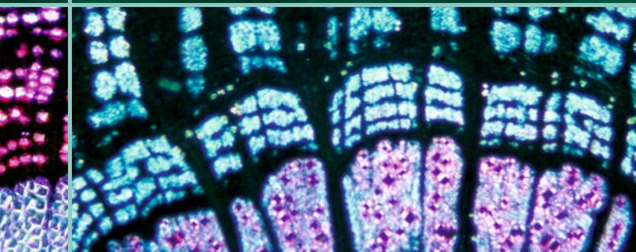
Fritz H. Schweingruber
Peter Steiger · Annett Börner




# Bark Anatomy of Trees and Shrubs in the Temperate Northern Hemisphere

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Fritz H. Schweingruber
Institute of Forest, Snow
and Landscape Research - WSL
Birmensdorf, Switzerland

Peter Steiger
Landscape architect
Rodersdorf, Switzerland

Annett Börner
Calyptra Pty Ltd.
Melrose Park, Australia

| | |
|---|---|
| Fritz Schweingruber | all microscopic content |
| Peter Steiger | all macroscopic content |
| Annett Börner | editing and layout |

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Cover illustration
Spine: Xylem and phloem in polarized light
Frontcover, top: Crystal druses in the phloem of *Paulownia tomentosa* (polarized light)
Middle left: Xylem and phloem of *Malva moschata*
Middle right: Phloem of *Salix foetida*

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# Content

# 1 Introduction

Bark is an essential part of all plants with secondary growth. Young bark, especially the cortex, plays an active role in plant metabolism. Parenchyma cells store photosynthetic products and young bark is photosynthetically active. Barks protect sensitive meristems mechanically and chemically against fire and frost, and defend essential physiological tissues such as the xylem, phloem and cortex against pathogens. Barks are also a habitat for fungi, algae, mosses, lichens, vascular plants and invertebrates. Since prehistoric times, bark has been used by humans for fibers, resins, rubber, medicinal products, dyes, tannins and cork.

Why a new book about the anatomy of bark? There is an obvious lack of books about taxonomic bark anatomy. The reference list of studies on general bark anatomy is long (see Angyalossy *et al.* 2016), and many books present the macroscopic aspect of barks (e.g. Vaucher 1990), but most of those publications focus on general phloem anatomy or on the characterization of a few genera or species (e.g. Ravaomanalina *et al.* 2017). However, Holdheide 1951 and Crivellaro & Schweingruber 2013 are the only publications with regional anatomical inventories. The former concentrates on Central European species, the latter on Eastern Mediterranean species.

In contrast, there is a wealth of publications and atlases describing the anatomical structures of the xylem, featuring many species in large and diverse regions (e.g. Grosser 1977, Schweingruber 1978, 1990 and 2005). Recently, two studies described a comprehensive number of bark features occurring in the phloem and periderm. Crivellaro & Schweingruber 2015 chose a pragmatic way, describing all bark features observed in double-stained slides (Astrablue/Safranin) of trees, shrubs and herbs from all climatic zones of the Northern Hemisphere. Angyalossy *et al.* 2016 take a more academic approach, describing anatomical bark features observed in differently stained slides of trees from a worldwide collection. Unfortunately, the two approaches are at least partially difficult to compare. The masterpiece of bark characterization remains the book by Esau (1969).

In this new book, we try to give an overview over the variability of the macroscopic and microscopic aspect of bark, especially in phloem structures, from the temperate zone of the Northern Hemisphere.


F. H. Schweingruber et al., *Bark Anatomy of Trees and Shrubs in the Temperate Northern Hemisphere*, https://doi.org/10.1007/978-3-030-14056-4_1

## Species selection and the biomes featured in this book

The original concept of this book only included a wide variety of Central European and Mediterranean trees and shrubs. Because many readers may be of East Asian or North American origin, the selection of species was extended to these regions, also giving the book a broader view of the whole Northern Hemisphere. Because of the inclusion of other regions beyond Europe, the species were grouped by their geographical origins, such as Central Europe, the Mediterranean, Eastern Asia and Northern America. In each biome chapter, the species are separated into conifers and angiosperms. Within these two groups, the species follow in alphabetic order of their Latin names.

The number of species in this book is not reflecting the much greater biodiversity of Eastern Asia and Northern America compared to Europe, simply because the majority of the sampled bark material and photos compiled over the years by the two Swiss authors is of European origin.

Two of the chosen biomes are forming circumpolar belts, stretching from Europe continuously to Northeastern Asia and Northern America. There is the forest biome with the far biggest surface on earth—the **boreal taiga**. Consequently, the species selected for this chapter in the book are of Eurasian or North American origin. The boreal taiga is characterized by vast areas of species-poor coniferous forests, mostly of the genera *Picea*, *Pinus* or *Larix*, with a few deciduous pioneer trees such as *Populus tremula* or *Betula papyrifera*, and some widespread shrubs such as *Pinus pumila* or *Arctostaphylos uva-ursi*.

The **subarctic biome** is a circumpolar, treeless belt north of the taiga. This book includes only dwarf shrub communities, with most of the species having a circumpolar or at least Eurasian range. Ecologically similar conditions can be found in **subalpine dwarf shrub** communities of high mountain ranges above the tree line, also south of the subarctic, such as in the Alps, the Caucasus, the Altai Mountains, Siberian and Alaskan mountain ranges, the Northern Rockies or mountain tops in Maine.

The following biomes are more or less limited to one continent, with the exception of the Mediterranean Basin, where Northern Africa comes into close contact with Europe across the Strait of Gibraltar, in the same way as the Caucasus itself is sitting on the border of Europe and Asia, and the Greek and Turkish mountain ranges are close to one another. The **mountain systems of Eurasia** are represented in this book only by European species, with the exception of *Cedrus atlantica* from the Mediterranean mountains. The dominant conifers of the pine family in this biome are accompanied by various deciduous shrubs. Central Asian and Himalayan mountains are not included in this book, simply because of a lack of available bark material.

The main focus of this book, due to the huge variety of sampled bark material, is the **deciduous forest of temperate Europe**, represented by a variety of deciduous trees and shrubs. In many areas of Central Europe, *Fagus sylvatica* is able to form vast, pure stands, whereas in Atlantic or more continental areas, mixed oak forests dominate. Geographically and ecologically very close and difficult to separate is the biome of the **deciduous forest of submediterranean Europe**, centered in the higher, frost-influenced areas of the Mediterranean, the Balkans and the Southern Alps, with a few thermically favored islands in Central Europe, such as the Pannonian Basin. These forests are usually more species-rich then those in Central Europe, and are often dominated by deciduous oaks, *Castanea sativa*, *Ostrya carpinifolia* and *Fraxinus ornus*.

The **deciduous forest of Eastern Asia** with its enormous biodiversity and subtropical influences reaching far north, is represented in this book only by a small selection of typical species, with the purpose to include some of the plant families centered in Eastern Asia, and also some species with a worldwide distribution and familiarity as planted trees and shrubs.

A similar, limited representation is given to the **deciduous forest of Eastern America**, although its level of biodiversity and species richness lies somewhere in between Eastern Asia and Europe. Due to a marked continental or Mediterranean summer drought, the **coniferous forests of Pacific North America** are represented by a unique variety of conifers, including the tallest known trees, marked not only by many members of the pine family but also by outstanding members of the cypress family, such as the giant sequoia and coast redwood.

Finally, the **Mediterranean hard-leaved forest** is well represented by hard-leaved trees and shrubs, naturally often dominated by *Quercus ilex*, growing in a sometimes only narrow zone below the frost-influenced areas around the Mediterranean Basin, together with a few conifers and deciduous species such as *Platanus* x *hispanica* or *Punica granatum*. With the exception of some circum-Mediterranean species, species are often centered either in the western or eastern half of the basin.

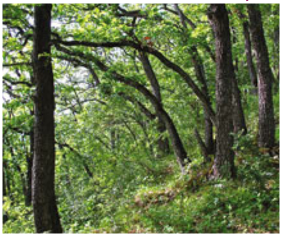
Boreal taiga

Subalpine and subarctic dwarf shrubs

Mountain systems in Eurasia

Deciduous forest of temperate Europe

Deciduous forest of submediterranean Europe



Deciduous forest of Eastern Asia

Deciduous forest of Eastern America

Coniferous forest of Pacific North America

Mediterranean hard-leaved forest

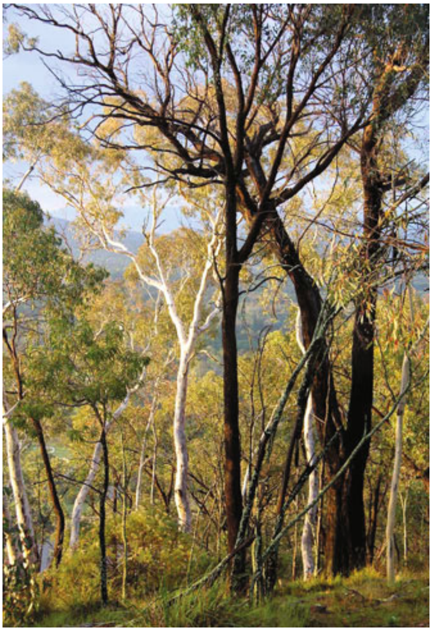
# Macroscopic bark aspects

The contemplation of tree and shrub bark is as fascinating as the study of individual human skin, both reflecting life stories that are getting richer with age. A species' typical bark textures and colors tell—besides an often impressive process of aging—an individual story for each tree and shrub. Its bark is reflecting an often century-long process influenced by the specific locality and soil, light and shadow, competition with neighboring trees, average climate, weather extremes, catastrophic events such as fire, flood, avalanches or attacks by animals and fungi. As a result of all these influences, a bark may be instantly recognizable as a certain species but may also show an impressive variety of individual colors and structures, often additionally characterized by lichen, mosses or higher plant epiphytes.

Some barks, such as this bark of *Pinus cembra*, are very distinct with age.

This *Juniperus thurifera* is at least several hundred years old.

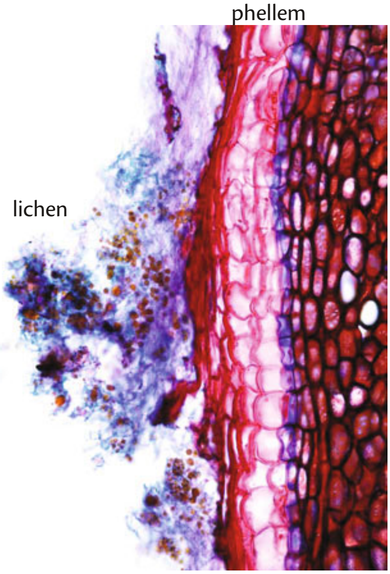
Some barks are unmistakable, such as the orange red, papery scaling bark of the genus *Arctostapylos*.



In species-rich genera, such as the Australian *Eucalyptus*, the bark can be very helpful to distinguish species or groups of closely related species.

Fruticose lichen on a branch of a subalpine *Picea abies*. Bark characteristics are no longer visible because the surface is covered with various lichen species.

Crustaceous lichens on an old *Acer* stem, a food resource for snails. Bark characteristics can be recognized but the original color is falsified by the color of the lichens.



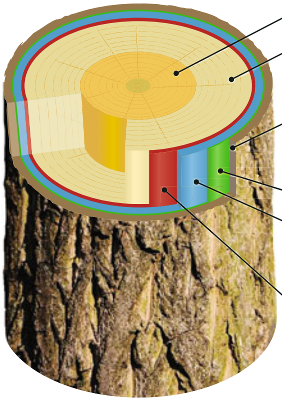

Microscopic aspect of the crustaceous lichen *Phlyctis argena* on a young *Fraxinus* twig. The lichen consists of hyphae (blue cells) with chloroplasts. It sticks to the cork layer (red phellem cells) without penetrating it.

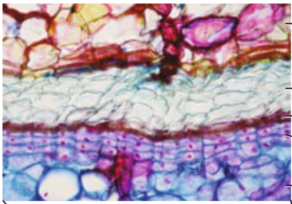
# Microscopic bark aspects

Bark consists of the following principal parts: The outermost juvenile part of the bark are the **epidermis** and the **cortex**. The innermost part outside of the cambium is the **living phloem**. Between the cortex and the phloem is the **periderm**. The adult phloem consists of a living and a dead part. The **phellogen** is a meristem separating the living from the dead phloem, and, in earlier stages, the phloem from the cortex. The phellogen is a tertiary cambium that produces the periderm; the **phelloderm** towards the inside and the **phellem** towards the outside.

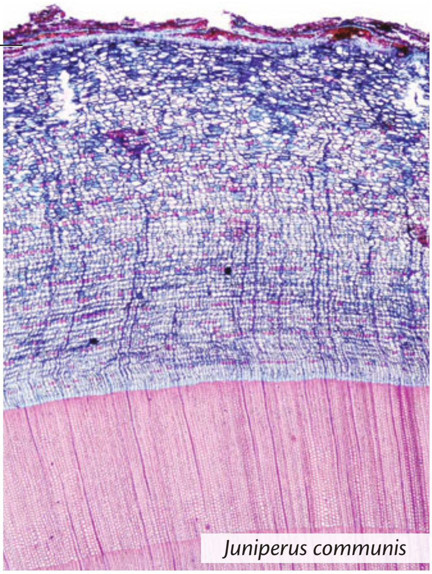
**Bark** is a general term and includes all tissues outside of the cambium. The **inner bark** includes the living part of the phloem, and the **outer bark** the dead part of the phloem. The outer bark is also called **rhytidome**. **Bast** is the colloquial term for the living part of the phloem.

Wood and bark terminology



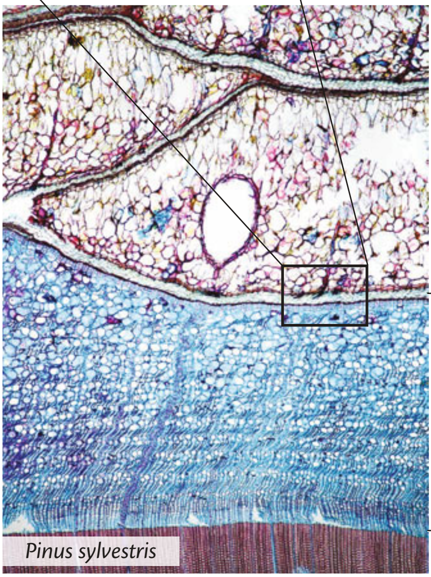




Young bark




*Juniperus communis*

Adult bark




*Pinus sylvestris*

## Principal bark elements and their function

Xylem and phloem are principally composed of similar tissues. The only qualitative anatomical difference in the phloem is the presence of sieve elements instead of vessels and tracheids. Several cell types characterize the xylem and the bark. All of them have been previously described, e.g. by Evert 2006, Crivellaro & Schweingruber 2015 and Angyalossy *et al.* 2016. The following descriptions are based on these sources.

**Parenchyma cells** are long-lived and perform their function while living. Parenchyma cells store, transport and remobilize assimilates, and produce various excretes such as resin and gum. Parenchyma cells are easily recognizable because they contain nuclei in living tissues. Cell-wall thickness, cell shape and size vary. Axial parenchyma cells occur in the bark (cortex, phloem) and in the xylem. Radially oriented parenchyma cells form the rays which occur in the phloem as well as in the xylem. Parenchyma cells are stem cells and are able to differentiate into meristems, parenchyma cells, sclereids and excretion cells (Eschrich 1995, Evert 2006, Schweingruber *et al.* 2013).

**Sieve elements** (sieve cells or sieve tubes) are short-lived and transport assimilates from all plant parts with chlorophyll to storage elements (parenchyma cells) elsewhere in the plants. Sieve elements are only active in the innermost, conductive part of the phloem near the cambium. They are large cells, but rapidly change their form due to cell collapse while they lose their functionality.

**Sieve cells** are axially elongated cells in the phloem of conifers. Their sieve plates occur on radial walls. Sieve cells in the phloem are the equivalent of axial tracheids in the xylem. Small, living **Strasburger cells** occur adjacent to sieve cells.

**Sieve tubes** are axially elongated cells in the phloem of angiosperms. Their sieve plates occur primarily on transverse walls at different inclinations. Sieve tubes in the phloem are the equivalent of vessels in the xylem. Small, living **companion cells** occur adjacent to sieve tubes.

**Sclerenchyma cells** (fibers and sclereids) are short-lived stabilizing cells and protect the tissue against physical and biological damage.

**Fibers** are elongated cells with pointed ends, produced in the cambial differentiation belt. Fibers occur in the phloem and in the xylem. **Gelatinous fibers** are a special type of fiber, characterized by an unlignified secondary layer. Gelatinous fibers occur in phloem, cortex and xylem of specific taxa.

**Sclereids** are thick-walled cells of various forms. They derive from living parenchyma cells that thicken their cell walls and lose cell content. Sclereids are restricted to the pith, phloem and cortex. They are mostly absent in the xylem. In the bark they occur predominantly outside of the conductive phloem.

**Excretion cells** are parenchyma cells specialized in the production of various substances such as resin, slime or gum. They occur surrounding ducts or in the form of long cells (laticifers). They are found in cortex, phloem and xylem.

**Crystals** of various forms (prismatic, acicular, raphids, sand etc.) mostly have the same chemical composition (calcium oxalate). They occur in cells of the cortex, phloem and xylem of various species. Crystals have two functions—calcium regulates the transport of organic molecules, and calcium oxalate is an end product of metabolic processes.

The **periderm** is formed by the tertiary cambium and consists of an external belt of parenchyma and cork cells. The outermost layer of the periderm, the **phellem**, varies in dimension, but it is mostly the dominating tissue.

The **rhytidome** is the dead part of the bark. It largely determines the macroscopic aspect of the bark. The periderm and the rhytidome protect the living phloem from dehydration, solar radiation and mechanical damages.

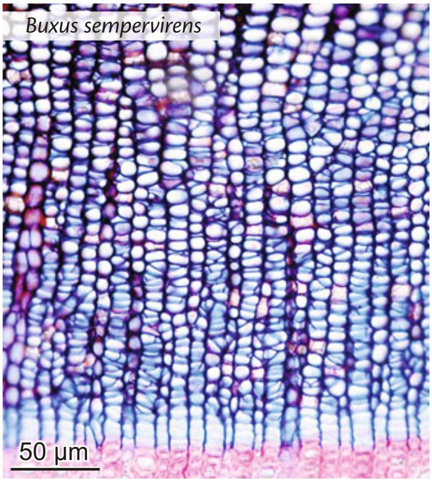
# Illustrated overview of microscopic bark features

The following features are visible in high-quality, double-stained sections. The features and codes in brackets relate to Crivellaro & Schweingruber 2015.

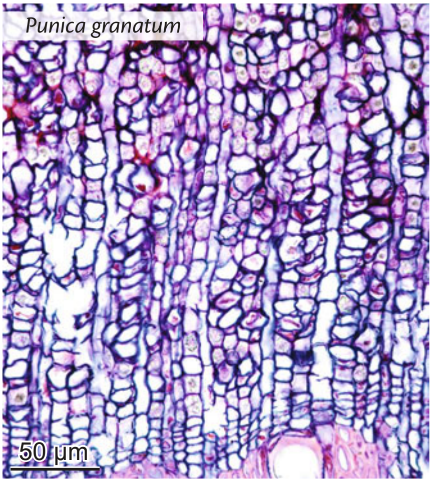
## Homogeneous structure (Cr,Sg B.3, B.14)

Tissue without tangential layering. Sieve tubes and parenchyma cells irregularly or radially arranged. Sclerenchyma absent.

*Sieve tubes and parenchyma radially arranged*



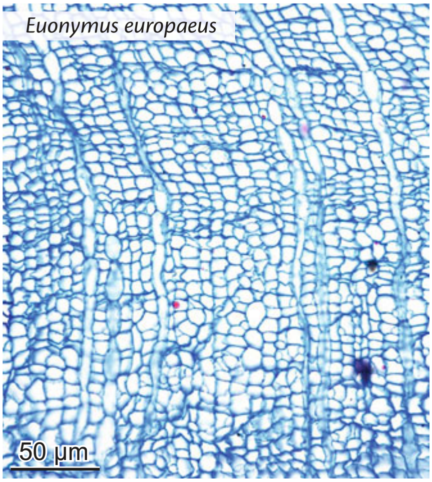

*Sieve tubes & parenchyma irregularly alternating*




## Tangential layering

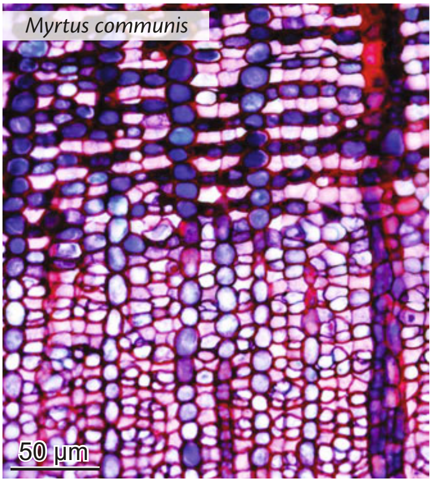
*Multiseriate layers without sclerification* (Cr,Sg B.9.1)

Several rows of parenchyma cells alternating with one or two rows of collapsed sieve tubes.




*Uniseriate layers without sclerification*

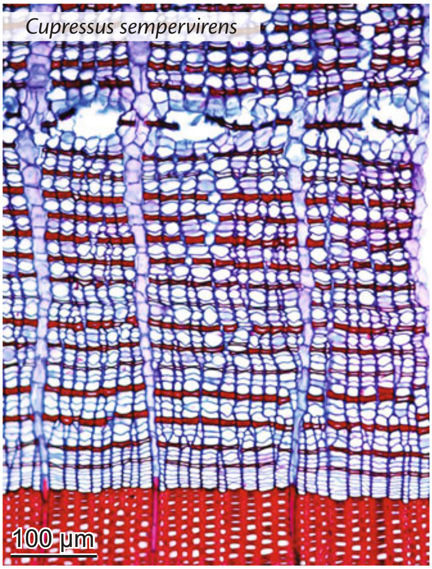
Sieve tubes and parenchyma cells alternating.

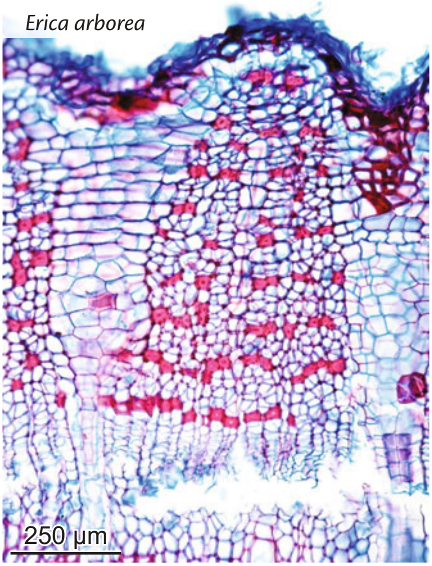


## Tangential layering

*Fibers uniseriate*

Uniseriate layers of fibers alternating with layers of sieve cells and parenchyma cells.

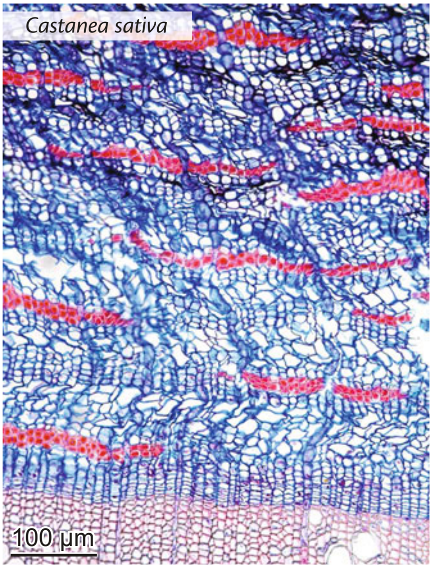



*Small layers of fibers with less than 3 cells*

(Cr,Sg B.18)

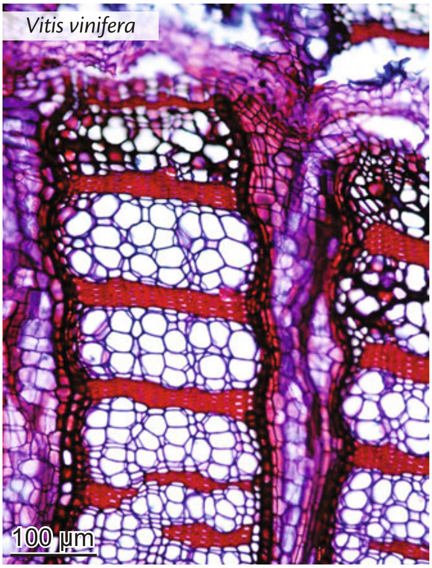
1–3 layers of fibers in tangential bands alternating with layers of sieve tubes and parenchyma cells.




*Large layer of fibers with >3 cells*

(Cr,Sg B.17.4)

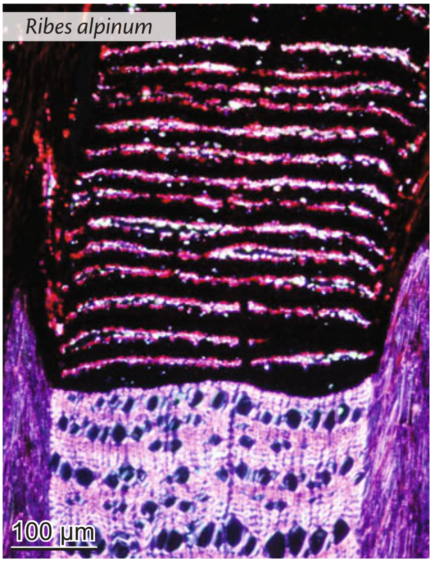
Layers of different widths alternating with tangential bands of sieve tubes and parenchyma cells.



## Tangential layering

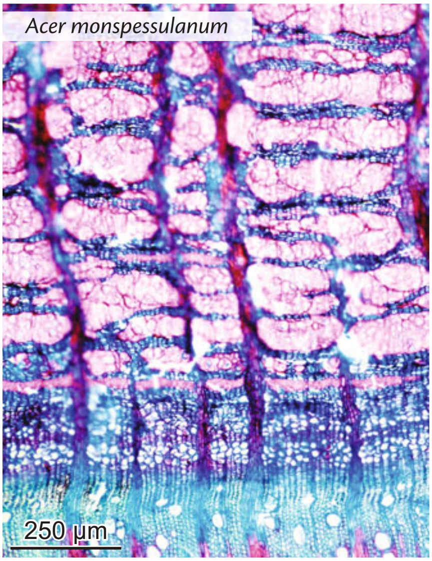
*Small layers of sclereids with less than 3 cells*

Small layers of sclereids alternating with a few layers of sieve tubes and parenchyma cells.




*Large layers of sclereids with >3 cells*

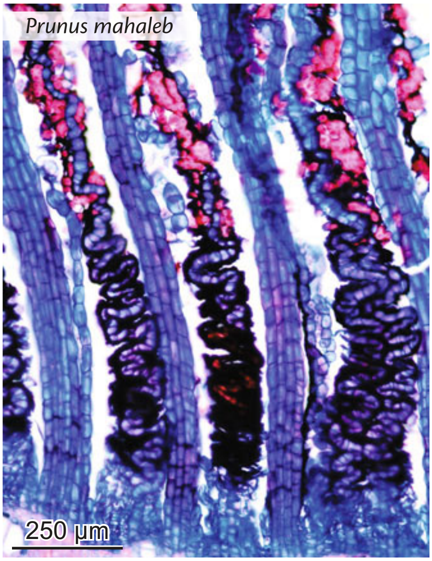
Small layers of sclereids alternating with a few or many rows of sieve tubes and parenchyma cells.




## Radial orientation of sclereids

(Cr,Sg B.29.2)

Sclereids arranged in radial stripes or blocks.

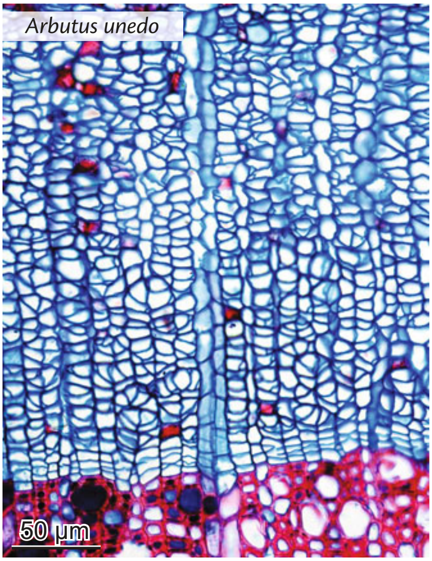



## Grouping of sclerenchyma

*Fibers solitary*

(Cr,Sg B.15)

Individual fibers distributed irregularly within a tissue of sieve tubes and parenchyma cells.

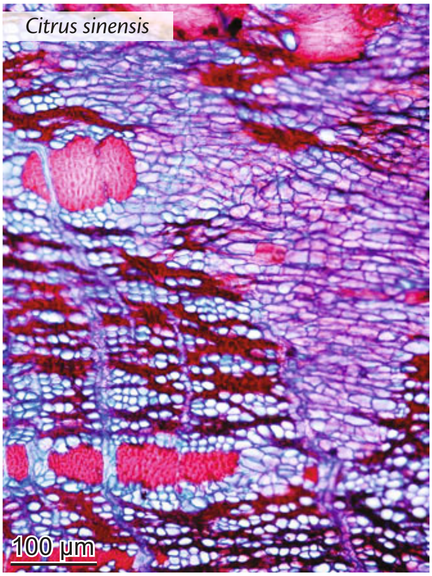


## Grouping of sclerenchyma

### *Fibers in groups*

(Cr,Sg B.27)

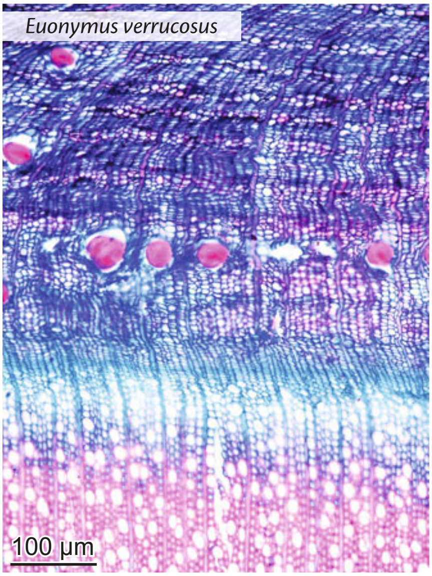
Fibers in small or large clusters.




### *Sclereids solitary*

(Cr,Sg B.27)

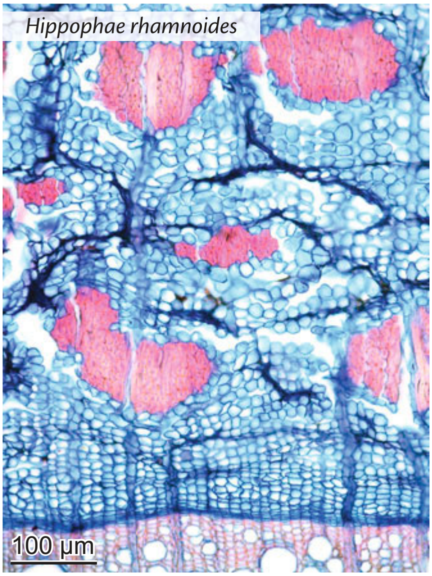
Sclereids solitary within a tissue of sieve tubes and parenchyma cells.




### *Sclereids in groups*

(Cr,Sg B.28,29)

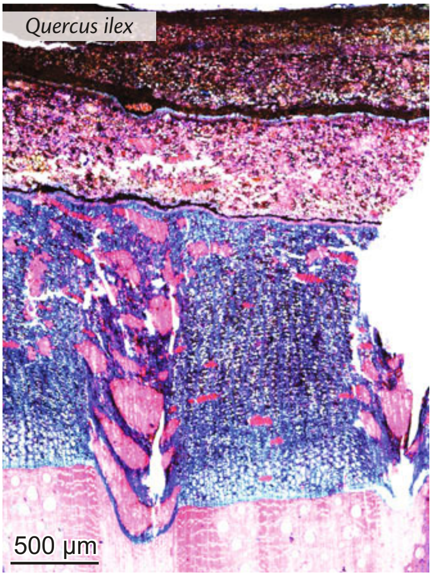
Sclereids in round to oval clusters.




### *Sclereids in large rays or aggregate rays*

(Cr,Sg B.41)

Sclereids of any form restricted to ray zones.

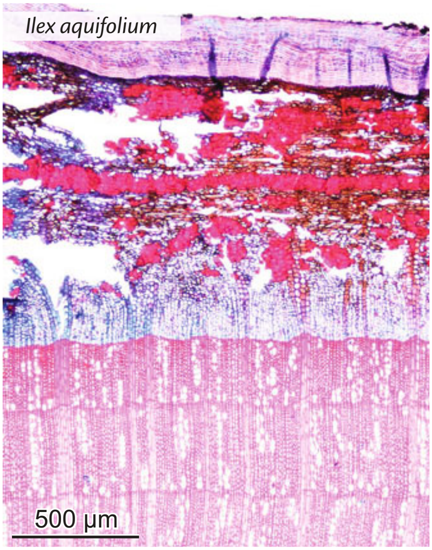


## Grouping of sclerenchyma

*Sclereids in large, irregularly distributed groups*

(Cr,Sg B.29.3)

Groups of sclereids of any form irregularly distributed.

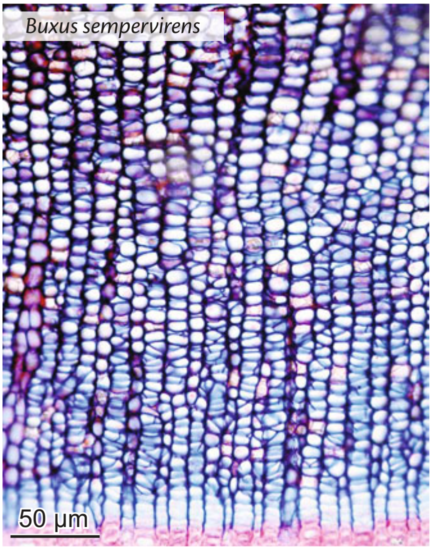



## Rays

*Rays absent or unrecognizable*

(Cr,Sg B.30)

Rays not differentiated from radially arranged tissue of sieve tubes and parenchyma cells.

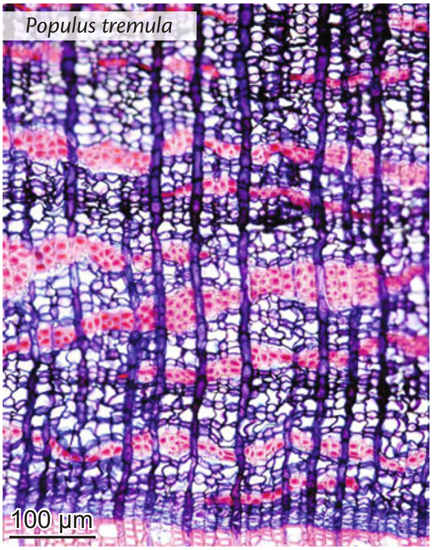



## Rays

*Rays straight*

(Cr,Sg B.31)

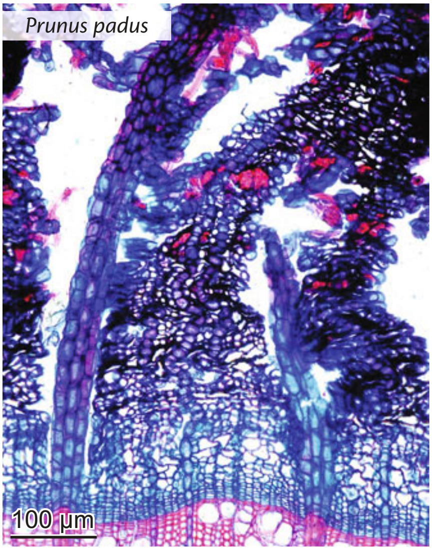
Ray course not influenced by mechanical forces of other elements.




*Rays wavy or bent*

(Cr,Sg B.32,45)

Rays wavy due to radial and lateral compression.

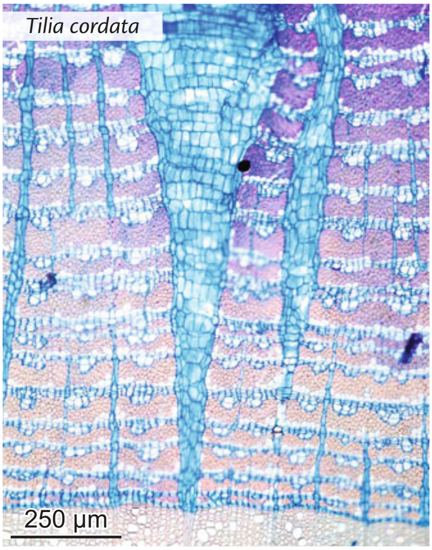


## Dilatation

*Ray dilatation*

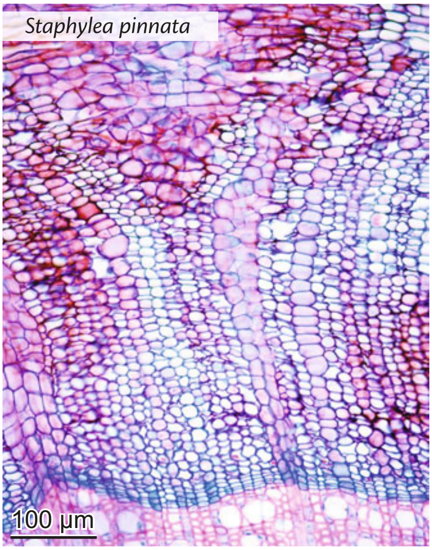
(Cr,Sg B.37–39)

Rays dilating by forming new cells from an intercalary meristem.




*Dilatation origin in axial parenchyma cells*

Tissues dilating by forming new cells from axial parenchyma cells.

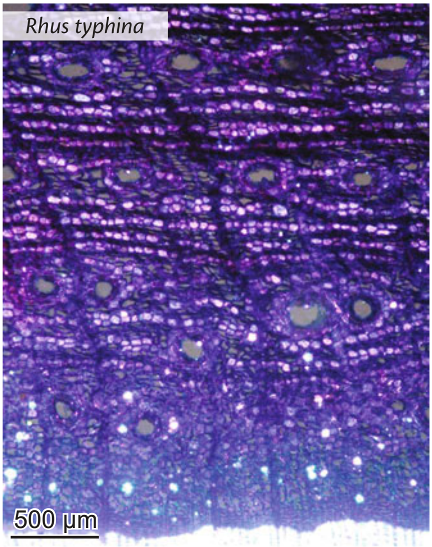



## Ducts and laticifers

*Ducts*

(Cr,Sg B.47)

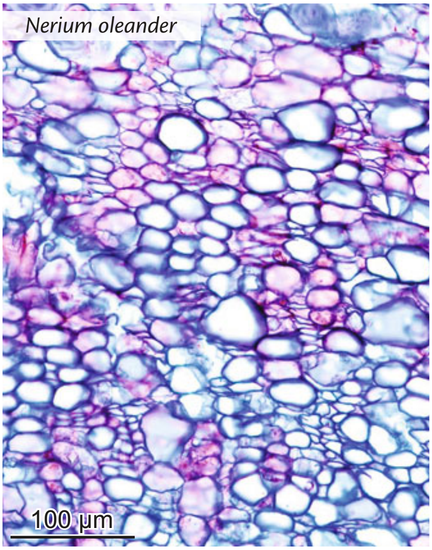
Ducts are surrounded by small excretion cells.




*Laticifers*

(Cr,Sg B.48)

Laticifers consist of single, axially elongated excretion cells.

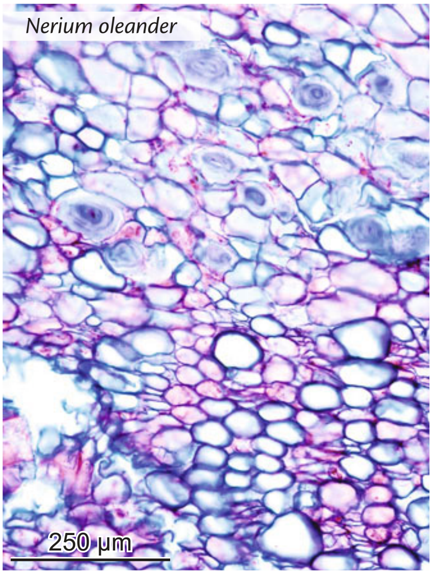


## Special cells

### *Gelatinous fibers*

(Cr,Sg B.64)

Unlignified, round fibers resembling tension wood.

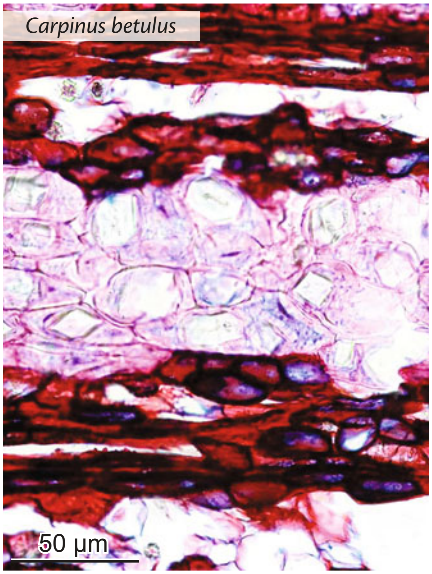



## Crystals

### *Prismatic crystals in sclereids*

(Cr,Sg B.53)

Crystals surrounded by dense, sclerotic cells.

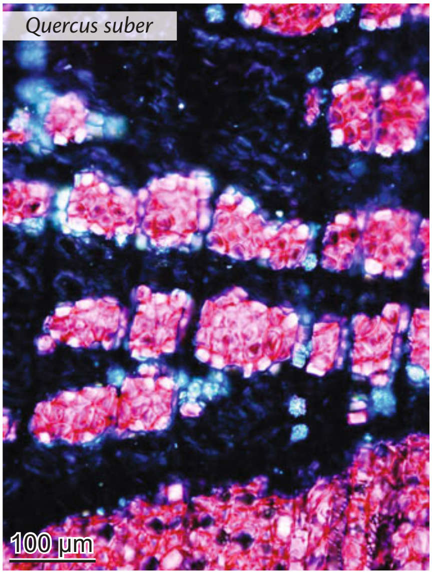



## Crystals

### *Prismatic crystals around sclerenchyma*

(Cr,Sg B.55)

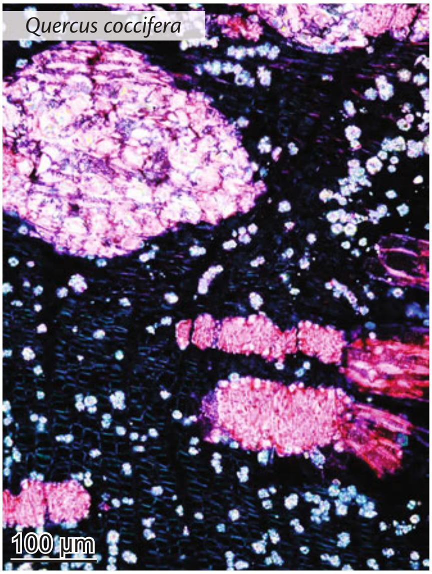
Groups of sclereid surrounded by layers of crystals.




### *Crystal druses*

(Cr,Sg B.63,64)

Druses associated with rays or unlignified axial tissues.

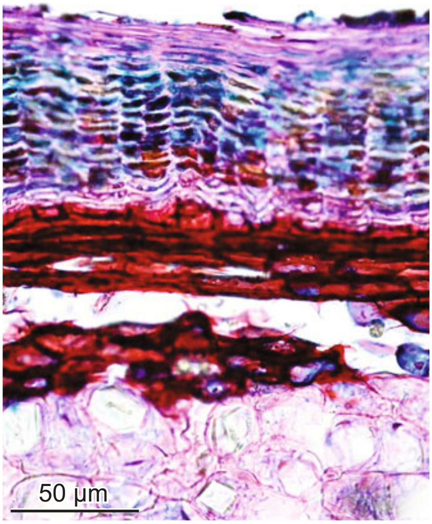


## Periderm

*Radially arranged rectangular cells*

(Cr,Sg B.134,138)

*Carpinus betulus*

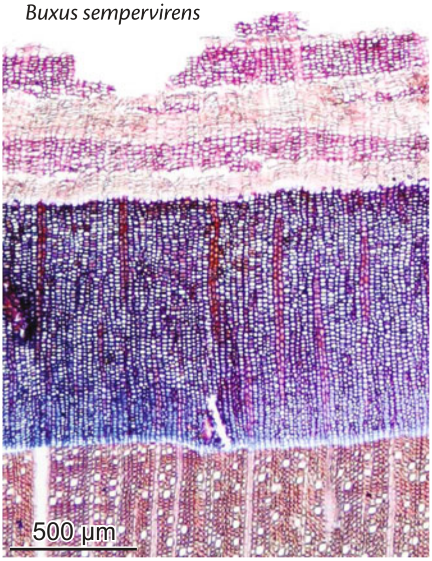



## Rhytidome

*Regular layers of old phloem compartments*

(Cr,Sg B.131,137)

*Buxus sempervirens*



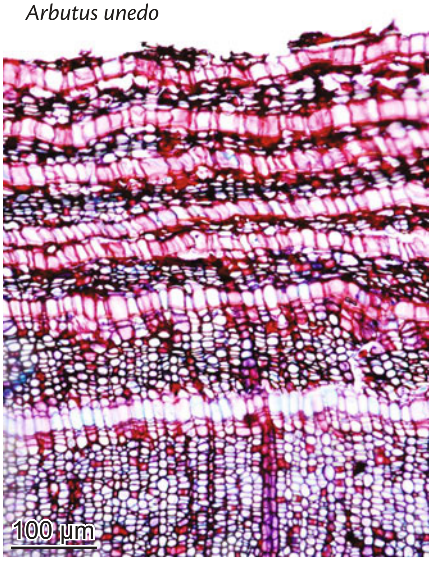

## Rhytidome

*Phelloids*

(Cr,Sg B.132)

Rows of large square cells alternating with many rows of small cells.

*Arbutus unedo*




*Irregular*

(Cr,Sg B.133)

Groups of irregularly shaped cells separating compartments of phloem.

*Betula pendula*

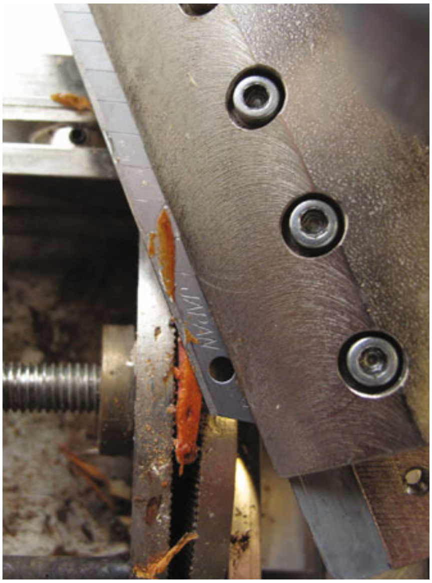
# Microscopic preparation techniques

There are many publications on the anatomy of wood, but not many on the anatomy of bark. One likely reason for this discrepancy lies in the technical difficulty of sectioning bark. Bark is a very heterogeneous material—very tough tissues, with a density of around 1 g/cm³, are embedded into soft tissues with a very low density of 0.3 g/cm³. If the microtome knives are just slightly blunt, the denser tissues will tear the more fragile tissues during sectioning, rendering these sections scientifically useless.

All bark sections shown in this atlas were prepared from freshly collected samples. The material was sectioned with paper-knife blades, fixed in a sledge microtome with a special blade holder (Gärtner & Schweingruber 2013). All sections were stained with a one-to-one mixture of Safranin/Astrablue for several minutes. Staining and dehydration of the samples with ethanol 96%, absolute alcohol and xylene happens directly on the microscopic glass slide, reducing the amount of work. All slides were embedded in Canada Balsam for preservation, making them permanent and comparable even after many years. Photographs were taken in transmitting, normal and polarized light with an Olympus BX51 microscope. Sections were documented under 40, 100, 200 and 400 times magnification.

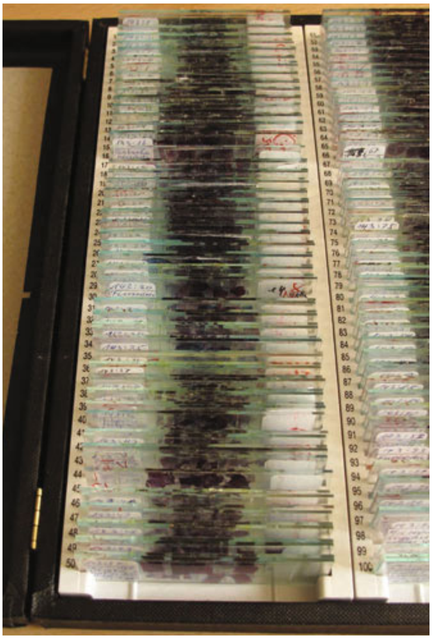
The use of sharp disposable paper-knife blades and the chemical sample preparation directly on the microscopic slide make it possible to produce many high-quality slides in a short amount of time. Detailed preparation techniques are described in Gärtner & Schweingruber 2013.

Microtome designed by Gärtner *et al.* 2015, featuring a blade holder for disposable paper-knife blades.



Sectioning of a sample with a high-quality disposable paper-knife blade.

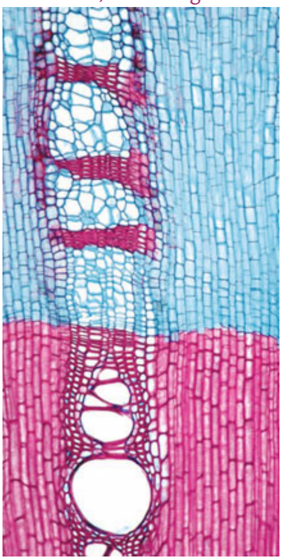
Staining and dehydration of the samples happens directly on the microscopic glass slide.



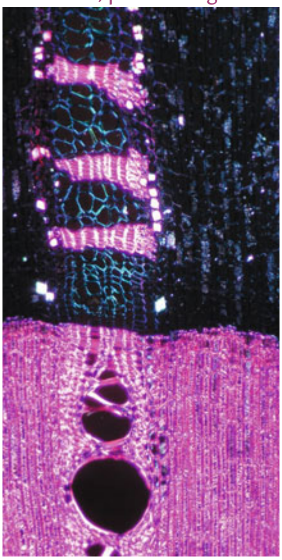
Storage of microscopic slides in boxes. All slides are entered into a digital database with their taxonomical, morphological, geographical and anatomical characteristics.

Unstained slide


Stained with Safranin/ Astrablue, normal light



Stained with Safranin/ Astrablue, polarized light



The **boreal taiga** is characterized by vast areas of species-poor coniferous forests, mostly of the genera *Picea*, *Pinus* or *Larix*, with a few deciduous pioneer species such as *Populus tremula* or *Betula papyrifera*, and some wide-spread shrubs, such as *Pinus pumila* or *Arctostaphylos uva-ursi*.


F. H. Schweingruber et al., *Bark Anatomy of Trees and Shrubs in the Temperate Northern Hemisphere*, https://doi.org/10.1007/978-3-030-14056-4_2

# 2 The boreal taiga

# *Juniperus communis* L. Cupressaceae

juniper, Gewöhnlicher Wacholder, genévrier commun, ginepro comune, enebro comun

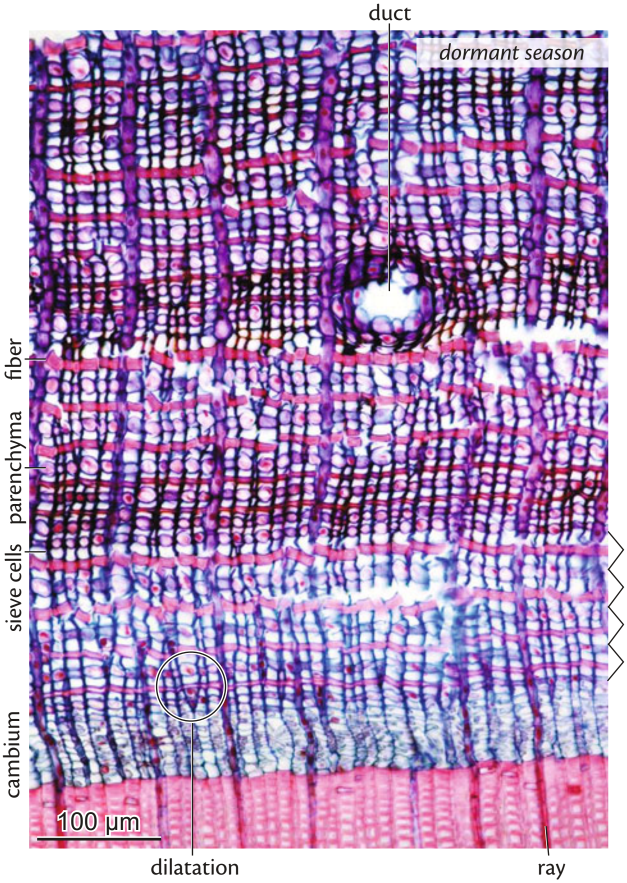
**Form:** Conifer, usually a very columnar shrub, rarely a small tree, to 12 m tall; the dwarf subsp. *nana* is always a low-spreading dwarf shrub.

**Features:** Needles evergreen, stiff, short, sharply pointed in subsp. *communis*, to 2 cm long, upper side with a white waxy streak giving the needles a bluish appearance; needles in subsp. *nana* curved, without sharply pointed tip. Flowers dioecious, female and male flowers in tiny yellowish globes, to 5 mm wide. Cones with a berry-like, light bluish structure of coalescing scales.

**Habitat:** Subspecies *communis* in nemoral and boreal Eurosiberia, from Morocco eastwards to the Ob and Yenisei rivers; subsp. *nana* in subarctic Siberia, Greenland and North America, south only in high mountain ranges.

Subspecies *communis* on dry or wet soils, mostly on rocky, gravelly or sandy soils, also in bogs in full sun, to 1800 m; subsp. *nana* only in alpine or subarctic tundra, to 4200 m.

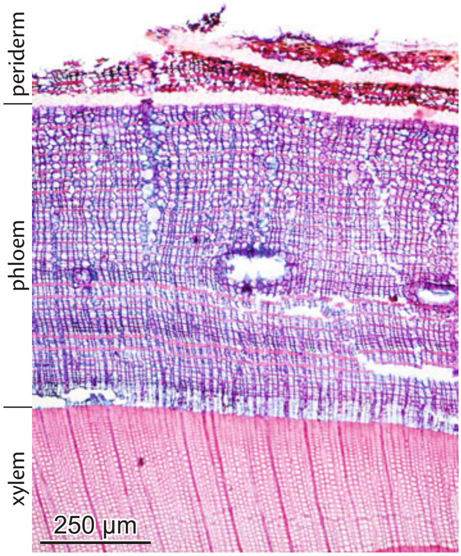
**Bark:** Young glossy, silvery or dark red brown, later light gray brown, with fine longitudinal fissures.

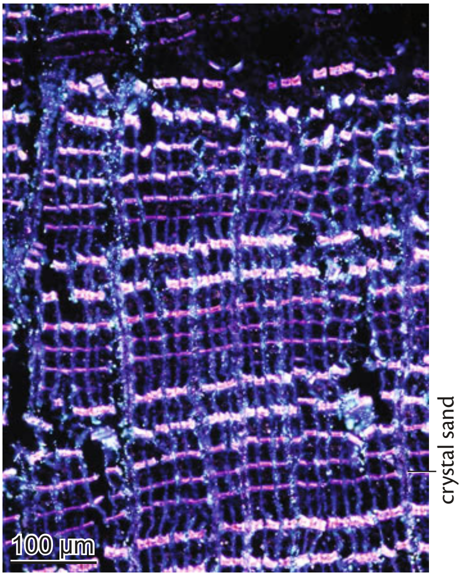



**Bark anatomy:** Regular tangential layers of sieve cells, fibers, and parenchyma cells are characteristic for Cupressaceae.

Sieve cells thin-walled, rectangular. Parenchyma cells round to oval. Fibers thick-walled, square and rectangular. Sieve cells tending to collapse. Uniseriate rays dilating in later stages. Rays remaining straight. Rarely with large ducts. Crystal sand in radial intracellular layers.

Annual rings mostly indistinct. Ring boundaries of fast-growing trees indicated by thick-walled fibers in the early phloem. Phellem cells thin-walled, irregular shaped.



## *Larix sibirica* Ledeb. — Pinaceae

Siberian larch, Sibirische Lärche, mélèze de Siberie, larice siberica, alerce de Siberia

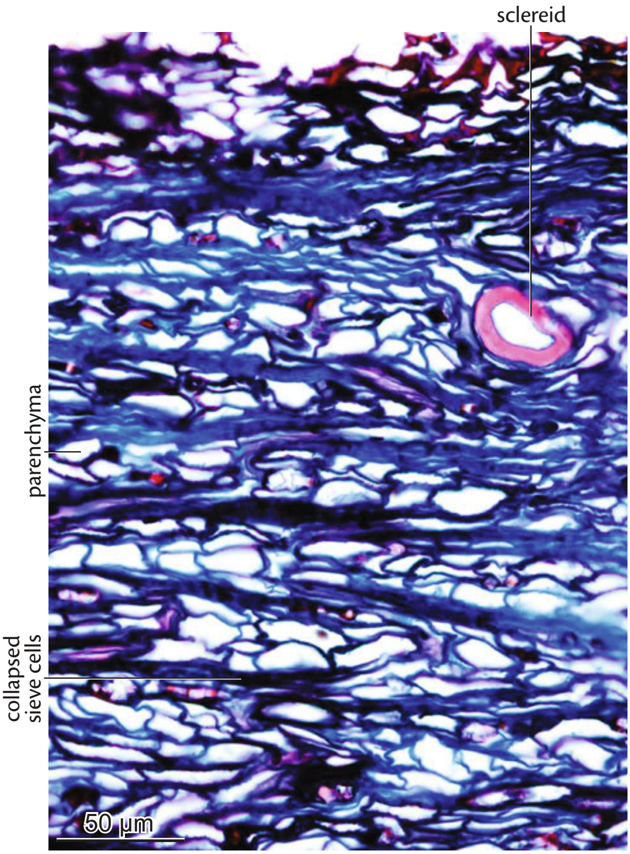
**Form:** Conifer, crown broadly columnar, later rounded, with horizontal branches and hanging twigs, to 45 m tall.

**Features:** Needles deciduous, soft, to 5 cm long, in star-shaped bundles of 20–40 on short buff shoots. Flowers monoecious, female cone upright, red, 1–2 cm long, male cone hanging, yellow, globular, to 2 cm long. Seed cones soft, globular, red to gray brown, to 5 cm long.

**Habitat:** Boreal and subarctic Russia from the White Sea eastwards to the Ural Mountains, Yenisei River and Altai Mountains, eastwards gradually being replaced by the east-Siberian *L. dahurica*.

A typical pioneer on all soil types, to 2400 m.

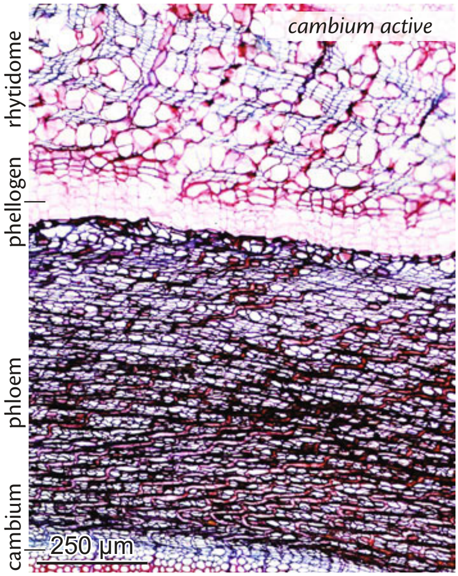
**Bark:** Thin and flaky, young yellowish or red brown, later gray brown, corky, with deep longitudinal furrows.

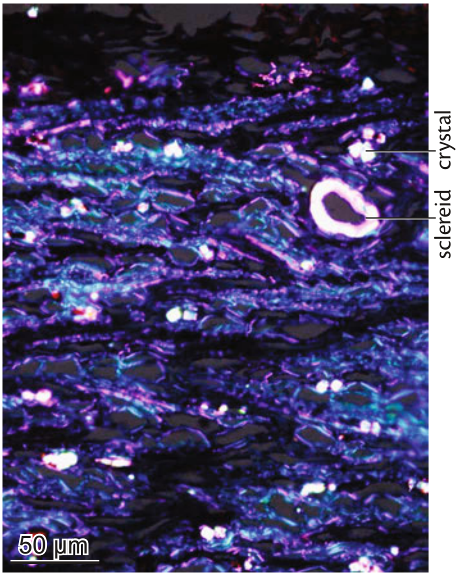



**Bark anatomy:** Regular tangential layers. The presence of isolated sclereids is characteristic, a rare feature in slow-growing trees.

Sieve cells rectangular, arranged in 3–5-seriate tangential rows, collapsing within a short time after formation. Parenchyma cells small, oval in the juvenile phloem, enlarged in the adult phloem. Fibers absent. Sclereids as isolated, round, very thick-walled, lignified cells. Rays radially wavy. Small prismatic crystals outside of sclereids.

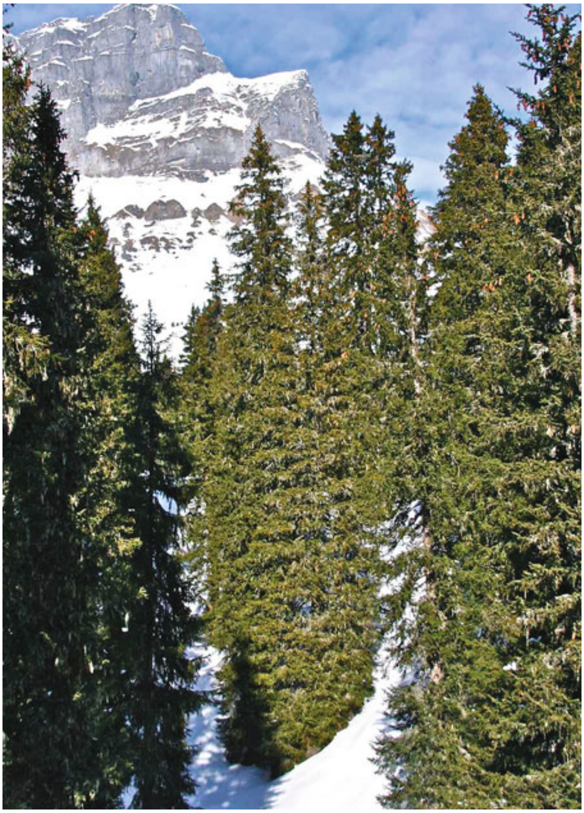
Annual rings indistinct in the present material. Periderm active for several years. Phellem cells rectangular, thin-walled.



# *Picea abies* (L.) H.Karst Pinaceae

Norway spruce, Fichte, épicéa, peccio, pícea europaea



**Form:** Upright conifer, crown narrowly to broadly conical, to 60 m tall.

**Features:** Needles evergreen, stiff, quadrangular in cross section, to 3 cm long. Flowers monoecious, female cone upright, crimson, to 4 cm long, male cone yellowish red, to 5 cm long. Seed cones brown, hanging, soft, to 15 cm long.

**Habitat:** Northern Europe and the Alps, from Scandinavia and Northwest Russia south to the Balkans, North Apennines and Massif Central.

On all soil types, often dominant in boreal and subalpine forest, to 2100 m.

**Bark:** Young red brown, fine scaly, later tessellated-flaky, gray brown.