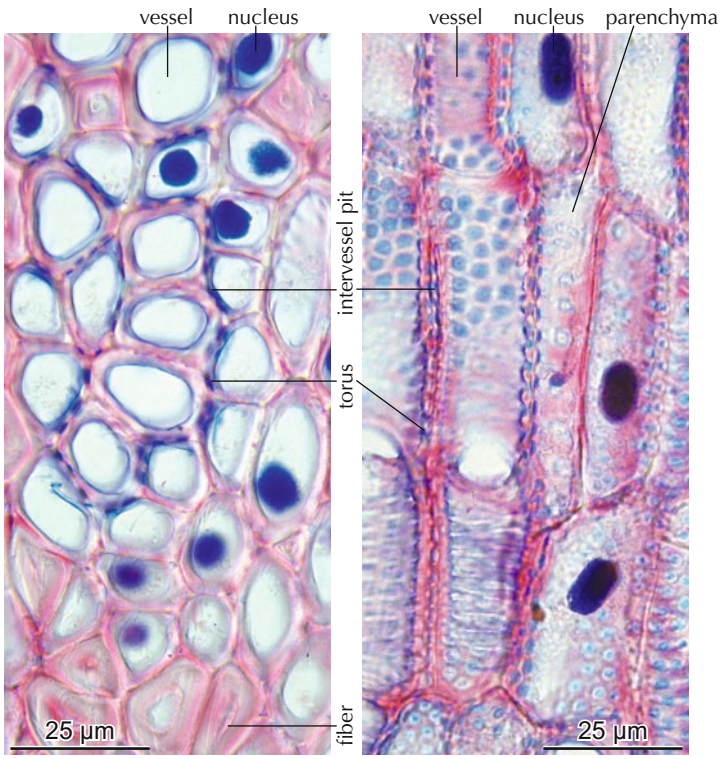
6.179 The final stage of the development near the cambium shows pits in axial tracheids and ray tracheids with large borders and unlignified tori in a radial section of *Pinus sylvestris*.



6.180 Final stage of the development of bordered pits in a transverse section of *Picea abies*. The borders are lignified, the tori are unlignified.



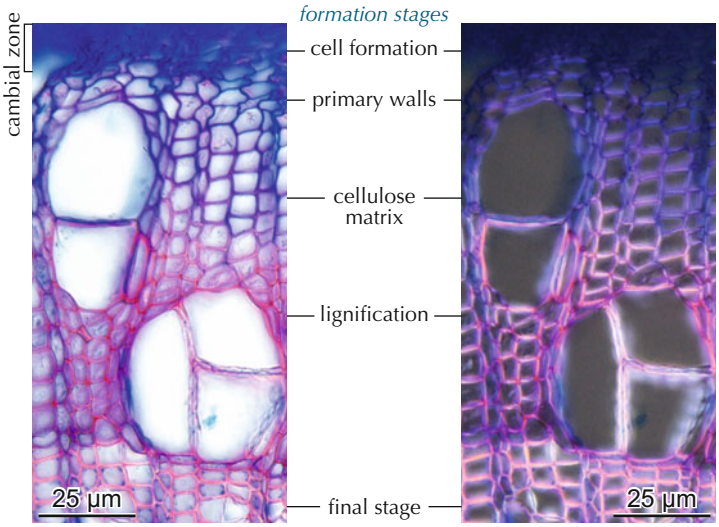
6.181 Tracheid pits with indistinct unlignified tori (blue) and ray tracheid pits with distinct, unlignified tori in a cross section (left) and radial section (right) of *Drimys piperita*.



6.182 Intervessel pits with distinct tori and vessel-ray pits with distinct, unlignified tori in a cross section (left) and tangential section (right) of *Viscum album*.

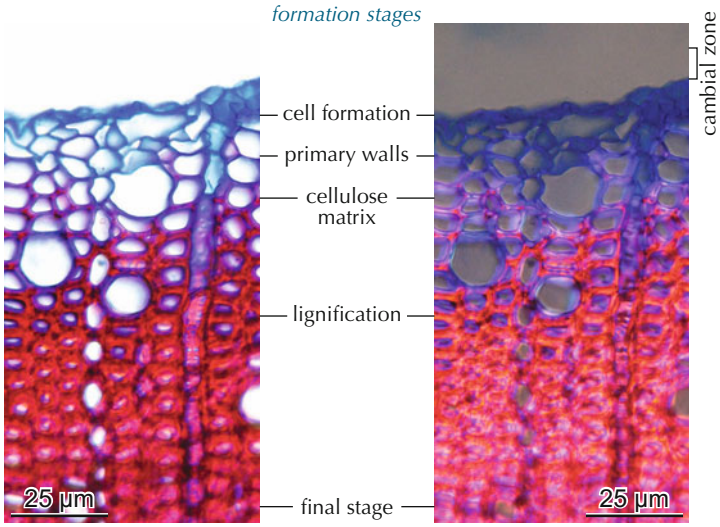
Cell-wall thickening and lignification are the last processes to take place. Lignification occurs immediately after or during the formation of the cellulose matrix. With the formation of the cellulosic matrix of the secondary wall, cell walls become thicker. This process is accompanied by the incrustation of lignin. It starts in primary walls in the corner of cells and expands towards the lumen of the cell. In conifers, all diffuse-porous species and in the latewood of ring-porous species, lignification occurs front-like behind the cambium. The lignification process is different in the earlywood of ring-porous species because the formation of earlywood vessels is asynchronous. Lignified vessels and the surrounding fibers of the first-formed cells stay side by side with newly formed, unlignified vessels.

Formation of the cellulose matrix and lignification of cells in angiosperms



6.183 Lignification of cell walls of vessels, fibers and rays in *Salix fragilis*. Ontogenetically young cells near the cambium are thin-walled and unlignified.

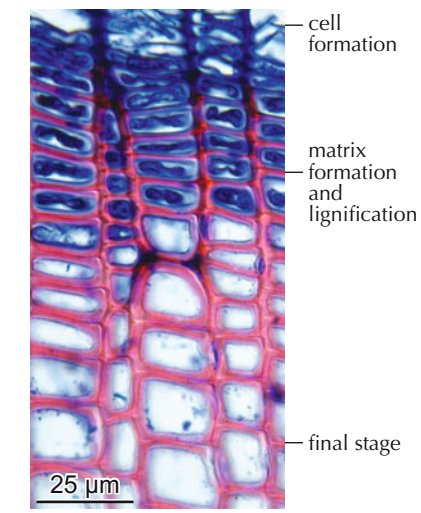
6.184 Cellulose-matrix formation is expressed by reflection in polarized light. Cellulose formation starts immediately after cell expansion is completed.



6.185 Cell-wall thickening, lignification of cell walls of vessels, fibers and rays in *Buxus sempervirens*. All cells near the cambium are thin-walled and unlignified. The thickening and lignification process occurs within 8–10 cell rows.

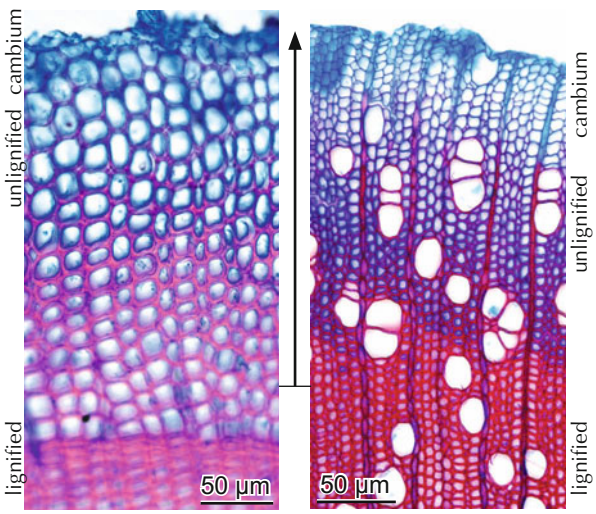
6.186 Cellulose-matrix formation is expressed by reflection in polarized light. Cellulose formation starts immediately after cell expansion is completed.

Conifers



6.187 Cells with protoplasts continuously produce cellulosic matrix and lignin. This process occurs during several months in *Picea abies*.

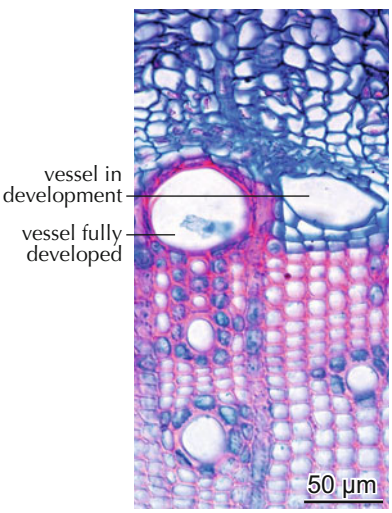
Continuous processes



6.188 Continuous cell-wall thickening and lignification in the conifer *Abies alba*.

6.189 Continuous cell-wall thickening and lignification in the diffuse-porous angiosperm *Prunus padus*.

Discontinuous processes



6.190 Cell formation and lignification occurs at different times in *Fraxinus excelsior*.

Ring formation in plants of seasonal climates is principally divided into a dormant and an active phase. Cell division by the cambium and cell growth (enlargement, lignification) are part of the active phase. The beginning of cambial activity is indicated by a large, anatomically undifferentiated cambial zone, while this zone is much smaller during dormancy. Genetic factors dictate the rhythm of cell-type formation (e.g. into fibers or vessels), and environmental factors modify the general principle and regulate the quantity and the size of cells.

The duration and occurrence of a ring-formation period varies*. It depends on:

- ***Taxonomy***. For example, in 2001, the cambial activity of *Prunus padus* trees in the lowland of temperate zones began in week 13 (late March), while that of *Juglans regia* trees began in week 23 (early June; Schweingruber & Poschlod 2005). Species-specific differences in timing in herbs can be much larger, e.g. *Erophila verna*, an annual small herb, fulfills its stem-formation cycle within three weeks in early March, and the small *Euphrasia cuspidata* within three weeks in August.
- ***Climate conditions***. Xylem formation in the arctic lasts for one to two months, in the temperate lowland four to five months, and in the tropical rain forests there often is no dormant period.
- ***Site conditions***. For example, the cambial activity of tall trees in the lowland of temperate zones begins mid-April and that of suppressed small individuals in June. Ring formation on south-facing slopes in the arctic starts in early July and in snow beds in early August.

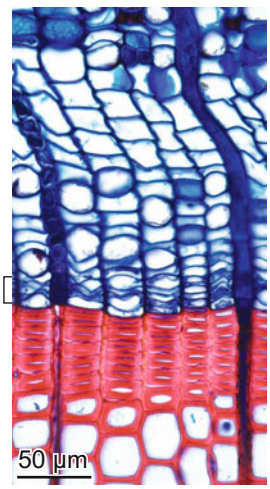
Cambium width

Modification of ring formation due to

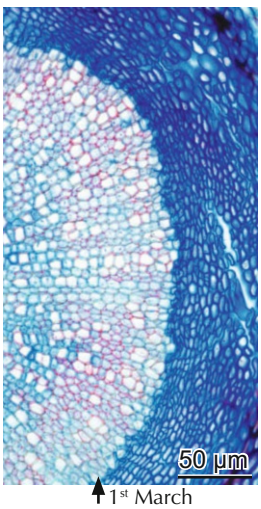
taxonomy

climate conditions

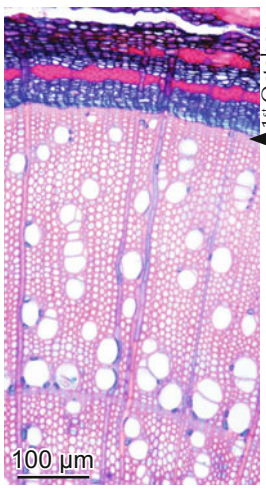
site conditions

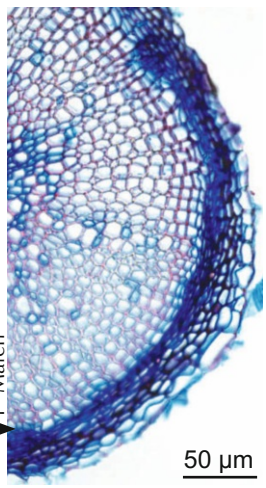


6.191 Small cambial zone during the dormant period in *Larix decidua*.



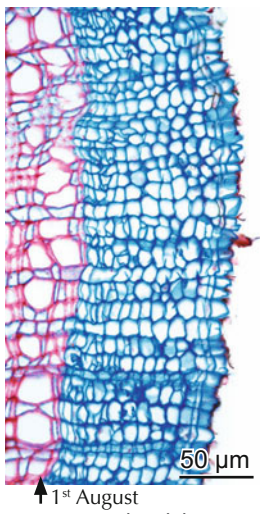
6.192 Ring formation is completed within three weeks in February in the annual herb *Erophila verna*.



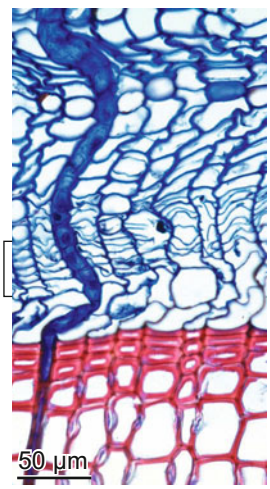


6.193 Ring formation occurs in temperate climates during four to five months from April to September. *Acer campestre*.

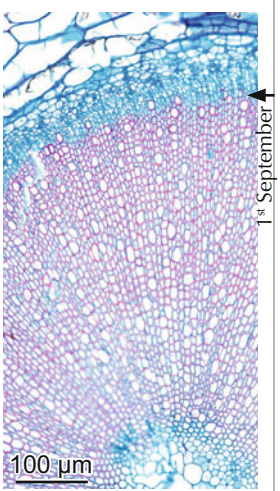
6.194 Almost completed ring in the herb *Thlaspi perfoliatum* at the end of February in the Mediterranean zone of Cyprus.



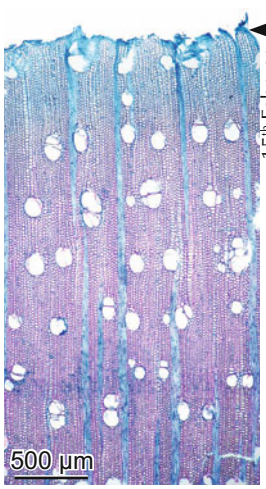
6.195 Completed last ring in *Arctostaphylos alpina* at the beginning of August on a sunny slope in Greenland.



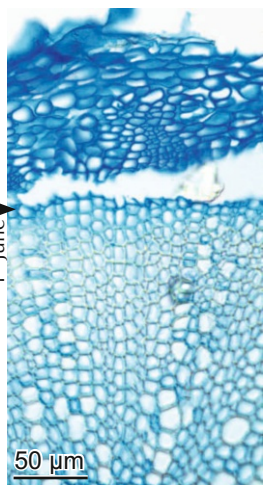
6.196 Large cambial zone in the active period in the earlywood of *Larix decidua*.



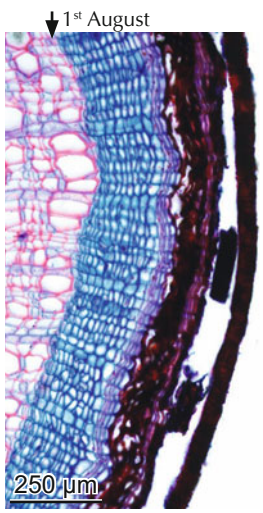
6.197 Ring formation is completed within four weeks in August in the annual herb *Euphrasia cuspidata*.



6.198 Ring in formation in the tree *Schefflera abyssinica* in a tropical rain forest. Ring formation lasts 11–12 months.



6.199 Incomplete ring in the herb *Thlaspi perfoliatum* at the end of April in the temperate zone of Switzerland.



6.200 Incomplete last ring in *Dryas octopetala* at the beginning of August in a snow bed in Greenland.

*All examples discussed on this page relate to Northern Hemisphere seasons.

6.2.6 Cell differentiation in the *phloem* – The multifunctional stem periphery

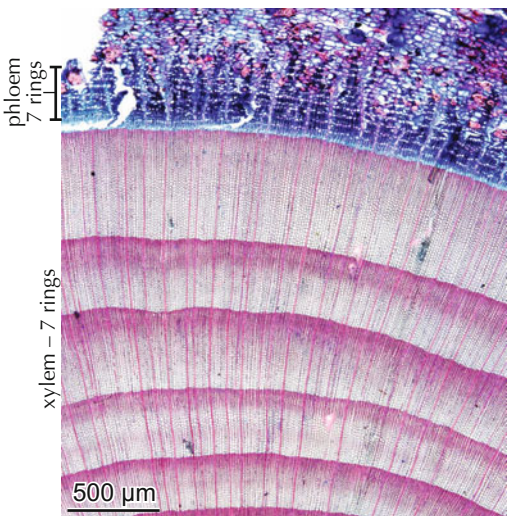
Most cell formation processes described for the xylem also occur in the phloem: cell type differentiation, cell-wall differentiation, nucleus differentiation, cell-wall enlargement, cell-wall thickening, lignification and formation of crystals are the basic steps.

The following aspects are different than in the xylem (Huber 1961):

- Phloem mother cells normally produce less new cells than the xylem mother cells.
- Annual rings are mostly less distinct and smaller in the phloem than in the xylem.
- Vessels are replaced by sieve elements and companion cells.
- Spatial restrictions often lead to more intensive cell-wall enlargement and lateral cell divisions in rays (dilatation).
- Bordered pits in tracheids or vessels are replaced in the phloem by lateral sieve areas; perforation plates in vessels are replaced by axial sieve plates.
- The xylem normally forms a dense block of tissue onto which the phloem gets pushed, which results in collapsed sieve elements. As soon as sieve tubes die they collapse due to the higher turgor of neighboring parenchyma cells, the pressure from newly formed cells and/or the strength of the phellem belt. The processes primarily take place in the juvenile stage between the cortex and the xylem and in adult stages between the xylem and the rhytidome (isolated dead tissues formed by the phellogen). (Holdheide 1951)

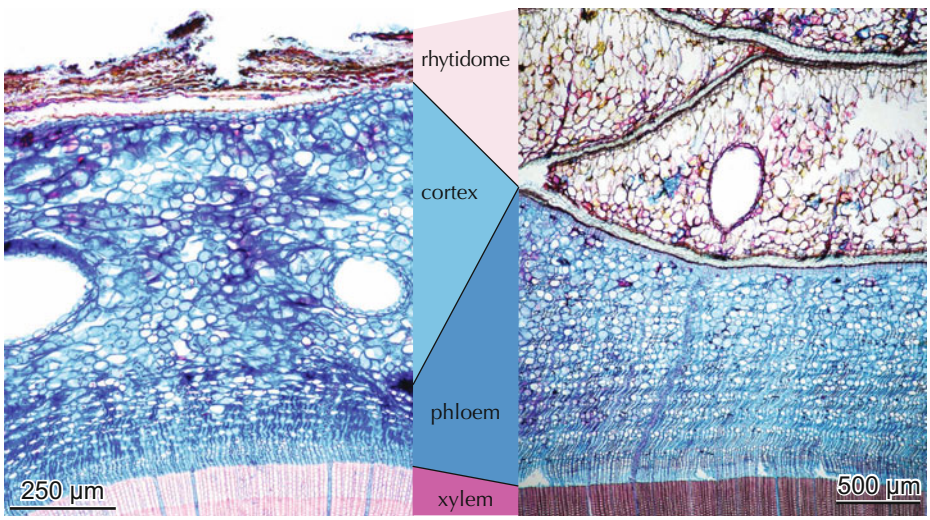
Shown below are the principal changes during the thickening and aging process for a conifer, and a diffuse-porous and a ring-porous angiosperm.

Proportion of xylem and phloem



6.201 Comparison of xylem and phloem rings in *Abies alba*. Xylem/phloem = 7:1, xylem rings distinct, phloem rings only distinct in first few years.

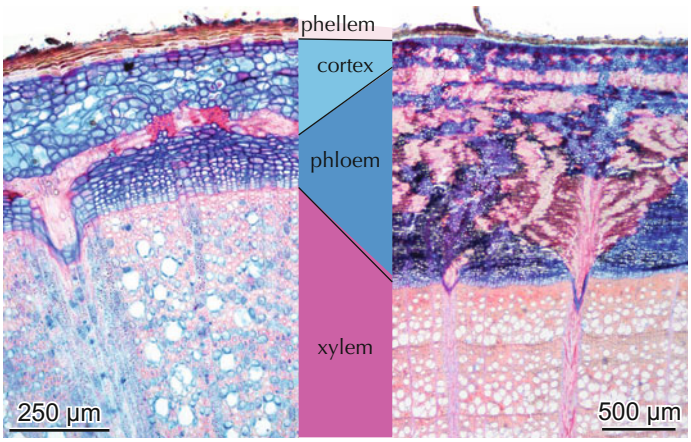
Differentiation during stem thickening and aging in conifers



6.202 Juvenile bark of the conifer *Pinus sylvestris*. Characteristic are the small phloem, a large cortex and a small rhytidome.

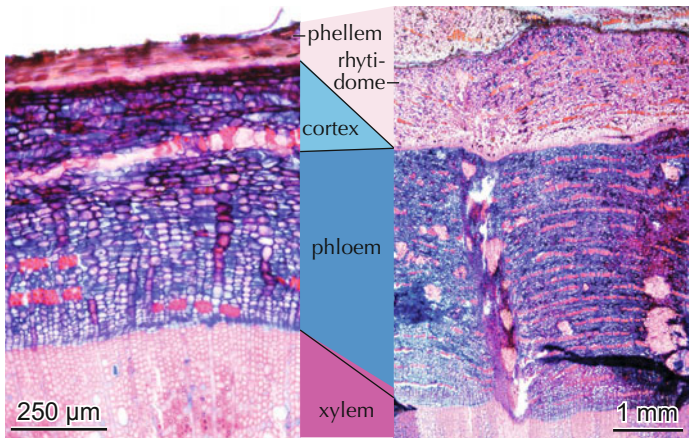
6.203 Adult bark of the conifer *Pinus sylvestris*. Characteristic are the large phloem, an absent cortex and a large rhytidome.

Differentiation during stem thickening and aging in angiosperms



6.204 Juvenile bark of the deciduous angiosperm *Fagus sylvatica*. Characteristic are a small phloem, a large cortex containing a continuous fiber/sclereid belt and a small periderm.

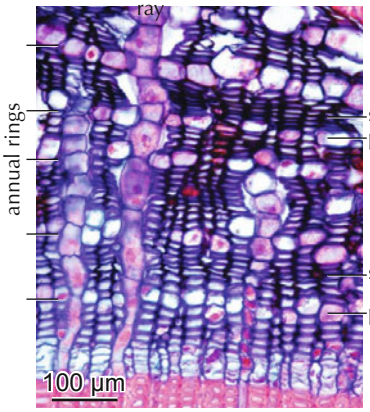
6.205 Adult bark of *Fagus sylvatica*. Characteristic are a large phloem with sclereid groups, a very small cortex with remnants of the juvenile fiber/sclereid belt and a small periderm; rhytidome is absent.



6.206 Juvenile bark of the deciduous angiosperm *Quercus robur*. Characteristic are a large phloem containing groups of fibers, a large cortex with a continuous fiber/sclereid belt and a small periderm; rhytidome is absent.

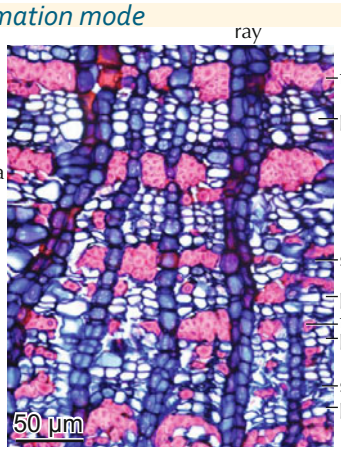
6.207 Adult bark of *Quercus robur*. Characteristic are a large phloem, consisting of many bands of groups fibers and a few groups of sclereids, and a rhytidome; cortex is absent.

Changing formation mode

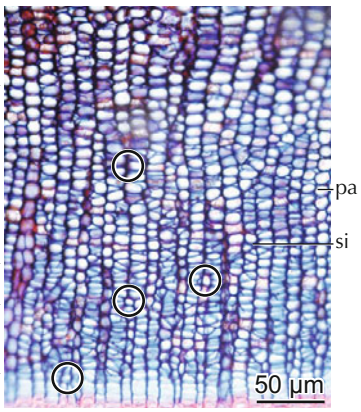


6.208 Annual rhythms in *Abies alba* are indicated by a tangential row of early-bark parenchyma cells and several rows of late-bark sieve cells.

6.209 Regular rhythms in *Juniperus communis* are indicated by thin-walled tangential rows of sieve cells, parenchyma cells (with nuclei) and thick-walled fibers. Annual growth rates are indistinct.

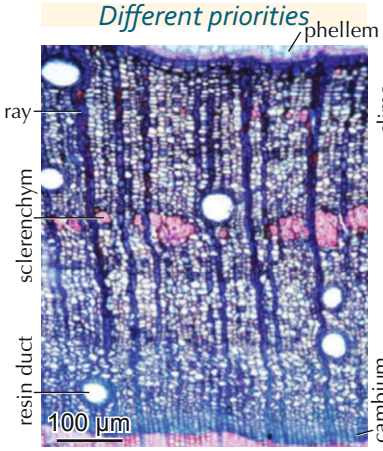


6.210 Rhythms are indicated in *Sorbus chamaemespilus* by poorly differentiated zones of sieve tubes and parenchyma cells and distinct groups of fibers. Fibers probably develop in the second year.



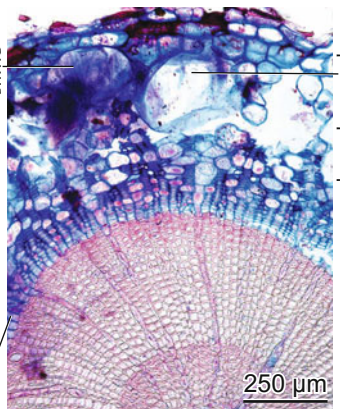
6.211 Arrhythmic formation of sieve tubes, companion cells and parenchyma cells in *Buxus sempervirens*. Radial rows are not permanent due to aperiodic lateral cell divisions and cell death (circles).

Different priorities

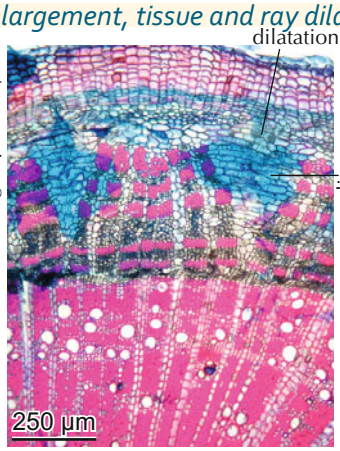


6.212 The general pattern in *Cotinus coggygria* changes periodically when the cambial mode changes to the production of resin ducts. In later stages, living parenchyma cells produce thick secondary walls (sclereids).

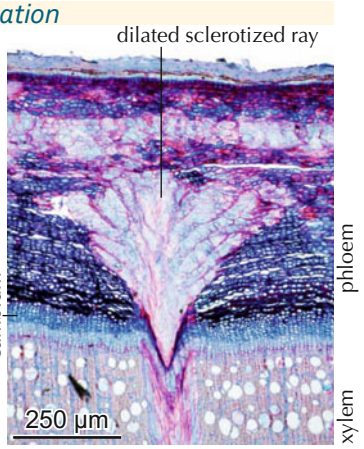
Cell enlargement, tissue and ray dilatation



6.213 Extensive cell enlargements of parenchyma cells in the cortex of *Abies alba*. The enlarged parenchyma cells produce slime.

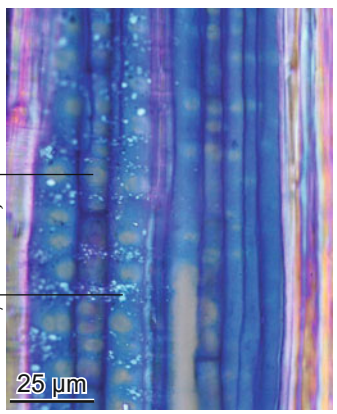


6.214 Lateral cell divisions and cell-wall expansion increase the circumference of the stem wedge-like in *Lavatera acerifolia*.

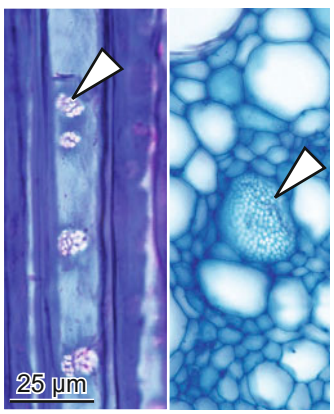


6.215 Ray dilatation and sclerotization in *Fagus sylvatica*.

Cell-wall differentiation and pit structure



6.216 Sieve tubes in the cambial zone of *Metasequoia glyptostroboides*. Calcium oxalate crystals seem to play a physiological role in the formation of the primary wall.

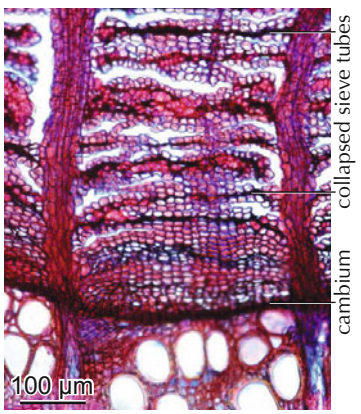


6.217 Left: Adult sieve plates on radial walls in *Larix decidua*.

Right: Sieve plate on the axial end of a sieve tube in *Nelumbo nucifera*.

Collapse of sieve tubes

6.218 Irregular pattern of collapsed sieve tubes in *Hippophae rhamnoides*. Sieve tubes in the cambial zone are not collapsed.



6.219 Tangential lines of collapsed sieve tubes in *Laburnum anagyroides*.

6.2.7 Formation of tertiary meristems, the cork cambium – A new skin

Tertiary meristems determine the face of tree stems because the formation mechanisms are species-specific.

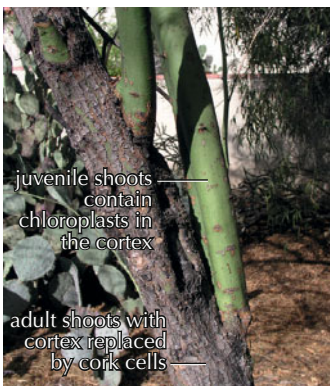
Periderms in the bark

Most plants with secondary growth form a tertiary meristem, which is located somewhere in the bark: the ***phellogen***. Toward the inside, the phellogen produces a few long-lived parenchyma cells, the ***phelloderm***, and towards the outside, it produces various amounts of short-lived cork cells, the ***phellem***. Their walls consist of cutin or suberin. Their origin are living parenchymatic cells. In young shoots, parenchyma cells of the cortex, and in older shoots, parts of the phloem get reactivated to meristems. The number of formed cells is normally much bigger towards the outside than towards the inside. The zone of phellogen, phelloderm and phellem is called ***periderm***. All dead phloem and cortex parts outside of the phellogen are called ***rhytidome***. This formation mode occurs in all growth forms of conifers and dicotyledons.

With continuous stem thickening and the associated tension, the external phellogen and adjacent phloem and cortex parts die and normally flake off. Rhytidomes are species-specific. Therefore tree species can be identified macroscopically by their bark: the face of the tree. Godet 2011 presents the bark of central European tree species.

Cork formation is essential for most perennial terrestrial plants because cork layers build a continuous mantle around the plant. It protects the plant lifelong against mechanical and biological damages.

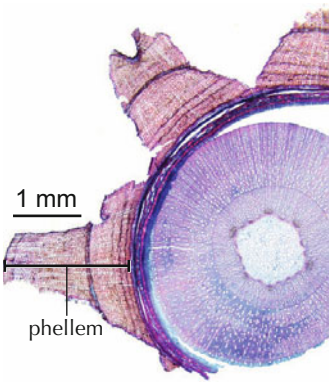
Morphology of the bark



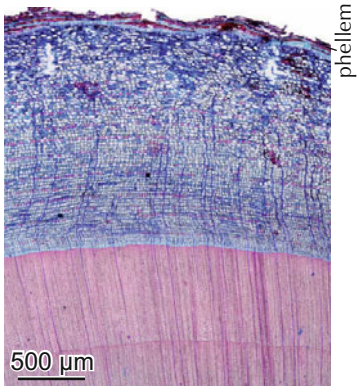
6.220 Juvenile shoots and adult bark in *Prosopis* sp.

6.221 The phellem in *Acer griseum* thinly flakes off.

Size of the cork mantle

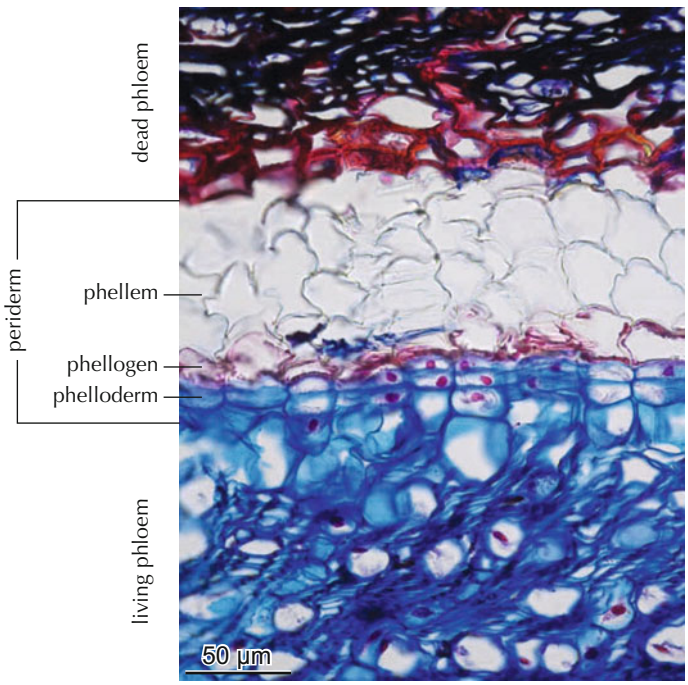


6.222 Large phellem in *Acer campestre*.



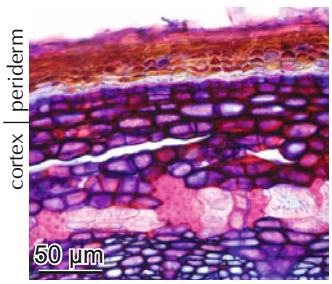
6.223 Small phellem in *Taxus baccata*.

Definition of the formation zone

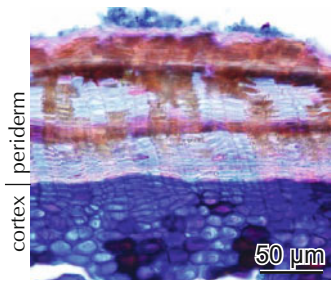


6.224 Bark of *Pinus mugo*.

Periderms formed in the cortex

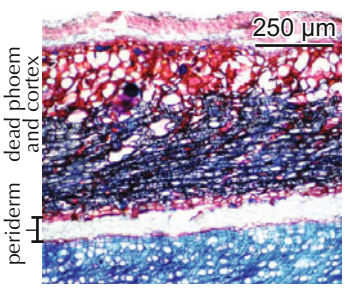


6.225 Bark of *Carpinus betulus*.

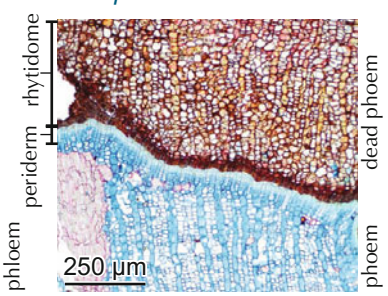


6.226 Bark of *Betula pendula*.

Periderms formed in the phloem



6.227 Bark of *Pinus mugo*.



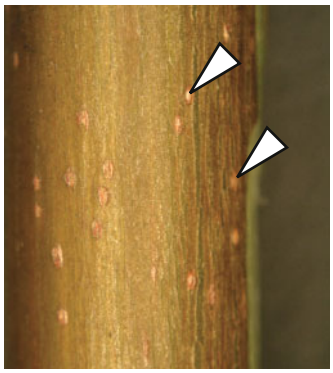
6.228 Bark of *Alnus glutinosa*.

Periderms form lenticels

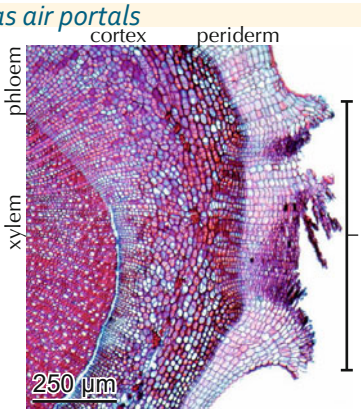
Phellem layers seal the stem. The phellogen locally creates perforations in the young twigs by accelerated cork-cell production: the lenticels. Lenticels occur on young twigs and especially on roots in wet environments. The phellogen locally forms an external tissue with numerous intercellulars, which permit the entrance of air to the cortex.

Lenticels as air portals

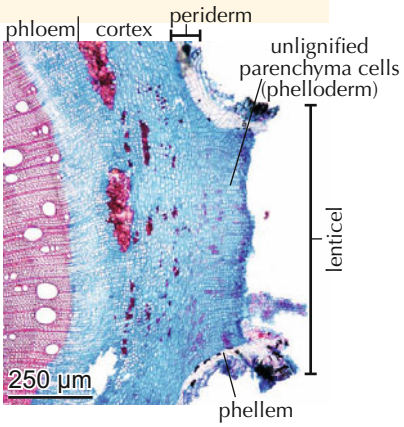
6.229 Twig with flowers of *Forsythia suspensa*.



6.230 Annual twig of *Acer pseudoplatanus* with lenticels.



6.231 Lenticel in a twig of *Forsythia suspensa*.



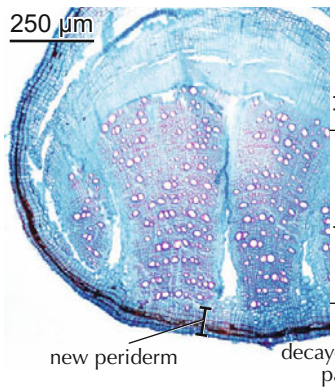
6.232 Lenticel in a root of *Alnus glutinosa*.

Periderms in stem centers

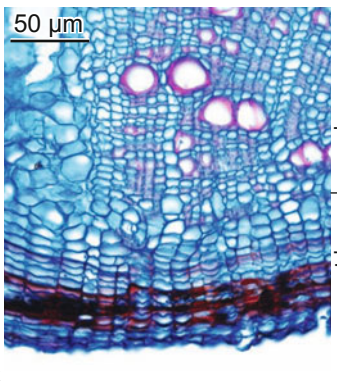
A special form of cork formation can occur, mainly in small, long-lived plants of certain families (e.g. Lamiaceae, Rosaceae, Fabaceae or Aceraceae) at high altitudes and northern latitudes. As soon as a plant is unable to maintain the metabolism of the stem as a whole, living parenchyma cells in the xylem get reactivated to form a cork cambium, the products of which separate part of the living tissue towards the inside. This process occurs repeatedly and forms an internal rhytidome inside the stem.

Periderms in stem centers as protection layers

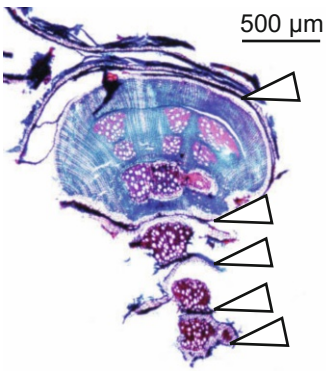
6.233 *Potentilla nitida*, Rosaceae, a 5 cm-tall alpine plant with a long-lived rhizome.



6.234 Rhizome of *Potentilla nitida* with a re-shaped, round stem. The original central part disappeared and the wood was sealed by a periderm.



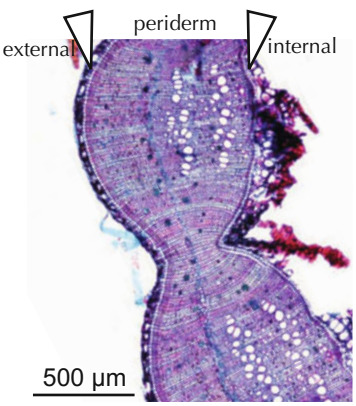
6.235 The new periderm in *Potentilla nitida* bridged vessel/parenchyma parts and enlarged rays.



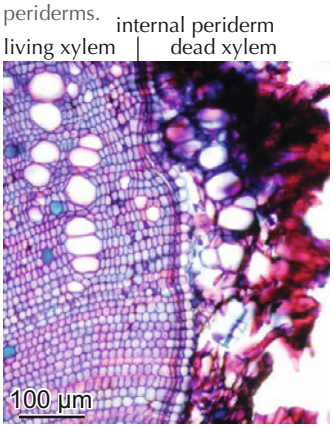
6.236 Rhizome of the alpine herb *Nepeta discolor*, Lamiaceae, with one active and four inactive central periderms.

6.237 *Epilobium angustifolium*, Onagraceae, with a long-lived rhizome.

6.238 Rhizome of *Epilobium angustifolium* with a small living part and many central dead periderms.



6.239 Living part of the rhizome of *Epilobium angustifolium*, with a central periderm.

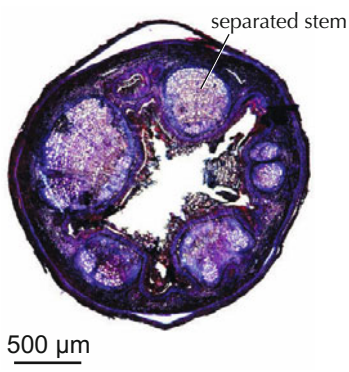


6.240 The central periderm of *Epilobium angustifolium*.

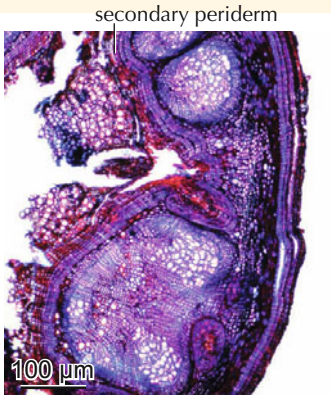
Periderms as protection layers

6.241 *Saussurea gnaphalodes*, Asteraceae, a 5 cm-tall alpine plant with a long-lived rhizome.

6.242 Rhizome of *Saussurea glanduligera*, composed of many separated partial rhizomes.



6.243 Stem separation by central periderms in *Potentilla crantzii*, Rosaceae.

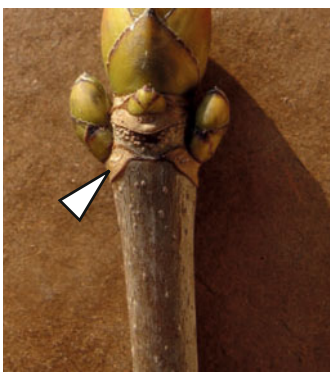


6.244 Stem compartments separated by secondary periderms in *Potentilla crantzii*.

Periderms as breaking zones for leaves

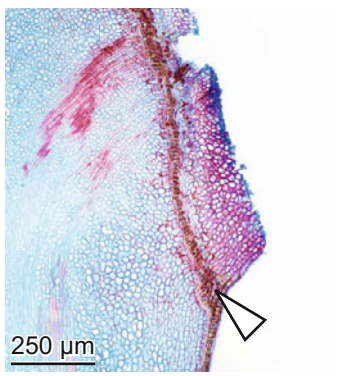
Just as important are the accelerated cork-formations at the break-off zones of leaves. Long before the leaves drop, the phellogen becomes active and forms a layer of phellem cells. As soon as the leaves drop, the potential wound is already sealed.

Breaking zones for leaves

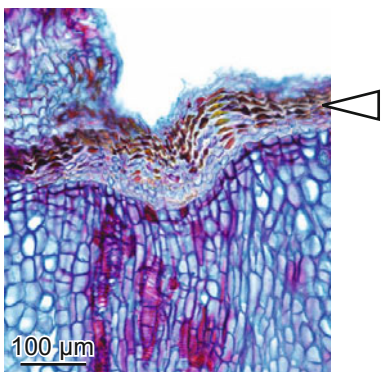


6.245 Leaf scar below a bud of *Acer pseudoplatanus*.

6.246 Leaf scars in a cabbage stem, *Brassica oleracea*.



6.247 Leaf of *Castanea sativa*, separated by a periderm.



6.248 Periderm on a leaf scar in *Castanea sativa*.

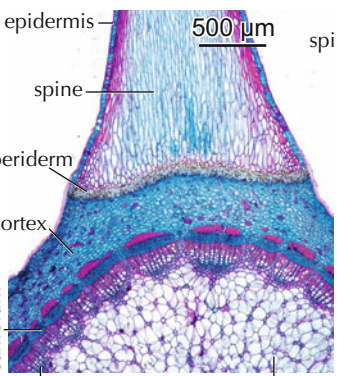
Periderms as breaking zones for spines

Spines are products of local periderms. In contrast to all other periderms they differentiate into special forms. Spines occur on stems, e.g. of *Bombax ceiba* (cotton tree), roses and others, and on fruits, e.g. of *Aesculus hippocastanum* (horse chestnut). The spine itself is a product of the hypodermis (cells just below the epidermis) and the breaking zone is the outermost part of the periderm, the phellem.

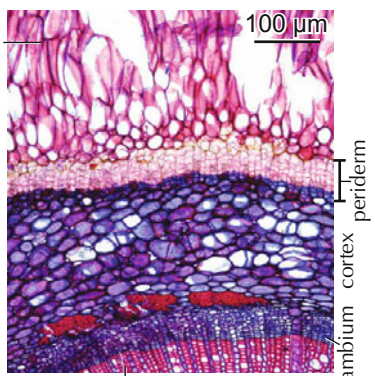
Breaking zones for spines

6.249 Spines on the stem of *Bombax ceiba*, Malvaceae.

6.250 Spines on a twig of *Rosa arvensis*, Rosaceae.



6.251 Spine on a twig of *Rosa arvensis*.



6.252 Breaking zone of a spine of *Rosa arvensis*.

In the following, the ***programmed cell death*** or ***apoptosis*** is anatomically described. ***Genetically predetermined cell death*** is behind all phenomena in which plants shed leafs, twigs or fruits. These processes have partially been described in Chapter 6.2.7 "Tertiary meristems". Death is part of any living organism. The physiologically driven dying process is called apoptosis or programmed cell death. The live span of the entire plant body is also genetically predetermined.

Aging processes, called ***senescence***, lead to the death of central parts of the stem (heartwood formation) or of entire plant bodies. Annual plants sometimes survive for only a few weeks, while perennials live for up to 5,000 years.

Externally induced cell death is behind all phenomena in which pathological factors or extreme ecological conditions determine cell death. This dying process is called necrosis or necrobiosis and is described in Chapter 10.6.

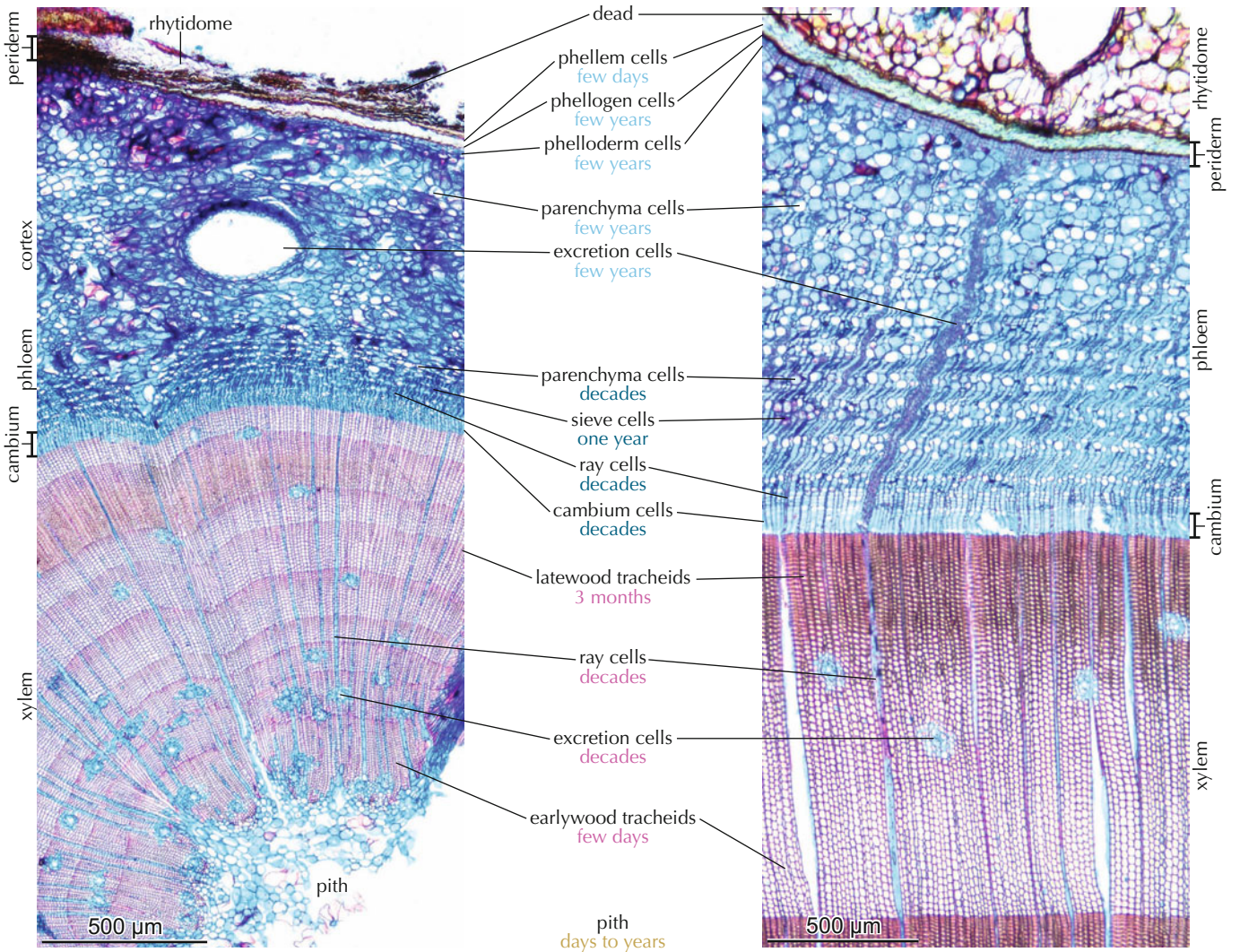
Programmed cell death within living parts of plants

A healthy, functioning plant body is based on a perfectly designed balance of living and dead cells. Genetically induced programs activate enzymes (caspases), which determine the longevity of cells. Meristematic cells of clonal plants theoretically can live forever. The life span of their derivates varies within a time range of a few days up to more than 100 years; in reality only parenchymatic cells have such a long life span. Xylem and phloem mother cells, conducting tissues (tracheids, vessels, cork cells and sieve elements) and sclereids have a short live span. Illustrated in the following is the age mosaic of juvenile and adult tissues in conifers and deciduous angiosperms.

Programmed cell death separates living and dead parts – Heartwood formation

The macroscopic characteristics of heartwood are described in Chapter 6.2.1, and of heartwood substances in Chapter 5.6.5 (Fig. 5.99–5.118). For deeper insight into heartwood formation processes see Fromm 2013.

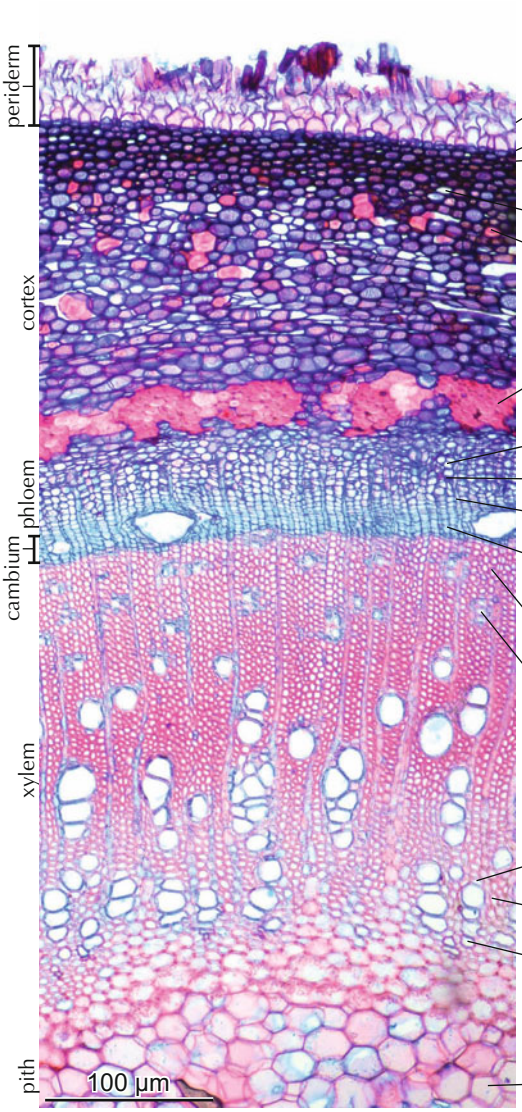
Longevity (days, months and years) of different cells in the xylem, phloem, cortex and periderm of conifers



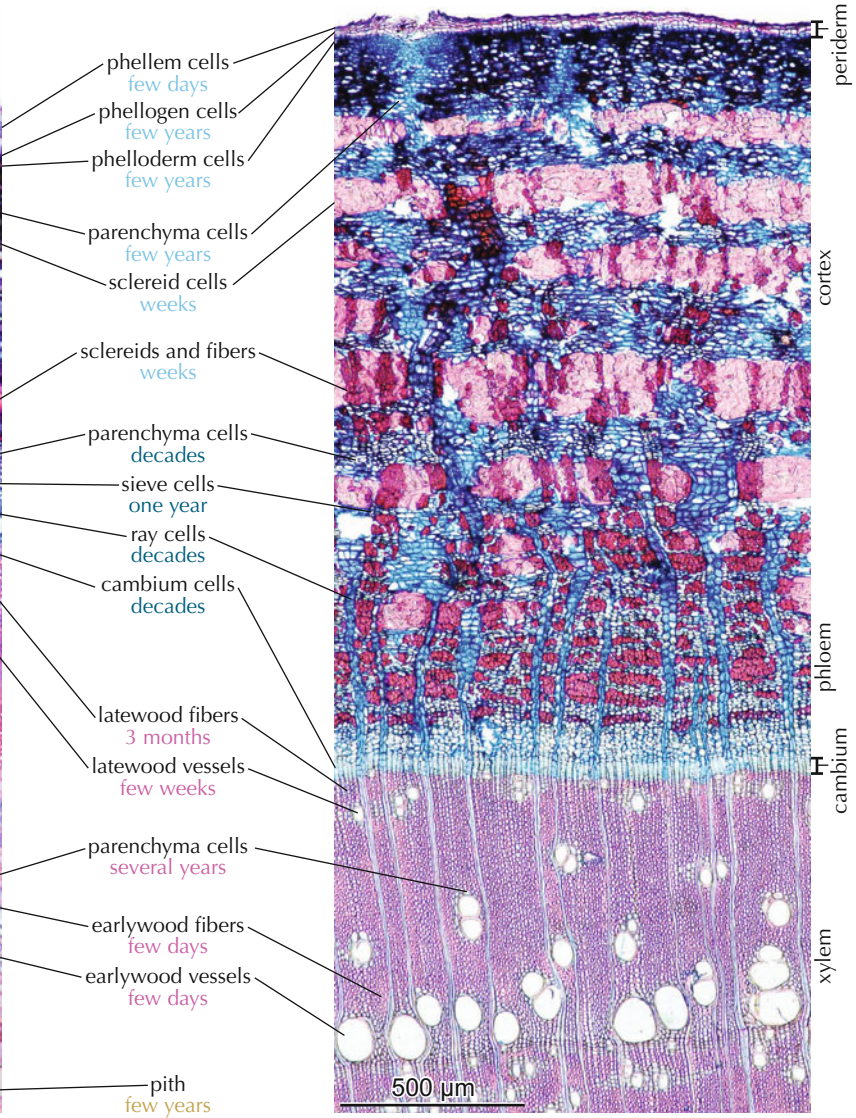
6.253 Juvenile tissues in a nine-year-old twig of *Pinus mugo*.

6.254 Adult tissue in a 60-year-old stem of *Pinus sylvestris*.

Longevity (days, months and years) of different cells in the xylem, phloem, cortex and periderm of dicotyledons

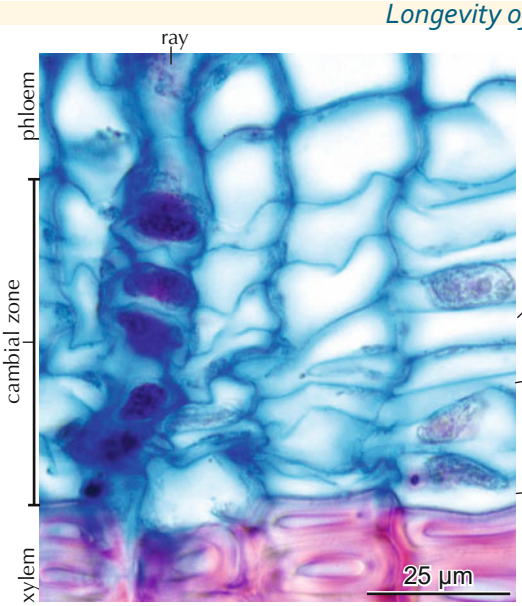


6.255 Juvenile tissue in a one-year-old twig of *Fraxinus excelsior*.

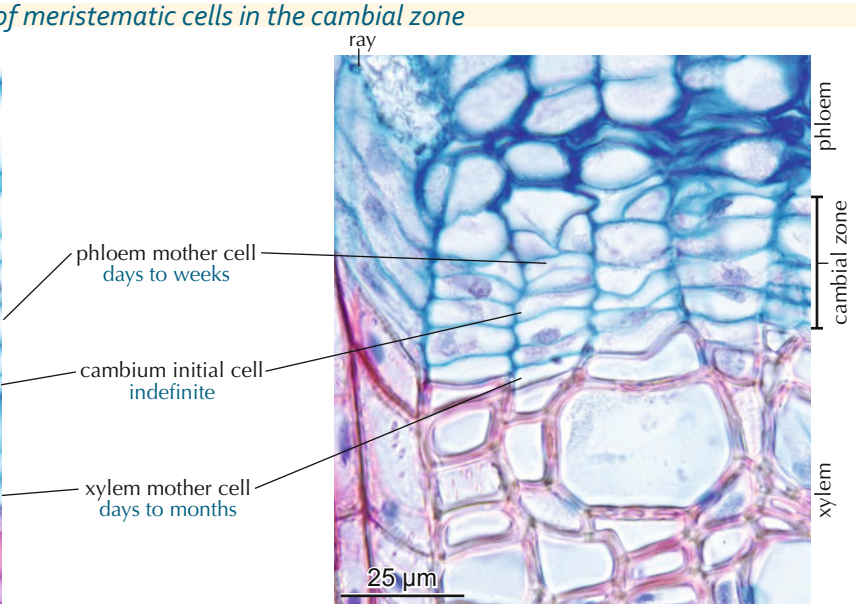


6.256 Adult tissue in a 30-year-old stem of *Fraxinus ornus*.

Longevity of meristematic cells in the cambial zone



6.257 Conifer *Pinus sylvestris*.



6.258 Dicotyledonous *Sambucus nigra*.

6.3 Cambial variants – Phloem elements within the xylem

Within the groups of palm ferns (Cycadopsidae) and dicotyledonous angiosperms species exist in which the cambium does not constantly produce a centripetal xylem and a centrifugal phloem. This group principally contains two formation modes which each include many different subtypes.

One cambium periodically produces centripetal bark elements

A phloem containing sieve cells, companion cells and parenchyma cells, or cork cells. The normal formation mode (vessels, fibers, parenchyma) is expanded to elements of the phloem or the periderm.

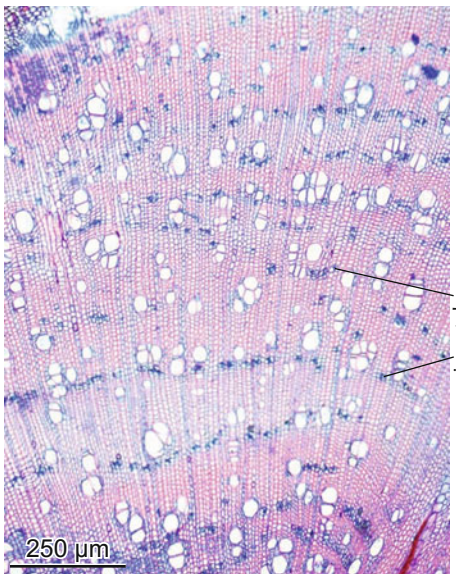
Several circular arranged cambia simultaneously produce xylem and phloem

This group comes under the term plants with ***successive cambia***. Within this unit there are principally two groups:

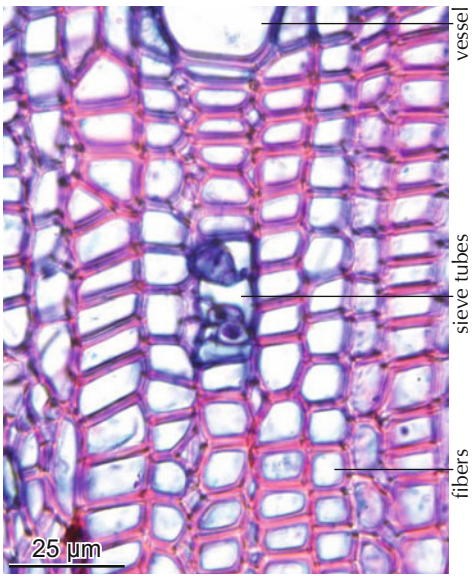
- The cambia periodically produce single collateral vascular bundles, which are located within a parenchymatic tissue. However, specific taxonomic groups anatomically modify these modes. Of special interest are monocotyledonous representatives (Agavaceae), which continuously produce concentric vascular bundles.
- The cambia produce tangential bands of xylem and phloem within a parenchymatic tissue.

One cambium produces fibers, vessels and, periodically, groups of sieve tubes and parenchyma cells or bands of cork

6.259 The herb *Gaura lindheimeri*, Onagraceae.

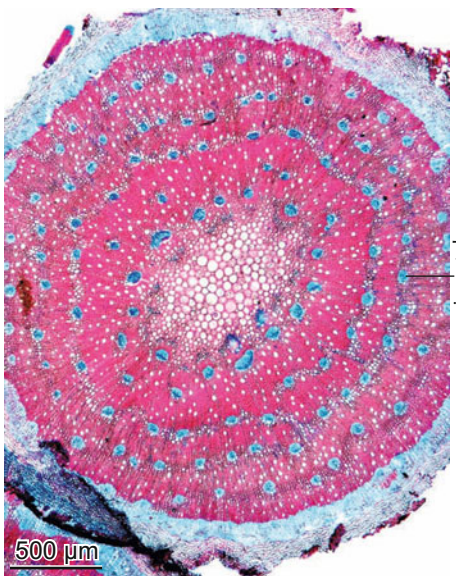


6.260 Tangential rows of groups of sieve tubes in *Gaura lindheimeri*.

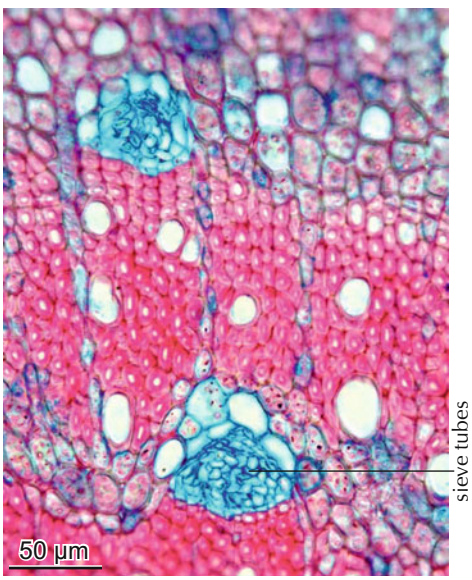


6.261 Group of sieve tubes with companion cells containing nuclei in *Gaura lindheimeri*.

6.262 The shrub *Simmondsia chinensis*, Simmondsiaceae.



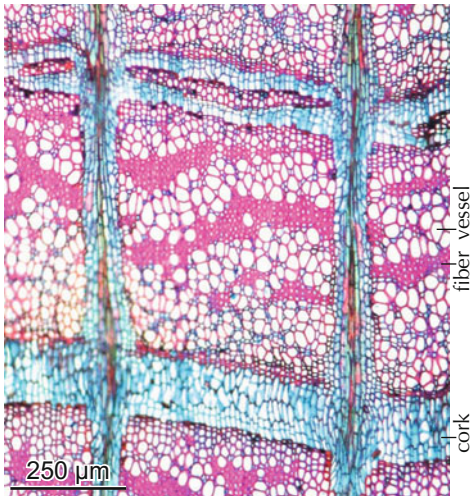
6.263 Circular rows of groups of sieve tubes in *Simmondsia chinensis*.



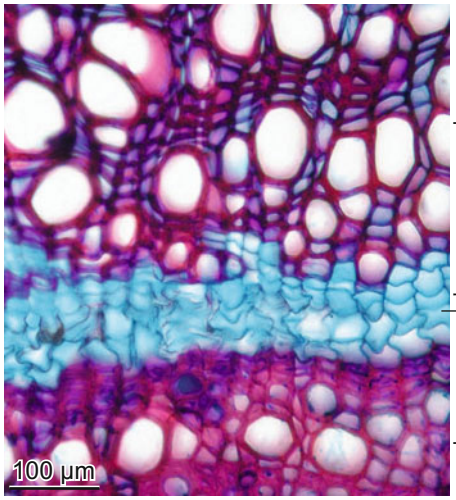
6.264 Groups of sieve tubes and parenchyma cells within a dense fiber/vessel tissue in *Simmondsia chinensis*.

One cambium periodically produces xylem and bands of cork

6.265 The dwarf shrub *Artemisia tridentata*, Asteraceae.



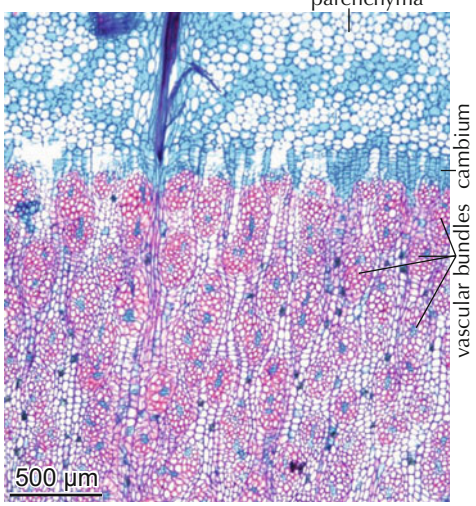
6.266 Tangential bands of cork cells between a vessel/fiber tissue in *Artemisia tridentata*.



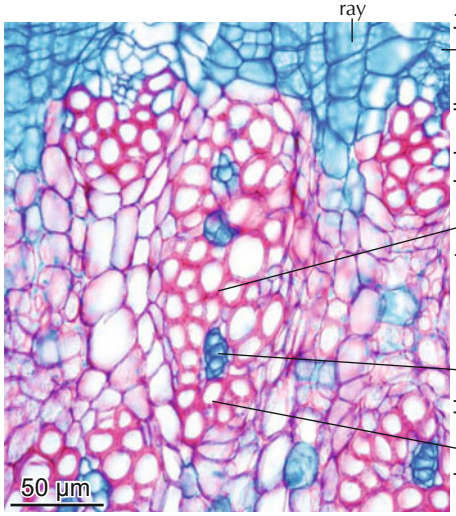
6.267 Thin-walled cork cells in the xylem of *Tanacetum millefolium*.

One cambium produces concentric vascular bundles

6.268 The monocotyledonous tree *Dracaena serrulata*, Asparagaceae.

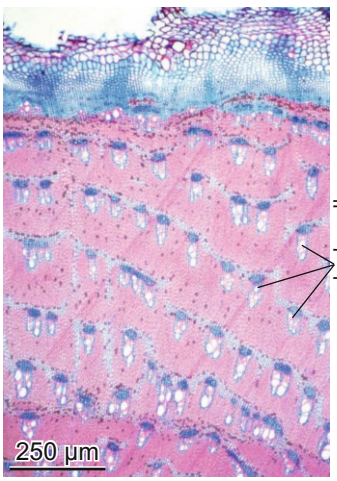


6.269 Xylem and cortex of *Dracaena serrulata*.

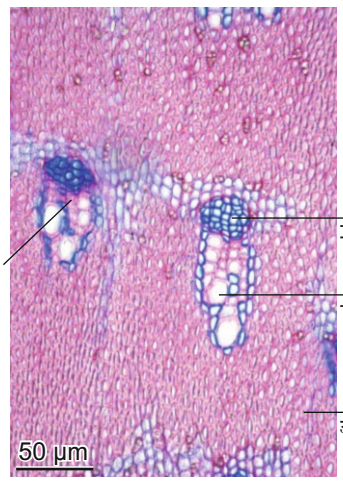


6.270 Single concentric vascular bundles between rays in *Dracaena serrulata*.

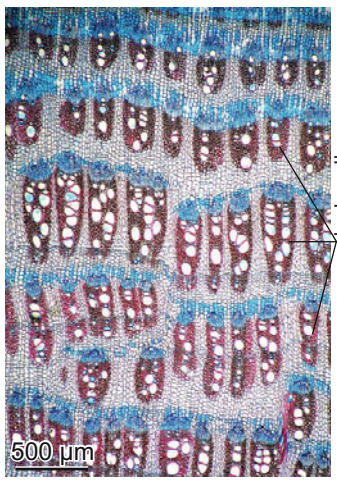
Several cambia periodically produce single collateral vascular bundles, fibers and parenchyma cells



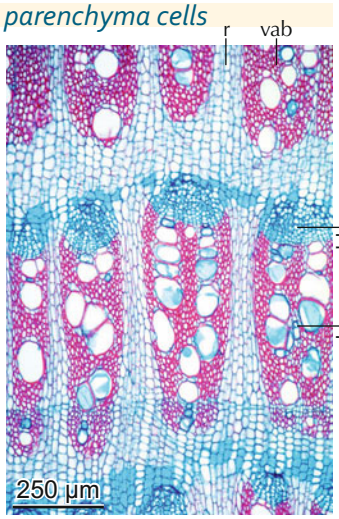
6.271 Isolated vascular bundles within a dense fiber tissue in *Bassia prostrata*, Amaranthaceae.



6.272 Vascular bundles within a dense fiber tissue in *Bassia prostrata*.



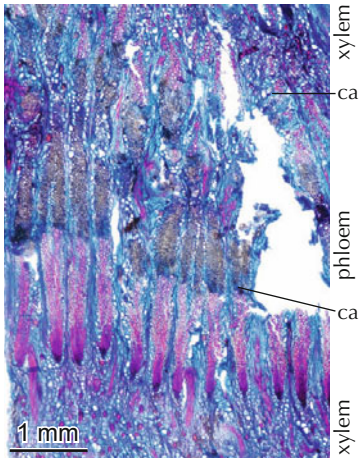
6.273 Tangentially arranged vascular bundles in *Bosea cypria*, Amaranthaceae.



6.274 Vascular bundles between rays in *Bosea cypria*.

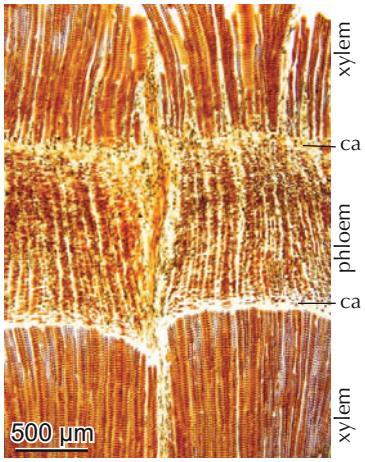
Several cambia periodically produce bands of xylem and phloem

6.275 *Welwitschia mirabilis*, Welwitschiaceae. Photo: P. Poschlod.



6.276 Two tangential rows of vascular bundles in *Welwitschia mirabilis*.

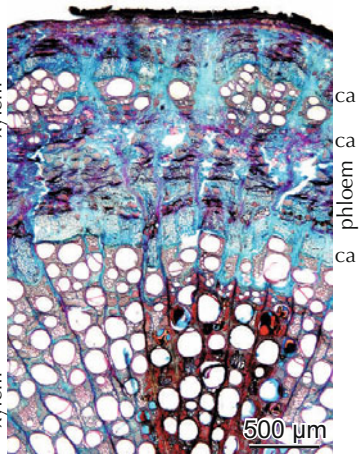
6.277 *Macrozamia moorei*, Cycadaceae.



6.278 A band of phloem between two bands of xylems in *Macrozamia moorei*.

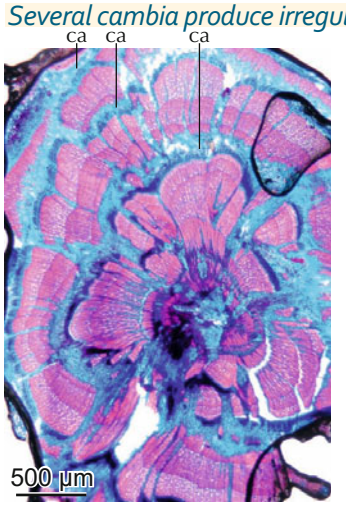
Several cambia periodically produce bands of xylem and phloem

6.279 Several concentric rows of cambia produce bands of xylem and phloem in the herb *Atriplex prostrata*, Amaranthaceae.

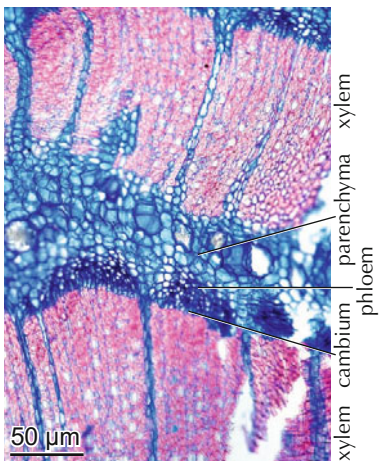


6.280 Two cambia produce xylem/phloem belts in the subtropical liana *Pueraria hirsuta*, Fabaceae.

Several cambia produce irregular bands of xylem and phloem



6.281 Irregular bands of internal cambia in the herb *Polycarpaea divaricata*, Caryophyllaceae.

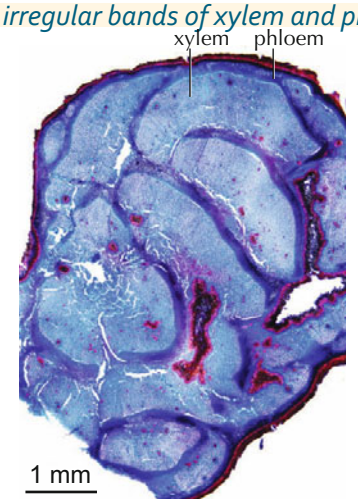


6.282 The zone between xylem belts in *Polycarpaea nivea* consists of a cambium, a phloem and an unlignified parenchymatic belt.

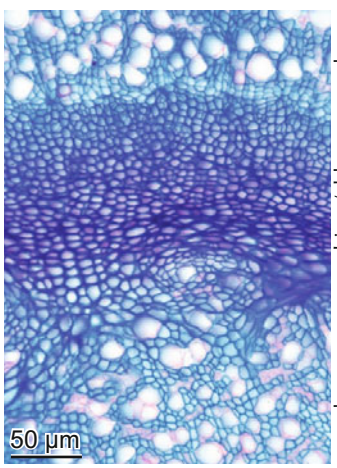
Several cambia periodically produce irregular bands of xylem and phloem

6.283 Alpine cushion plant *Silene acaulis*, Caryophyllaceae.

6.284 Cushion of *Silene acaulis* with taproot.



6.285 Irregular bands of internal cambia in *Silene acaulis*.



6.286 The zone between the two xylems in *Silene acaulis* consists of an anatomically undifferentiated cambium-phloem belt.

6.4 Intercalary meristems – Longitudinal growth far behind the tips in shoots and roots

Intercalary meristems are a special form of meristems. Intercalary meristems occur in grasses above nodes between leaf initials, in nodes on horsetails, and in root collars of mistletoes. Theses meristems originally are a product of apical meristems, which retain their meristematic activity far behind the inactivated apical meristems. Their activity is obvious in the elongation phase of the culm of grasses and horsetails. A long time after the formation of the flowers and the inactivation of apical meristems the culms are getting longer and longer due to the activity of intercalary meristems. In grass species with several nodes, multiple intercalary meristems are active until the culm reaches its final length.

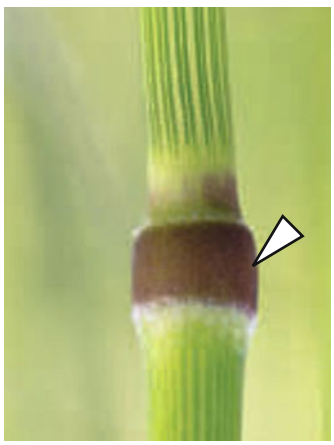
Mistletoes can only survive if the elongation of root collars follows the thickening of radial growth of the host. As soon as a haustorium touches the cambium of the host xylem, cells incorporate the foreign body. The mistletoe's strategy is to avoid isolation by forming new tissues in between its shoot and root. The original place of haustoria attachment remains, but the root elongates and enlarges in the cambial zone of the host.

Macroscopic aspect of intercalary meristems

Horsetails

6.287 Initial phase of stem elongation in a fertile shoot of *Equisetum telmateia*.

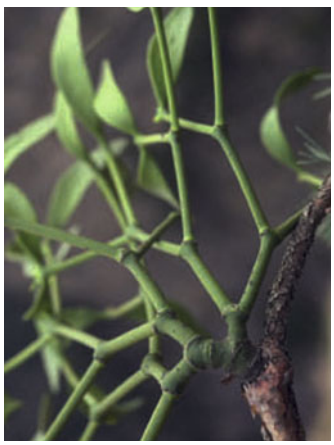
Monocotyledons



6.288 Node of a Poaceae culm. The intercalary meristem is located above the node.

6.289 Adult phase of stem elongation in shoots of a giant bamboo.

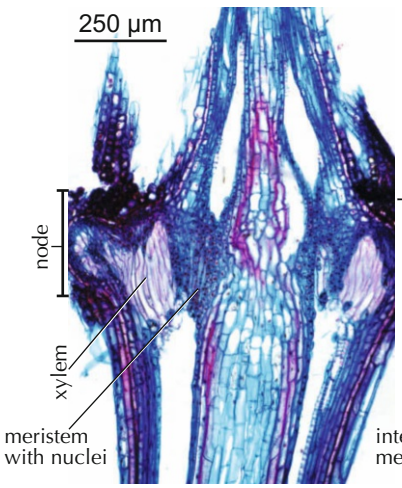
Mistletoe



6.290 Mistletoe *Viscum album* on a branch of *Pinus sylvestris*.

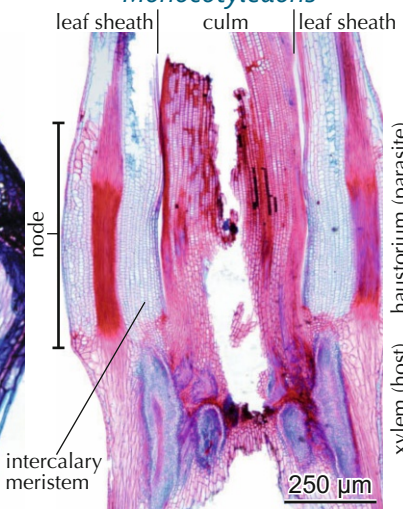
Microscopic aspect of intercalary meristems

Horsetails



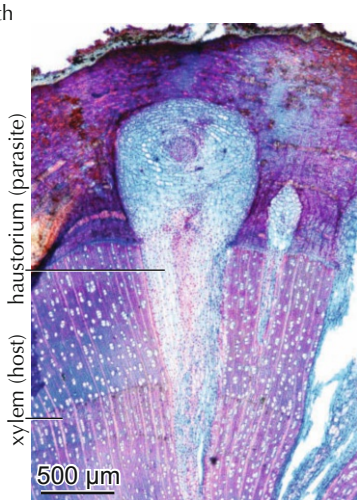
6.291 Internal structure of a node in *Equisetum arvense*.

Monocotyledons

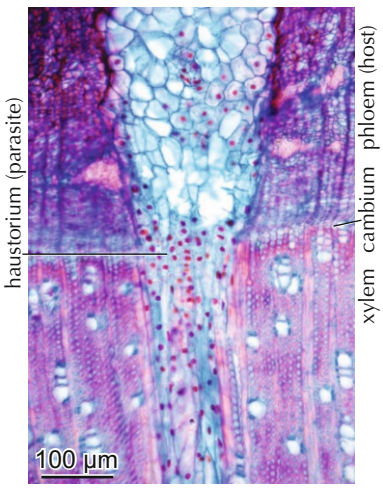


6.292 Elongation zone with unlignified meristematic cells in leaf sheaths of the grass *Milium effusum*.

Mistletoes



6.293 Mistletoe haustoria of *Viscum album* in the xylem and phloem of an apple tree (*Malus domestica*).



6.294 Concentration of nuclei in the thin-walled haustorium of the parasite in the cambial zone of the host.