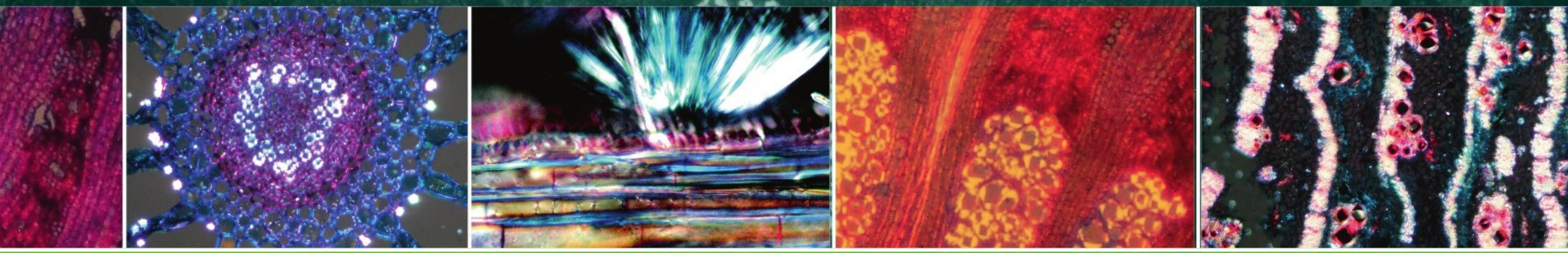
Volume 1



Fritz Hans Schweingruber · Annett Börner
Ernst-Detlef Schulze

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Atlas of Stem Anatomy in Herbs, Shrubs and Trees

Springer

F. H. Schweingruber A. Börner E.-D. Schulze

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Volume 1

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Volume 1

With over 2000 colour illustrations

Springer

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Cover illustrations (from right):
Cross-section of a dwarf shrub stem with successive cambia. Vessels and fibers are stained red, parenchyma cells are stained blue. *Chenopodium frutescens*, Amaranthaceae, grows in the Mongolian steppes.
Cross-section of an old rhizome of an herb. The large red stained rays separate yellow stained radial vessel/fiber zones. *Peucedanum venetum*, Apiaceae, grows in the dry meadows of the Southern Alps.
Radial section of a liana stem. Radially arranged crystals in the vessel of a vine. *Vitis vinifera*, Vitaceae, grows in Mediterranean riparian zones.
Cross-section of a water plant stem. Vessels in the center of the stems are surrounded by the phloem and an air-conducting tissue. The white dots represent calcium oxalate crystals. *Myriophyllum alternifolium*, Haloragaceae, grows in ponds.
The picture to the left is part of *Peucedanum venetum*.
All slides were stained with safranin and astra blue and photographed in polarized light.

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by Fritz Schweingruber

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Abbreviations

ae	aerenchym
bpit	bordered pit
ca	cambium
cal	callus, parenchymatic cells
clu	cell lumen, cell lumina
co	cortex
cork	
ct	conjunctive tissue
cry	crystal
csi	collapsed sieve tubes
cu	cuticula
di	(ray) dilatation
ds	dark-stained substances
duct	
ep	epidermis
en	endodermis
ew	earlywood
ewv	earlywood vessel
ewt	earlywood tracheid
ft	fiber tracheid
f	fiber
ge	gelatinous fibers
gr	growth ring
grb	growth ring boundary
he	helical thickenings
ivp	intervessel pit
la	laticifers
lf	libriform fiber
lcw	lignified cell wall
lw	latewood
lwv	latewood vessel
lwt	latewood tracheid
mu	mucilage
nu	nucleus
p	perforation
pa	parenchyma
ph	phloem
phe	phellem
phg	phellogen
pit	
pith	
r	ray
rd	resin duct
sc	sclereid
sf	septate fibers
shc	sheet cell
si	sieve tube, sieve element
spit	simple pit
ta	tannins
te	tension wood
tr	tracheid
ty	tylosis
ulcw	unlignified cell wall
v	vessel
vab	vascular bundle
vat	vascular tracheid
vrp	vessel-ray pits
xy	xylem

1. Introduction

Xylem and phloem are the "highways" for transport and communication in all higher plant species. The transport system is substantially important for plant functioning to an extent that as plants germinate, a protophloem and a protoxylem is being formed at the very beginning. However, as soon as a cambium develops, xylem cells are formed for water transport, which is the structure, generally known as wood. Phloem cells are formed outside of the cambium for transport of assimilates. After loosing their function, phloem cells and a secondary cambium contribute to the formation of bark.

Wood structure has been investigated since the days of early anatomy, and most woody species have been described anatomically (Wheeler et al. 2007). Nevertheless, despite of the long history of wood investigations, the term "wood" remains not well defined. Generally, the term "wood" designates an intensively lignified xylem which excludes a partial lignification that is characteristic for most species. Obviously, there is a continuum from intensively lignified to partially lignified stems, and this gradient of stem anatomy has neither been studied adequately nor has the expression of stems with differently lignified stems been studied in relation to climate and habitats where these plants grow. It is this shortcoming which prompted us to investigate the products of secondary growth of plant stems in a large variety of families and species representing the full range of life forms and plant sizes, ranging from herbaceous to truly woody species in a broad range of climatic conditions. Thus, we can make the attempt to investigate the anatomy of plant stems not only in a taxonomic and morphological but also in a climatic context. Many of the anatomical features are genetically fixed and characteristics of the respective species. It remains unclear how these features relate to the evolution and taxonomy of these species. Some anatomical features are plastic. The environment may modulate them, but it is not understood, if specific environmental conditions just cause the replacement of species or genotypes having additional features, or if single species can respond with their stem anatomy to the environment. Obviously, our understanding of why plant stems are that different can only be advanced if we place the anatomy in the context of the environmental conditions in which these species grow. Thus, the main focus of the present taxonomic, morphological and anatomical features to the environmental conditions of dicotyledonous plant form the new and old world in which these species live, even though, it was not possible to study the plasticity of anatomical features within a species.

In contrast to the extended literature on woody xylem, anatomical studies of the phloem and bark are rare (Esau 1969, Roth 1981, Trockenbrodt 1990, Junikka 1994). In this book we try to close this gap with a description of the bark, where possible.

Sampling Design of the Present Study

A major aim of this study is to create a collection of slides containing transverse, tangential and radial sections from a large number of species according to a uniform and standardized methodology of collection, preparation, and the location where the stem was cut. The establishment of this collection has been a major task for Fritz Schweingruber for the last 40 years.

Most of the material (96%) was collected from natural sites, harvesting one or few individuals of average size. An examination of replicated individuals shows that anatomical variation exists, but this could not be followed up in a systematic manner.

Fresh material is the basis for the preparation of all cross-, tangential- and radial sections. Only 5 out of 1658 species were taken from xylothecs because the habitats were not accessible.

The investigations are carried out on the basis of cutting the stem in the zone of the hypocotyls (root collar). Rhizomes were cut at the oldest stage.

Most sections were stained with Safranin, which makes lignin visible and with Astrablue which stains cellulose. All slides were embedded in Canada Balsam.

Plant samples were collected in the course of field tours and expeditions of Fritz Schweingruber. Species were identified according to local identification keys and confirmed, if needed, by comparison with herbarium specimens. The collection encompasses most but not all families of the Angiosperms including the Magnoiliid complex, Eudicots, the Rosoid clade, the Eurosides and a few families of the Asterid clade. The phylogeny follows Judd et al. (2002) and Strassburger et al. (2008), which are based on the APG III system. The figure opposite shows for which families representatives were described.

Emphasis was put on smaller plant statures (5-150 cm) because these had mostly been neglected in the past. Thus, the collection contains 1292 species of small stature and only 366 species of tall stature. According to the biodiversity of the floral regions, more Mediterranean than arctic species were collected.

The collection focuses on the European region, ranging from the arctic to the Sahara, and including the Canary Islands. Some material was collected in North America (Rocky Mountains), South America (Andes) and in Siberia.

Plant height and the environmental conditions of the growing habitat were recorded for each specimen. Climatic conditions were classified according to biomes (Walter and Breckle 1991). Most anatomical features were recorded as presence or absence of a trait, except for morphological features such as plant age and annual ring width, which were recorded on a continuous scale. Vessel size, vessel number as well as fiber-wall thickness and ray width were classified in groups.

For all species the anatomy of xylem, phloem, cortex and, in some cases, the pith was described. Plant age was determined based on annual rings.

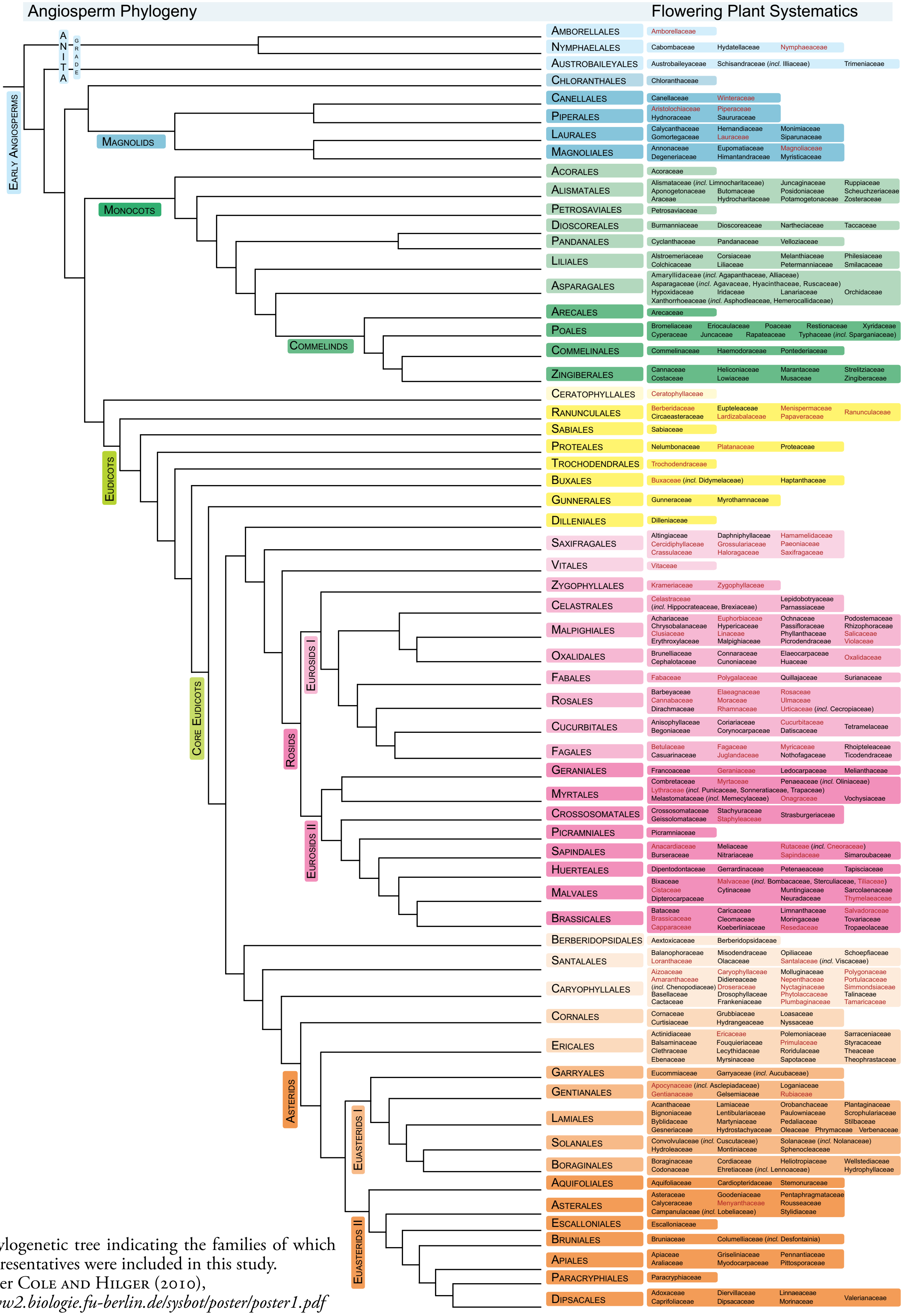
Limitations of the Study

The study started with a focus on woody species, but over time the emphasis changed from woody towards herbaceous species. Thus, at each sampling location not all species were collected quantitatively, but it was the aim to get at least one sample per species. Not described are Monocots, Proteaceae and Cactaceae, and other families which are not represented in the European flora. However, the main objective was to obtain a representative collection of species for each family. It was not possible to collect all taxa within a family.

For comparison, the number of known taxa and species occurring worldwide and in Europe is indicted at the beginning of each family described.

The age of stems was determined using polar roots of annuals (therophytes), perennial herbs (hemicryptophytes), and dwarf shrubs. The data do not represent the full range of ages, and not the maximum possible ages, because the sampling was not conducted to find the oldest specimen of a given species. Nevertheless, the range of ages gives a first insight into the longevity of species in the European non-woody flora. Ages were not determined for shrubs and trees.

The collection is based on healthy individuals growing on "typical" sites. We avoided crippled individuals. Also, extreme habitats in terms of nutrition (extremely poor habitats as well as fertilized habitats) were avoided.



Phylogenetic tree indicating the families of which representatives were included in this study.
After COLE AND HILGER (2010),
www2.biologie.fu-berlin.de/sysbot/poster/poster1.pdf

Comparison with Other Studies

Following references served as guidelines throughout this study:

Gregory (1994) and the updated Kew Bibliography (http://kbd.kew.org/kbd/login.do) give an excellent overview on xylem anatomy, which served as basis for the present analysis.

Metcalf and Chalk (1957) summarized the basic anatomical features of plant families.

Most studies (e.g. Carlquist and Hoekman 1985, Carlquist 2001, Baas and Schweingruber 1987) focused on woody species (trees and shrubs) only, while Schweingruber and Poschlod (2005) and Krumbiegel and Kästner (1993) gave a summary of the herbaceous species based on cross section photography. Here we extend these studies with features seen in longitudinal sections. An extended bibliography concerning dwarf shrubs and herbs is given by Schweingruber and Poschlod (2005).

The INSIDE WOOD database characterizes thousands of woody species with micro-photographs and IAWA-code numbers (see *http://insidewood.lib.ncsu.edu/search*). This database especially served as comparison for the present study. It remains a problem that the IAWA code (Wheeler et al. 1989) focuses mainly on trees and not on dwarf shrubs and herbs. Comparisons are possible for families where most species belong to woody species (trees and shrubs) such as Ericaceae, Cistaceae and others. The comparisons fail wherever the IAWA database is centered around woody species for a given family, but this study is focused on all existing life forms. This study includes many families containing mainly therophytes and hemicryptophytes e.g. Amaranthaceae, Brassicaceae, Cucurbitaceae. It emerges that comparisons are only useful if the material originated from the same biome.

Holdheide (1951) is the main bark monograph for European species. However, many of the species, which are described in this collection, are not included in the Holdheide monograph.

The collection, which is primarily focused on a representation of different families and the range of taxa, does not include the anatomical variability within species growing in the full range of habitats. It was beyond the scope of this study to comprehensively investigate this plasticity of traits within species in relation to the range of habitat conditions in which these species grow. We are aware that such plasticity exists.

2. Material and Methods

Geographic Origin of the Material

Plant material was collected during numerous field tours and expeditions. The geographic origin of the investigated specimens and the species nomenclature are summarized in **Table 1**. Details are given at *http://www.wsl.ch/dendro/xylemdb/index.php*. Clearly, the largest fraction of plants (about 80%) originated from Europe. Species from outside Europe served mainly to enlarge the taxonomic range and to demonstrate anatomical similarities between tectonically early separated regions.

Table 1. Geographic origin of the sampled species.

Continent	Region	Country	No. of species	Nomenclature
Europe	Scandinavia and Svalbard	Sweden, Finland, Norway, Russia	3	Tutin et al. 1964
	Western Siberia	Russia	81	Tutin et al. 1964
	Central	Austria, France, Germany, Hungary, Poland, Romania, Slovakia, Slovenia, Switzerland	812	Aeschimann et al. 2004 Lauber and Wagner 2001 Eggenberg and Möhl 2007 Rothmaler, 2005
	West	England	13	Tutin et al. 1964
	South	Greece, Italy, Portugal, Spain, Ex-Yugoslavia	242	Tutin et al. 1964
	Macaronesia	Canary Islands, Madeira	160	Bramwell and Bramwell 2000 Hohenester and Wels 1993 Schönfelder and Schönfelder 1997
Africa	North	Algeria, Egypt, Etiopia, Libya, Marocco, Tunesia	49	Ozenda 1983
	Arabian Peninsula	Oman	38	Miller and Morris 1988 Jagiella and Kürschner 1987
Asia	Central	Mongolia	3	determined by H. Heklau, Halle, Germany
	Near East	Georgia, Iran, Israel	52	Flora of Georgia
	South East	wood collection various countries	5	
America	North	USA, Canada	184	Weber 1976 Epple 1995
	South	Argentina, Chile	13	determined by Prof. F. Roig sen.
Oceania	Australia and New Zealand	Australia (New South Wales) and New Zealand (South Island)	2	Costerman 1989 NZ species determined by H. Ullmann, Würzburg, Germany
Total			**1657**	

Families and Number of Species Treated in this Volume

Aizoaceae	5
Amaranthaceae	62
Amborellaceae	1
Anacardiaceae	10
Apocyanaceae	10
Asclepiadaceae	11
Aristolochiaceae	6
Berberidaceae	16
Betulaceae	25
Brassicaceae	161
Buxaceae	6
Cannabaceae	2
Capparaceae	8
Caryophyllaceae	100
Celastraceae	10
Ceratophyllaceae	1
Cercidiphyllaceae	1
Cistaceae	35
Clusiaceae	18
Cneoraceae	2
Crassulaceae	31
Cucurbitaceae	7
Droseraceae	4
Eleagnaceae	4
Ericaceae	59
Euphorbiaceae	48
Fabaceae	211
Fagaceae	22
Gentianaceae	26
Geraniaceae	20
Grossulariaceae	15
Haloragaceae	2
Hamamelidaceae	8
Juglandaceae	1
Krameriaceae	1
Lardazibalaceae	6
Lauraceae	6
Linaceae	10
Loranthaceae	8
Lythraceae	5
Magnoliaceae	6
Malvaceae	25
Menispermaceae	1
Menyanthaceae	2
Moraceae	8
Myricaceae	3
Myrtaceae	1
Nepenthaceae	2
Nyctaginaceae	5
Nymphaeaceae	3
Onagraceae	14
Oxalidaceae	4
Paeoniaceae	3
Papaveraecae	23
Phytolaccaceae	1
Piperaceae	3
Platanaceae	3
Plumbaginaceae	10
Polygalaceae	7
Polygonaceae	41
Portulacaceae	3
Primulaceae	
Ranunculaceae	63
Resedaceae	9
Rhamnaceae	28
Rosaceae	158
Rubiaceae	33
Rutaceae	8
Salicaceae	39
Salvadoraceae	1
Santalaceae	9
Sapindaceae	15
Saxifragaceae	27
Simmondsiaceae	1
Staphyleaceae	2
Tamaricaceae	9
Thymelaceae	15
Tiliaceae	5
Trochodendraceae	2
Ulmaceae	6
Urticaceae	10
Violaceae	17
Vitaceae	5
Winteraceae	6
Zygophyllaceae	7
Total	1627

Families Treated in Vol. 2

Actinidiaceae
Adoxaceae
Apiaceae
Aquifoliaceae
Araliaceae
Asteraceae
Balsaminaceae
Boraginaceae
Campanulaceae
Caprifoliaceae
Convolvulaceae
Cornaceae
Diapensiaceae
Diervilleaceae
Dipsacaceae
Ebenaceae
Frankeniaceae
Garryaceae
Hydrangeaceae
Lamiaceae
Lentibulariaceae
Linnaeaceae
Myrsinaceae
Oleacea
Orobanchacea
Phrymacea
Pittosporaceae
Plantaginaceae
Polemoniaceae
Sapotaceae
Sarraceniaceae
Scrophulariaceae
Solanaceae
Styracaceae
Valerianaceae
Verbenaceae

Internet Data

Tables and pictures are an integral part of the present volume.

Microscopic pictures and the occurrence of anatomical features of all species analyzed with ecological characteristics (modified feature code of the IAWA-list (Wheeler et al. 1989) can be viewed in the internet.

In addition, a special table with all recorded anatomical taxonomic, morphological, environmental parameters is listed here.

- *http://www.wsl.ch/dendro/xylemdb/index.php*

Preparation of the Plant Material

For wood anatomical studies and for age determinations the most important plant part is the transition zone between root and stem, (root collar). For rhizomes the oldest end of the rhizome system has been used. For collection the plant was usually excavated.

Plant material was conserved in the field in 40% ethanol or any commercial alcohol, and stored and transported in thick-walled plastic bags which were collectively stored in plastic boxes.

Each sample was labeled with a sticker inscribed with a soft pencil (not alcohol soluble) containing the Latin plant name, the identification of the plant part (root, rhizome etc.), the plant life form according to Raunikiaer, plant height, phenology and obvious stem deformations, site conditions, altitude, location and sampling date.

The sample preparation was described in detail by Chaffey (2002) and Schweingruber et al. (2006).

All stems were cut as fresh material (not embedded in paraffin) into 1 cm^3 sections. Large stems were sectioned in pieces near the pith (juvenile wood) and near the cambium (adult wood). Thin stems were clamped in cork (*Quercus suber*). Sections were cut with a Reichert microtome or with the GSL-sliding microtom. The knives of the Reichert microtome were sharpened with the Leica knife sharpening machine. The GSL-microtome uses disposable paper knife blades.

The thin sections are placed on a glass object holder (slide) and covered with glycerol. Staining liquids are dropped in excess to run off into a container. The sections were stained with Astrablue (0.3 g in 100ml aqua dest. with 2 ml acetic or tartaric acid) and Safranin (0.4 g in 100 ml aqua dest.) mixed in a 1:1 ratio. A drop of the solution is placed on the section every 3 minutes.

The stained sample is washed with 95% alcohol and dehydrated with absolute alcohol. The absolute alcohol is replaced again by 95% alcohol mixed with 2,2-Dimethoxypropanaceton-dimethyacetat (Fluka). Finally, a drop of xylol tests for the presence of any water. Dehydration is incomplete, and requires more washing with absolute alcohol, if the xylol turns milky. A drop of Canada Balsam is placed on the dehydrated section with a cover glass pressed on top. To avoid buckling of the sample, two PVC-plastic stripes are placed above and below the slide and pressed together using two small magnets while drying in an oven at 60°C for 12 hours.

Specimens containing slimes (mucilage), starch or dark-stainingsubstances (phenols) were initially soaked in a drop of calcium hypochloride (Bleach, Javelle water) for 5-10 minutes. The section is then rinsed with water until any chloride smell disappears.

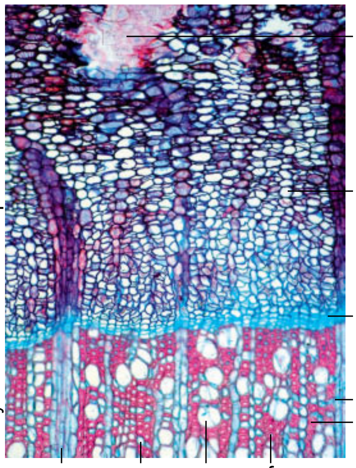
Sections were microscopically inspected using magnifications of 20-1000 (Olympus BX51 with camera Olympus C5050).

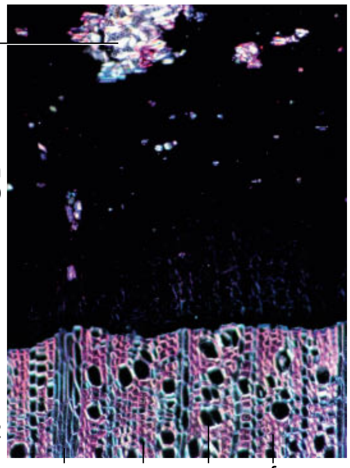
Polarized light is an extremely useful technique for the differentiation of the cell wall construction. Cell walls with a net-like, unordered fibril orientation disappear in polarized light. Cells with more ordered fibrils exhibit birefringency when illuminated with polarized light. Birefringence, or double refraction, is the decomposition of a ray of light into two rays when it passes through certain types of material. Therefore primary and tertiary walls (S1 and S3) and parenchyma cells with a non-crystalline fibril construction appear black and all cells with secondary walls (S2) and with parallel ordered fibrils appear lighter. The practical value of Astrablue/Safranin staining and the use of polarized light is demonstrated in the figure on the next page.

stained with Astrablue / Safranin

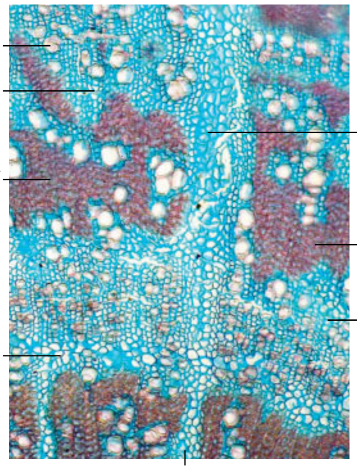
unpolarized light | polarized light

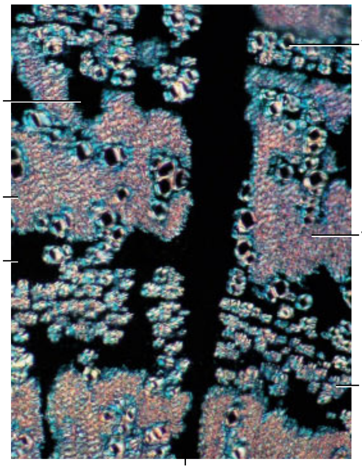
Apollonias barbujana
tree with dense wood



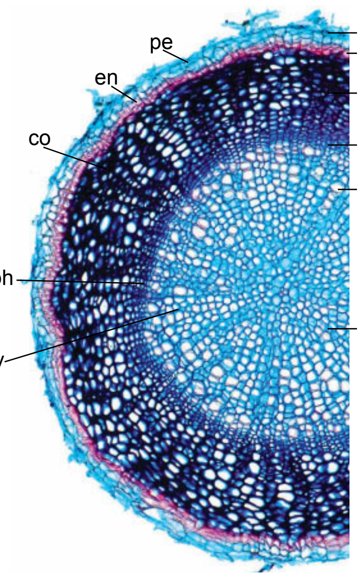


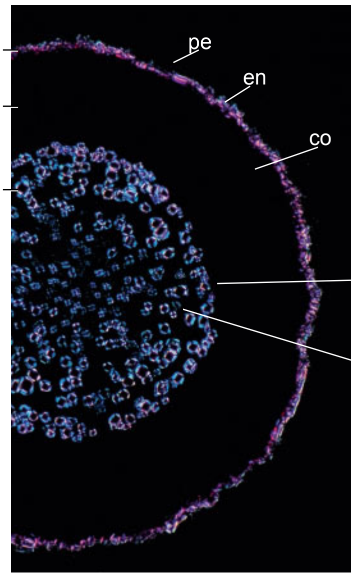
Erysimum crepidifolium
dwarf shrub with soft stem
chamaephyte





Cerastium semidecandrum
annual, fragile herb





3. Vegetation and Plant Parameters

Definition of Vegetation/Climate Types

We relate each analyzed species to vegetation/climate types, (Walther and Lieth 1967 and Walther and Breckle 1991). The following plant growth relevant parameters are presented in **Table 2** below.

- Mean January temperatures and precipitations indicate the severity of winter frosts and the water availability at the beginning of the growing season.
- Mean July temperatures and precipitations indicate the growing conditions in summer.
- Total annual precipitations indicate the general hydrological conditions.
- The number of arid months is an indicator for potential growth limitations.
- The number of winter month indicates the period without radial growth.

Table 2. Climatic values in relation to vegetation/climate types climatic data after Walter and Lieth (1967). The selection of climatic stations is in accordance with collected samples.

Classified vegetation types	Vegetation	Meteorological station	Elevation (m a.s.l.)	Jan temperature (°C)	Jan precipitation (mm)	July temperature °C)	July precipitation (mm)	Ann. precipitation (mm)	No. of arid months	No. of winter onths
arid	desert	Tucson, USA	739	10	22	30	60	293	10	-
subtropical desert		Tobruk, Libya	46	13	35	26	0	146	10	-
		Gat, Libya	561	15	0	33	1	10	12	-
	coastal desert below summer rain forest	Salalah, Oman	18	23	5	28	20	90	12	-
subtropical subtropical evergreen forest	laurel forest	La Laguna, Canary Islands, Spain	547	13	95	21	5	594	4	-
Mediterranean	evergreen oak forest	Santa Barbara, USA	37	12	100	25	0	371	7	2-3
thermomediterranean		Tripolis, Libya	18	13	25	25	5	625	5	2-3
		Faro, Portugal	153	12	50	25	0	363	6	2-3
		Athens, Greece	105	10	29	25	0	383	6	2-3
	succulent bush	St. Cruz de Tenerife, Canary Islands, Spain	50	18	35	22	0	290	8	-
		Las Palmas, Canary Islands, Spain	12	18	40	20	2	543	9	-
submediterranean	dry deciduous forest	Valence, France	126	5	40	21	45	904	1	3-4
		Turin, Italy	260	2	45	23	40	679	1	3-4
		Mostar, Croatia	70	6	100	25	40	1343	1	3-4
temperate hill zone	conifer forest	Astoria, USA	70	5	120	15	25	1935	-	5
warm temperate, humid	oak forest	Cardiff, U.K.	62	5	105	16	60	1043	-	5
	chestnut forest	Lugano, Switzerland	276	2	70	21	110	1725	-	5
temperate hill zone and	humid deciduous forest	Basel, Switzerland	343	1	45	18	95	815	-	4
temperate hill and mountain zone	dry pine forest	Sion, Switzerland	549	-1	55	20	50	590	-	4
temperate hill zone		St. Foy, France	430	4	80	20	60	938	-	4
	pine forest	Vienna, Austria	203	0	45	19	80	685	-	4
temperate mountain zone	pine forest	Barcelonette, France	1134	-1	45	17	40	731	-	5-6
temperate mountain zone	spruce forest	La Brévine, Switzerland	1077	-3	105	12	105	1446	-	5-6
	beech forest	Bachtel, Switzerland	1131	-1	100	12	110	1635	-	5-6
	spruce forest	Mittenwald, Austria	910	-2	70	14	105	1337	-	5-6
temperate alpine zone	meadow, fir forest	Mt. Ventoux, France	1912	-4	80	10	60	1228	-	7
temperate subalpine zone	*Rhododendron* bush	Grimsel Hospiz, Switzerland	1962	-7	105	9	105	2070	-	7
	larch, stone pine forest	St. Moritz, Switzerland	1853	-7	50	10	100	935	-	7
	spruce forest	Wolf Creek Pass, Colorado, USA	3100	-7	15	14	10	100	-	7
alpine zone	rocks, meadow	Säntis, Switzerland	2500	-8	110	5	115	2785	-	8
		Zugspitze, Austria	2962	-11	70	2	105	1350	-	8
boreal zone	pine forest	Irkutsk, Russia	467	-19	10	16	95	369	-	8
		Sljud, Russia	401	-18	5	14	105	474	-	8
	larch forest	Ochotsk, Russia	6	-23	3	11	60	238	-	8
	spruce forest	Fort Yukon, Canada	127	-30	5	15	30	172	1	8

The classification used for each species corresponds with the following descriptions.

Arid. Subtropical arid zone (desert), with 10-12 arid months, occasionally with night frosts. Rainfall is below 300 mm. The present dataset includes species from the following regions:

- Regions with two rain periods (Sonora desert, Southwest N-America), see **Tab. 3.1** Tucson. Land cover 20-40%. Shrubs and small trees, e.g. *Larrea divaricata* and many succulent species.
- Regions with one winter rain period (Northern Sahara, Marocco), see **Tab. 3.1** Tobruk. Land cover 20-30%. Shrubs and small trees, e.g. *Acacia* sp.
- Regions with one summer rain period (Dhofar, Oman), see **Tab. 3.1** Salalah. Land cover 10-40%. Shrubs and small trees, e.g. *Ficus salicifolia*, *Dodonea viscosa*.
- Regions without periodic rainfall (central Sahara), see **Tab. 3.1** Gat. Land cover <5%. Shrubs, e.g. *Leptadenia pyrotechnica*.

Subtropical. This zone has generally an arid season of 3 to 6 months, but no frost. The present dataset includes the following regions:

- Canary Islands: Warm, frost-free climate with minor seasonal temperature differences and without a distinct dry summer period. Permanent clouds on northern facing slopes of the Islands create fairly dense forest (Laurel forest). See **Tab. 3.1** La Laguna.
- Southern coast of Oman: Temperatures like on the Canary island but with high precipitation from July to September.

Mediterranean. Mediterranean climate has winter rains, and an arid summer period, but occasional cyclonal rains are possible all year long.

- Thermomediterranean (Macchia and chaparral). Winter frosts are not below -5°C. Distribution along coasts mainly on south-facing slopes up to approximately 200 m a.s.l. The vegetation in Europe is characterized by *Quercus ilex*, *Quercus suber* and macchia shrubs. See **Tab. 3.1** Santa Barbara, Tripolis, Faro and Athens.
The subtropical succulent bush zone at lower altitudes on the Canary Islands (Macaronesia) is included here because a long arid summer period mainly influences the composition of the vegetation. The zone is characterized by high winter temperatures and long summer droughts in the lowland on the Canary Islands (Macaronesia). See **Tab. 3.1** St. Cruz de Tenerife and Las Palmas. Land cover 10-40%. Shrubs, succulents e.g *Kleinia* sp. and many introduced European species.

- Submediterranean. Mediterranean climate with winter rains and a short dry summer period, without a distinct cold winter but occasionally with winter frosts but not below -10°C. See **Tab. 3.1** Valence, Turin, Mostar.
Wide region of southern Europe and the Black Sea at north facing slopes at low altitudes and on south-facing slopes at higher altitudes. The vegetation is characterized by *Quercus pubescens*.

Temperate Zone.
The temperate Zone has summer and winter rains, and a distinct growing season of 6 to 10 months. Frost may reach -30°.

Temperate hill zone. Warm temperate regions without drought periods. Distinct temperature- seasonality with a few frosts. Coastal and hill zone in Europe and North America. See **Tab. 3.1** Astoria, Cardiff and Lugano. Forests are dominated by:

- Tall conifers, e.g. *Sequoia sempervirens*, *Abies grandis* and *Pseudotsuga menziesii* along the Pacific coast in the USA.
- Oak (*Quercus robur*) in Great Britain.
- Chestnut (*Castanea sativa*) in the Southern Alps.

Temperate hill and mountain zone. Cold temperate zone without drought periods. Distinct temperature-seasonality with some frosts. Vegetation period lasts 6-8 month. January temperatures are around freezing point. July temperatures vary between 17-20°C and annual precipitations between 600-1000 mm. See **Tab. 3.1** St. Foy, Basel, Sion and Vienna. Forests are normally dominated by various species of summer green trees, e.g. *Fagus sylvatica* and *Quercus robur*, but on south-facing slopes by pines (*Pinus sylvestris*). The hill zone extends in the Alps from 200-1000 m a.s.l.

Temperate mountain zone. January temperatures are a few degrees below the freezing point. July temperatures vary between 12-16°C and annual precipitations between 1000-2000 mm. The duration of vegetation periods varies between 5-6 months. See **Tab. 3.1** Barcelonette, La Brévine, Bachtel and Mittenwald.
Forests are normally dominated by various species of summer green trees e.g. *Fagus sylvatica* and *Abies alba* but south facing slopes by pines (*Pinus sylvestris*). The hill zone extends in the Alps from 800-1600 m a.s.l.

Temperate alpine zone. The present classification includes the subalpine and alpine zone.

- Subalpine zone. Mean January temperatures vary between 5-9°C below freezing point and July temperatures between 9-12°C. Annual precipitation is mostly more than 1500-2000 mm. Growing seasons vary between 3-4 months. See **Tab. 3.1** Mt. Ventoux, Grimsel Hospiz, St. Moritz, Wolf Creek Pass.
Forests in humid regions are dominated by spruce (*Picea abies*), those in more continental regions by larch and stone pine and mountain pine (*Larix decidua*, *Pinus cembra*, *Pinus mugo*). Deforested areas are dominated by meadows and dwarf shrubs, e.g. *Rhododendron ferrugineum* and *Calluna vulgaris*. The subalpine zone extends in the Alps from 1600-2300 m a.s.l.

- Alpine zone. Mean January temperatures vary between 8-11°C below freezing point. July temperatures rarely reach 10°C and annual precipitation is mostly more than 2000 mm. The duration of growing season varies between 1-2.5 months. See **Tab. 3.1** Säntis and Zugspitze. Open meadows and rock fields are characteristic of the zone.

Boreal zone, Taiga.
The boreal zone has a growing season of 3-6 months with an average summer temperature of >10°C. Winter temperatures reach <30°C. See **Tab. 3.1** Irkutsk, Sljud, Ochotsk, Fort Yukon. Forests are dominated by spruce (*Picea obovata*, *P. mariana*, *P. glauca*) and various *Larix* species.

Arctic Zone, Tundra.
The arctic reagion has July temperatures <10°C, and a growing season of up to 3 months. Open meadows and rock fields are characteristic of the zone.

Definition of Life Forms (after Ellenberg et al. 1992)

P: Phanerophytes. Woody plants that grow taller than 4 m high (trees).

N: Nanophanerophytes. Woody, shrub-like 0.5-4 m high plants.

C: Chamaephytes. Herbaceous to semi-woody perennials. Dwarf shrub-like plants whose mature branch or shoot system remains perennially 25-50 cm above ground surface.

Z: Woody chamaephytes. Dwarf shrubs with less than 50 cm height.

H: Hemicryptophytes. Perennial herbaceous (including biennials) plants. With periodic shoot reduction to a remnant shoot system that grows relatively flat on the ground. Here we include most of the *geophytes (G)* whose surviving shoot system normally remains below surface. Also included are winter-annuals, which perform their life cycle between fall to late spring. These winter annual plants form two rings.

T: Therophytes. Annuals. Plants whose shoot and root system dies after seed production and which complete their life cycle within one growing season (spring, summer, fall). Included are only specimens with one tree ring.

Liana: Mostly perennials, plants with extremely long shoots, which need normally structural support by other species.

Definition of Plant Height (after Aeschimann et al. 2004)

Plant height is principally genetically fixed but ecological conditions can modify height in a certain range. Since we did not record the height of all plants analyzed in detail we classified each species in the following height classes:

Height variability	Height class
2-10 cm	5 cm
10-25 cm	20 cm
25-50 cm	40 cm
50-100 cm	80 cm
100-150 cm	150 cm
150-300 cm	300 cm
300->1000 cm	1000 cm

4. Definition of Anatomical Features

Precondition for a valuable comparison of anatomical structures is the definition and coding of features. Here, we separately define ring distinctness and microscopic features.

Classification of Ring Distinctness after Schweingruber and Poschlod 2005

Type a: Growth-ring numbers can be exactly determined: All ring boundaries are clearly demarcated (**Figs. 1-3**). In this case the number of observed growth rings corresponds to the true age of the plant tissue. Growth rings in the collar of primary taproots yield the ontogenetic age; growth rings in rhizomes provide the age of the preserved tissue.

Type b: There is some uncertainty in the determination of the age: Clearly demarcated rings are only visible along some radii and some rings may be ill-defined due to tangential intra-annual bands or wedging rings. In such cases, it is important to examine the complete cross section. **Fig. 4**

Type c: Age determination is uncertain. Ring numbers indicate a rough estimation. Growth zones may either look like annual rings, or be weakly expressed, or only visible in small areas of the cross section. **Figs. 5** and **6**

Type d: Age cannot be determined: Growth rings are invisible or growth-ring formation is insignificant. **Figs.** 7 and **8**

Type e: The growth zone of annual plants (therophytes) cannot be classified because only one zone is present. When therophytes germinate in autumn and flower in the next growing season they form two rings. In this case they may be classified as belonging to any one of the types a, b or c.

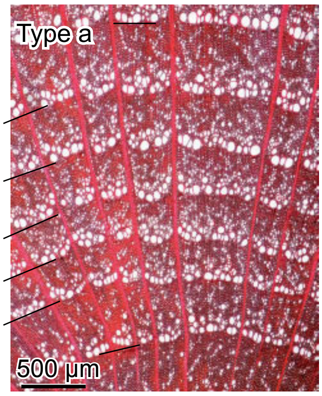


Fig. 1. *Berberis aetnensis*, Berberidaceae.

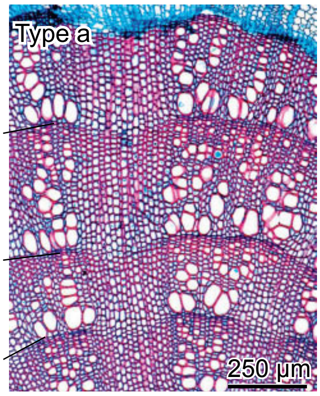


Fig. 2. *Helleborus viridis*, Ranunculaceae.

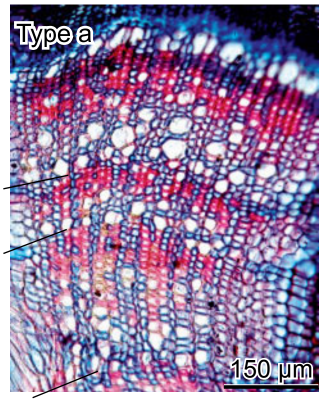


Fig. 3. *Viola odorata*, Violaceae.

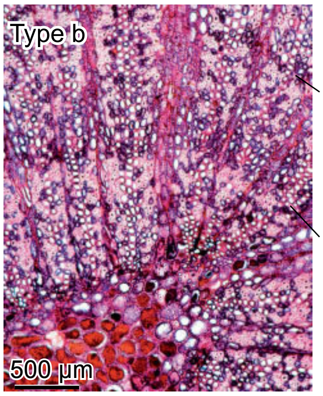


Fig. 4. Boundary marked by thick-walled fibers in the latewood and their absence in the earlywood. *Loranthus aphyllus*, Loranthaceae, dwarf shrub.

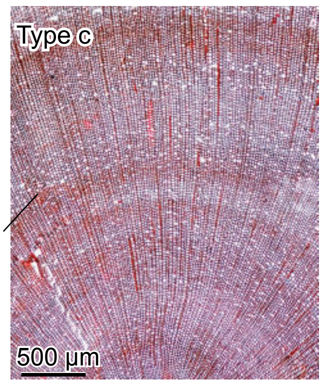


Fig. 5. Radial growth variations marked by zones with fibers of variable cell wall thickness. *Ixanthus viscosus*, Gentianaceae, dwarf shrub.

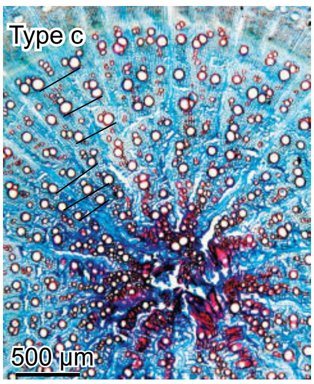


Fig. 6. Annual rings partially indicated by the difference in vessel size between latewood and earlywood. *Laserpitium gallicum*, Apiaceae, herb.

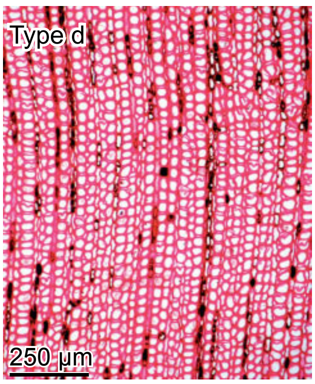


Fig. 7. Growth zones absent. *Amborella trichopoda*, Amborellaceae, small tree.

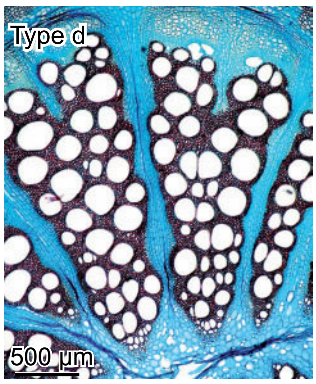


Fig. 8. Growth zones absent. *Aristolochia gigantea*, Aristolochiaceae, shrub.

Definition of Features According to the IAWA List (Wheeler et al. 1989), and Complements

2.1 Only one ring. Annual plants = therophytes.

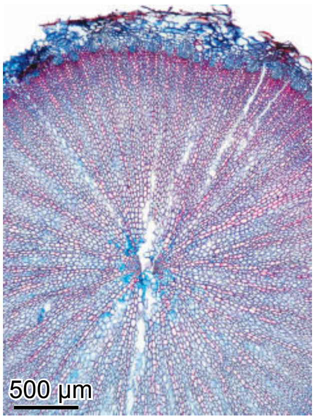


Fig. 9. Root collar, without pith. Very small vessels. *Adonis flammea*, Ranunculaceae.

Fig. 10. Root collar, without pith. Vessels in radial multiples *Fumaria officinalis*, Papaveraceae.

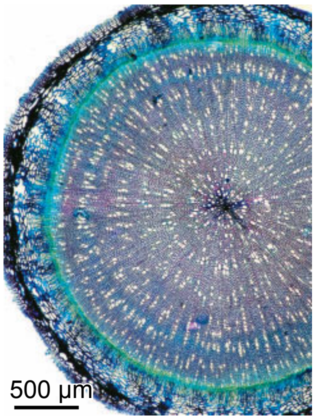


Fig. 11. Root collar, without pith. Vessels in tangential bands. *Capsella bursa-pastoris*, Brassicaceae.

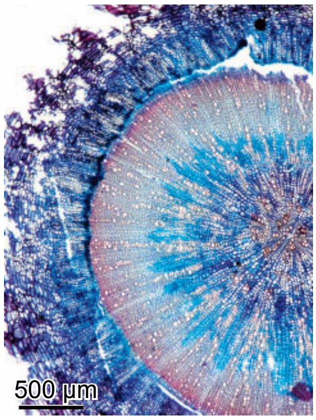


Fig. 12. Root collar, without pith. With pervasive parenchyma in the center. *Echium bonnettii*, Boraginaceae.

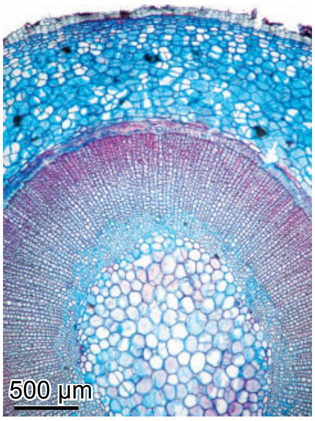


Fig. 13. Root collar, with pith. Vessels are absent in the latewood. *Umbilicus horizontalis*, Crassulaceae.

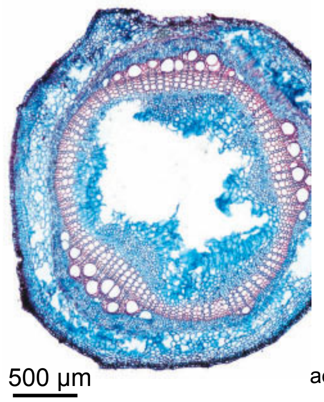


Fig. 14. Root collar, with pith. Vessel dimorphism. Large vessels in the second part. *Calystegia sepium*, Convolvulaceae.

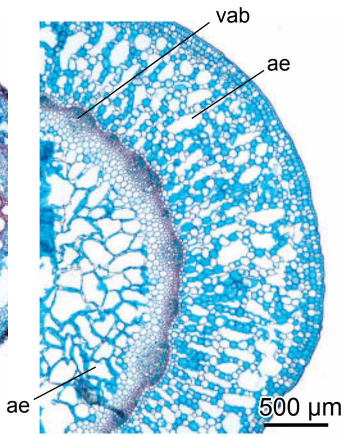


Fig. 15. Vascular bundles are connected by inter-vascular fiber zones. *Lysimachia thyrsiflora*, Primulaceae.

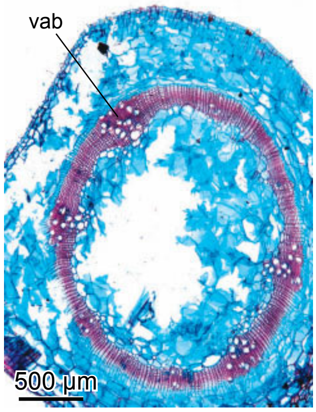


Fig. 16. Vascular bundles are connected by inter-vascular fiber zones. *Impatiens parviflora*, Balsaminaceae.

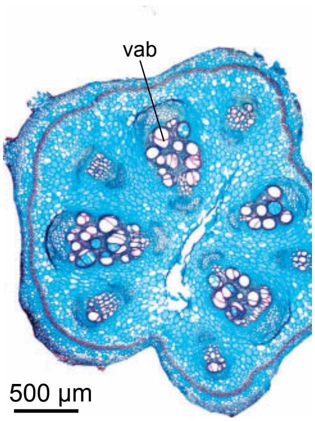


Fig. 17. Vascular bundles are connected by large inter-parenchyma zones. *Cucumis sativus*, Cucurbitaceae.

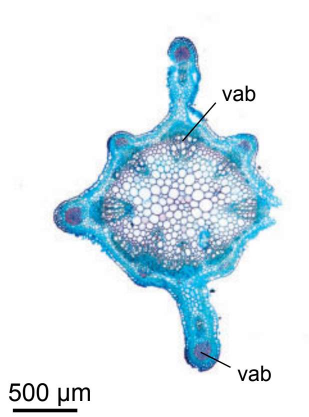


Fig. 18. Vascular bundles are connected by small inter-parenchyma zones. *Vicia hirsuta*, Fabaceae.

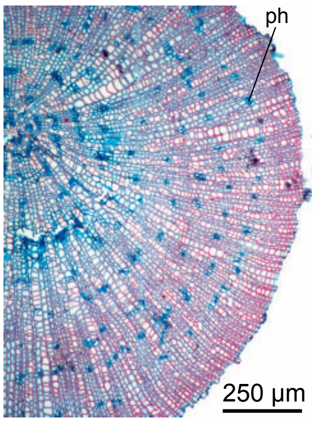


Fig. 19. Root collar without pith. Groups of inter-xylary phloem in tangential rows. *Plantago aschersonii*. Plantaginaceae.

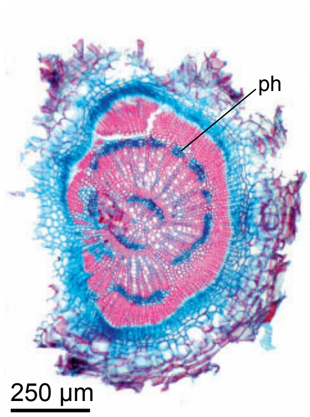


Fig. 20. Root collar without pith. Bands of inter-xylary phloem. *Sagina maritima*, Caryophyllaceae.

2.2 Without secondary growth.

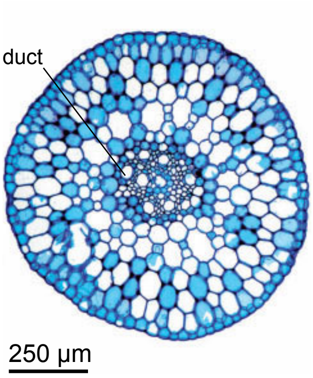


Fig. 21. Central vascular bundle with air ducts. Hydrophyte, *Ceratophyllum demersum*, Ceratophyllaceae.

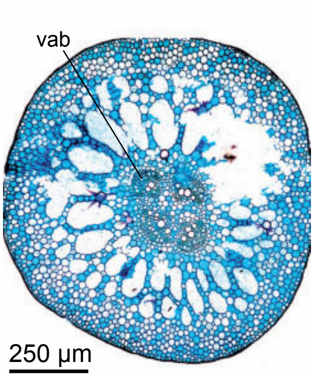


Fig. 22. Four centrally arranged vascular bundles. Helophyte, *Nymphoides peltata*, Menyanthaceae.

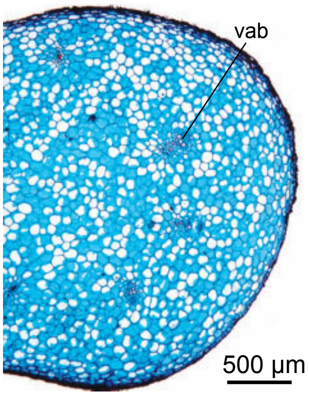


Fig. 23. Isolated vascular bundles in a parenchymatic tissue. Rhizome. *Anemone ranunculoides*, Ranunculaceae.

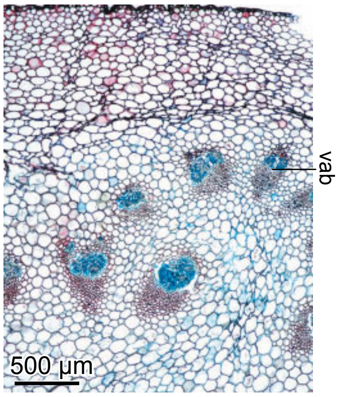


Fig. 24. Isolated vascular bundles in a parenchymatic tissue. Annual shoot. *Cistanche tinctoria*, Orobanchaceae.

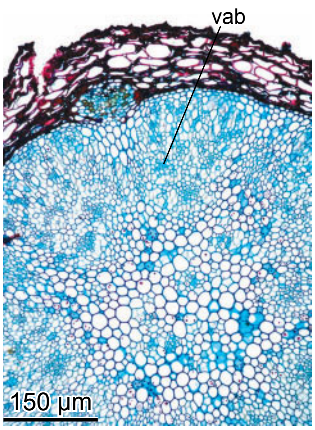


Fig. 25. Isolated vascular bundles in a parenchymatic tissue. Perennial shoot. *Drosera capensis*, Droseraceae.

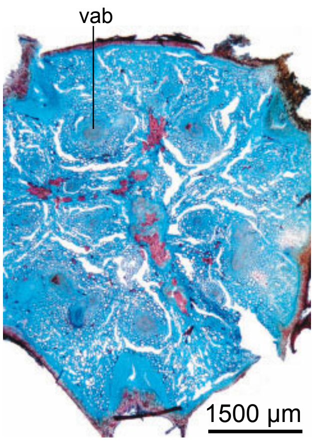


Fig. 26. Concentric vascular bundles within a parenchymatic tissue. *Primula hirsuta*, Primulaceae.

3 Ring-porous. Vessels in earlywood are 6 to >10x larger in diameter than those in the latewood.

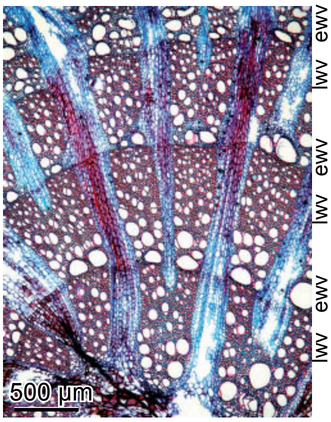


Fig. 27. *Aristolochia macrophylla*, Aristolochiaceae, liana.

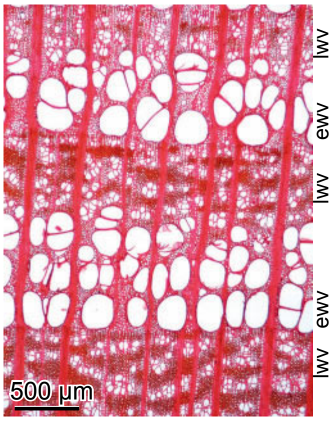


Fig. 28. *Morus alba*, Moraceae, tree.

4 Semi-ring-porous. Vessels in earlywood are 3 to 5x larger in diameter than those in the latewood. Transitions between semi-ring-porous and diffuse-porous may occur even within an individual.

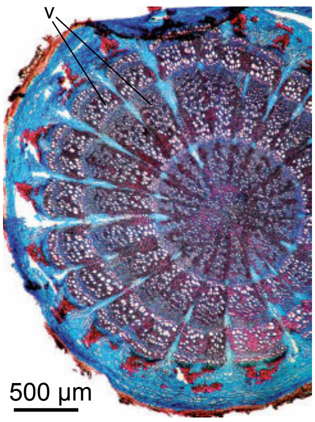


Fig. 29. *Aethionema thomasiana*, Brassicaceae, herb.

Fig. 30. *Sedum album*, Crassulaceae, herb.

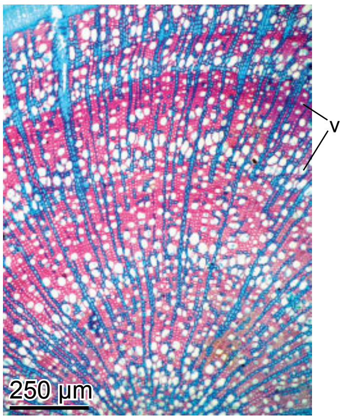


Fig. 31. *Adenolinum lewisii*, Linaceae, herb.

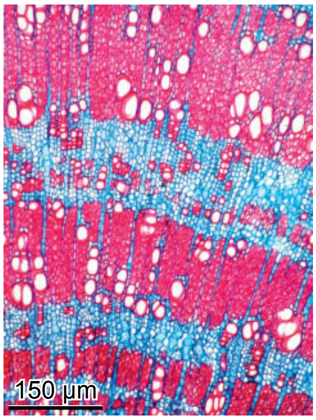


Fig. 32. *Euphorbia seguieriana*, Euphorbiaceae, dwarf shrub.

5 Diffuse-porous. Vessels diameter is constant throughout the growth ring.

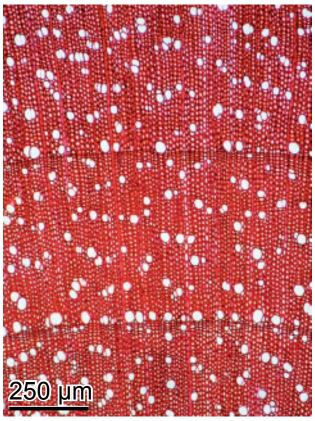


Fig. 33. *Ribes alpinum*, Grossulariaceae, small shrub.

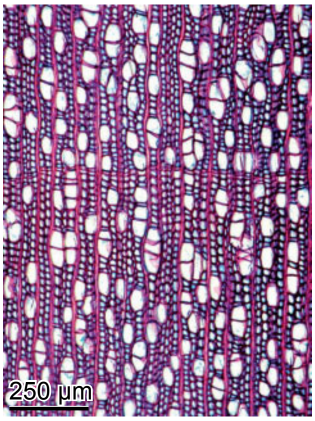


Fig. 34. *Aesculus hippocastaneum*, Sapindaceae, tree.

6 Vessels in intra-annual tangential rows. See also **Figs. 11**, **95** and **152**.

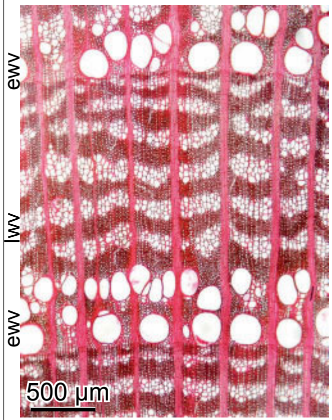


Fig. 35. *Ulmus laevis*, Ulmaceae, tree.

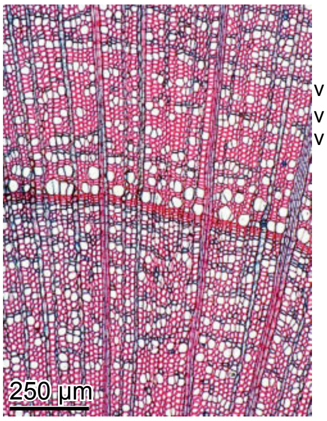


Fig. 36. *Enkianthus campanulatus*, Ericaceae, shrub.

7 Vessels in diagonal and/or radial patterns. Transitions between diagonal and dendritic distribution exist within an individual.

Fig. 37. *Mahonia bealei*, Berberidaceae, shrub.

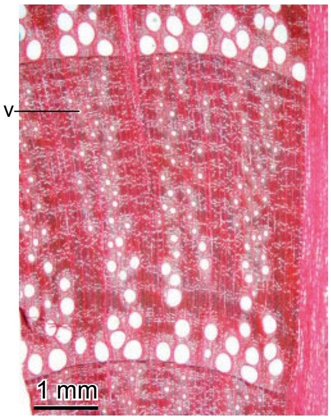


Fig. 38. *Quercus cerris*, Fagaceae, tree.

8 Vessels in dendritic patterns. Transitions between diagonal vessel distribution and semi-ring-porosity exist within an individual.

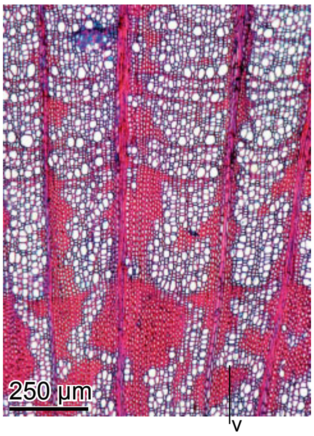


Fig. 39. *Berberis julianae*, Berberidaceae, herb.

Fig. 40. *Genista radiata*, Fabaceae, shrub.

9 Vessels predominantly solitary. See also **Figs. 101** and **120**.

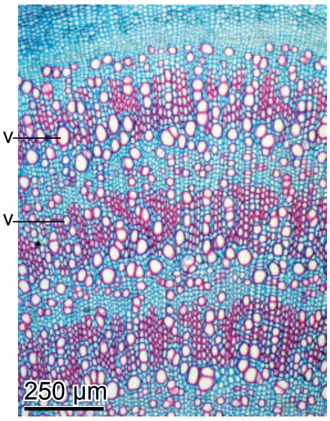


Fig. 41. *Silene maritima*, Caryophyllaceae, herb.

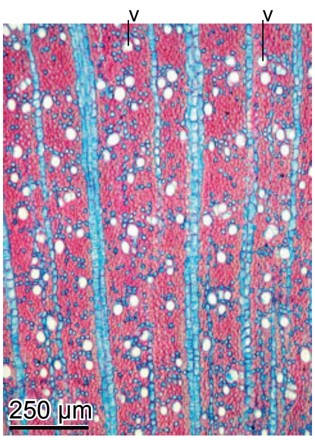


Fig. 42. *Zygophyllum fontanesii*, Zygophyllaceae, succulent chamaephyte.

9.1 Vessels in radial multiples of 2 to 4 common. See also **Figs. 95** and **117**.

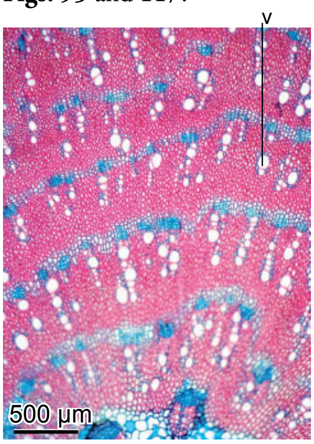


Fig. 43. *Atriplex patula*, Amaranthaceae, annual herb.

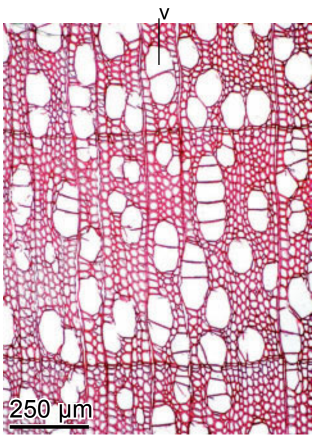


Fig. 44. *Populus suaveolens*, Salicaceae, tree.

10 Vessels in radial multiples of 4 or more common. See also **Fig. 10.**

Fig. 45. *Erodium ciconium*, Geraniaceae, annual herb.

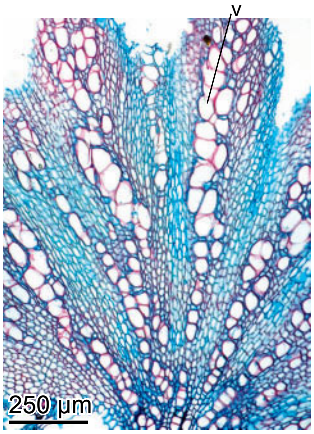


Fig. 46. *Asperugo procumbens*, Boraginaceae, annual herb.

11 Vessels predominantly in clusters. Groups of 3 or more vessels having both radial and tangential contacts.

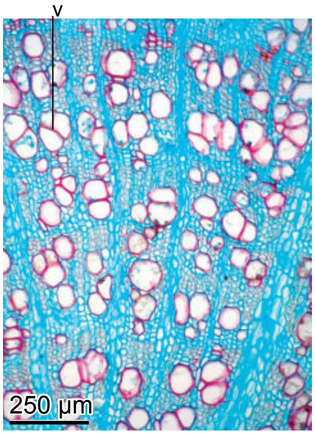


Fig. 47. *Euphorbia nicaeensis*, Euphorbiaceae, herb.

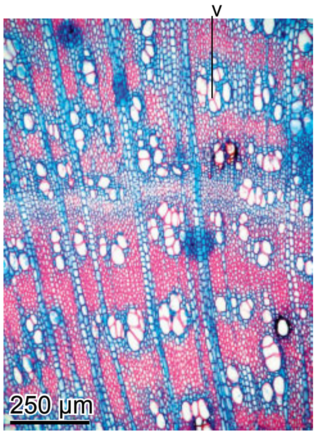


Fig. 48. *Malva moschata*, Malvaceae, herb.

13 Vessels with simple perforation plates. Perforation plate with a single circular or elliptical opening.

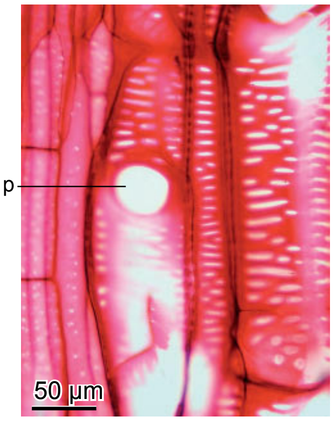


Fig. 49. *Euphorbia piscatoria*, Euphorbiaceae, shrub.

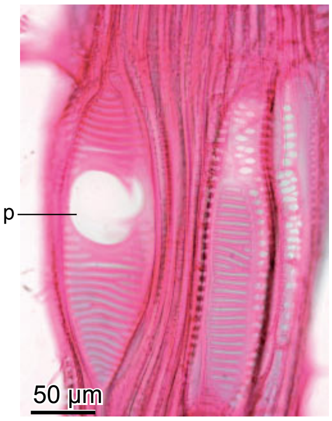


Fig. 50. *Parthenocissus inserta*, Vitaceae, herb.

14 Vessels with scalariform perforation plates. Numbers of bars are of some taxonomic value. Transitions to scalariform intervessel pits occur. See also **Fig. 92**.

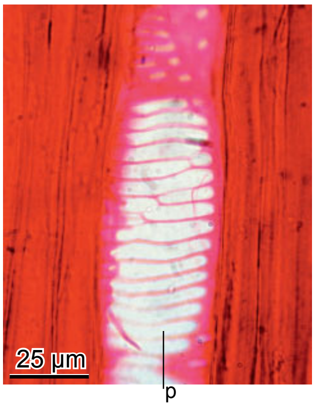


Fig. 51. Perforation plate with >10 bars. *Ribes alpinum*, Grossulariaceae, shrub.

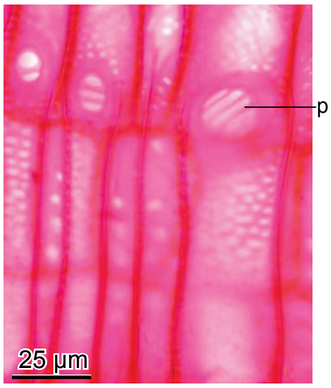


Fig. 52. Scalariform perforation plates with 1-3 bars. *Tolpis fruticosa*, Asteraceae, dwarf shrub.

20 Intervessel pits scalariform. Pits with horizontally elongated apertures. See also **Fig. 92**.

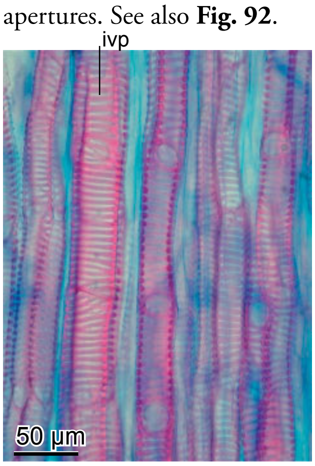


Fig. 53. *Viola calcarata*, Violaceae, herb.

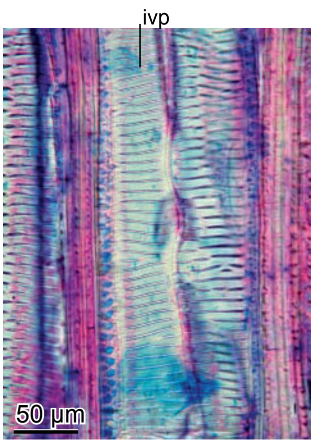


Fig. 54. *Parthenocissus tricuspidara*, Vitaceae, climber.

20.1 Intervessel pits pseudoscalariform to reticulate. Pits with enlarged apertures.

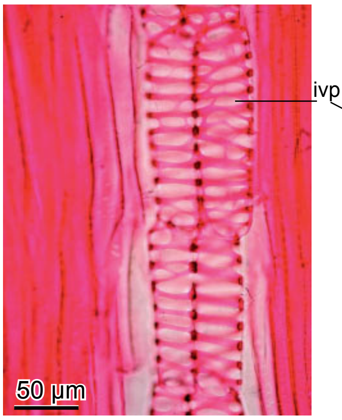


Fig. 55. *Aeonium urbicum*, Crassulaceae, dwarf shrub.

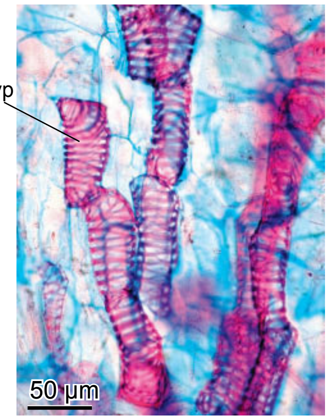


Fig. 56. *Orobanche canescens*, Orobanchaceae, annual herb.

21 Intervessel pits opposite. Arranged in horizontal rows across the length of the vessel.

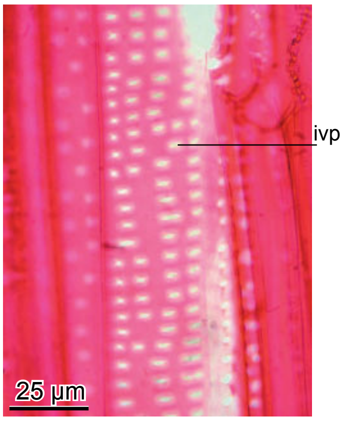


Fig. 57. Regular formed pits. *Platanus orientalis*, Platanaceae, tree.

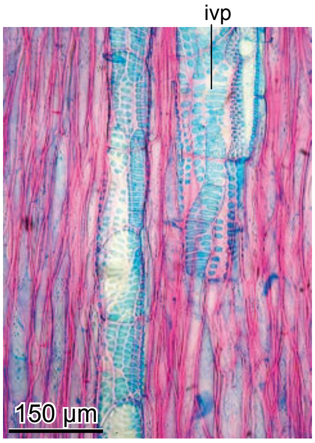


Fig. 58. Irregular formed pits. *Impatiens noli-tangere*, Balsaminaceae, annual herb.

22 Intervessel pits alternate. Arranged irregularly or in diagonal rows.

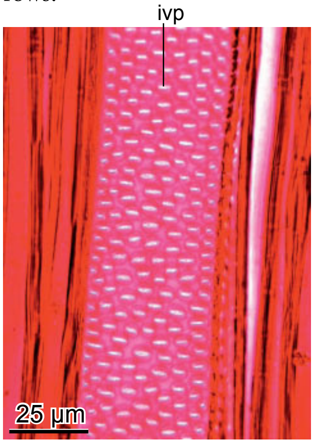


Fig. 59. *Reseda suffruticosa*, Resedaceae, shrub.

Fig. 60. *Salix planifolia*, Salicaceae, shrub.

31 Vessel-ray pits with large round apertures, *Laurus* type. Summarized are all forms from large round to irregular and to reticulate.

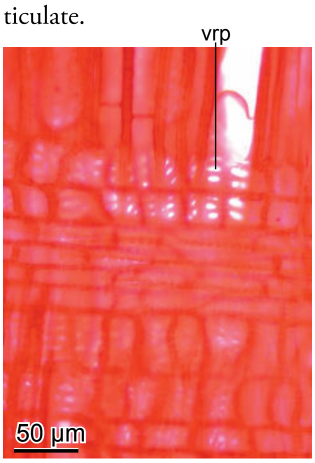


Fig. 61. *Olea europaea* ssp. *cuspidata*, Oleaceae, large shrub.

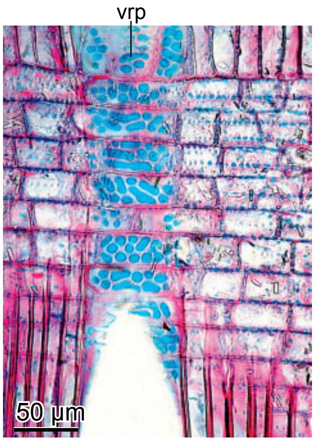


Fig. 62. *Laurus nobilis*, Lauraceae, tree.

32 Vessel-ray pits with large horizontal apertures, Hamamelidaceae type. All forms with one to several pits in one vessel-ray cross-field.

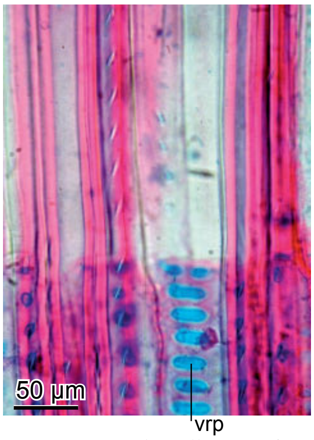


Fig. 63. *Fothergilla gardeni*, Hamamelidaceae, shrub.

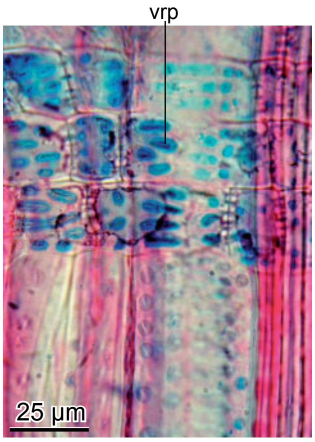


Fig. 64. *Fagus orientalis*, Fagaceae, tree.

36 Helical thickenings present. All types of thickenings e.g. very thin and thick spirals in small and large vessels.

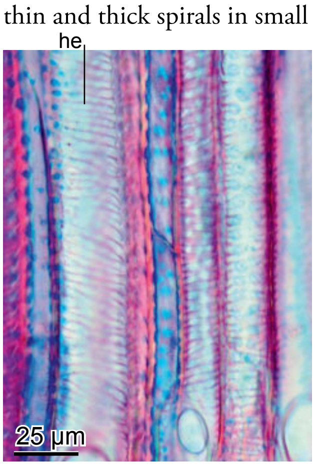


Fig. 65. *Nandina domestica*, Berberidaceae, shrub.

Fig. 66. *Corylus avellana*, Betulaceae, shrub.

39.1 Vessel cell-wall thickness >2 µm. Cell walls are thick in relation to the surrounding tissue. See also **Fig. 113**.

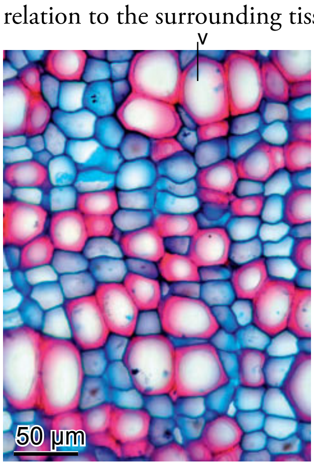


Fig. 67. *Pulsatilla vulgaris*, Ranunculaceae, herb.

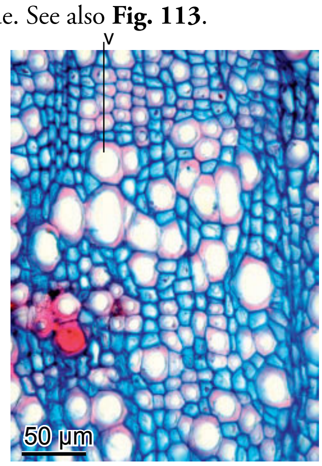


Fig. 68. *Armeria arenaria*, Plumbaginaceae, herb.

40.1 Earlywood vessels: tangential diameter <20 µm. See also **Fig. 30**.

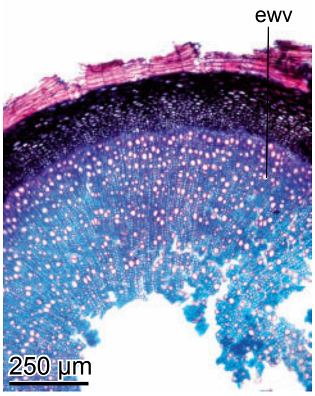


Fig. 69. *Arenaria ciliata*, Caryophyllaceae, herb.

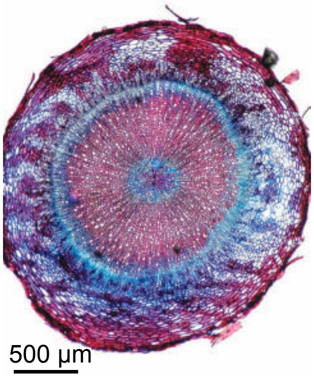


Fig. 70. *Neatostema apulum*, Boraginaceae, annual herb.

40.2 Earlywood vessels: tangential diameter 20-50 µm. See also **Fig. 31**.

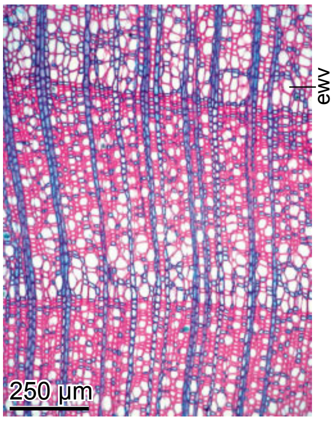


Fig. 71. *Paeonia suffruticosa*, Paeoniaceae, shrub.

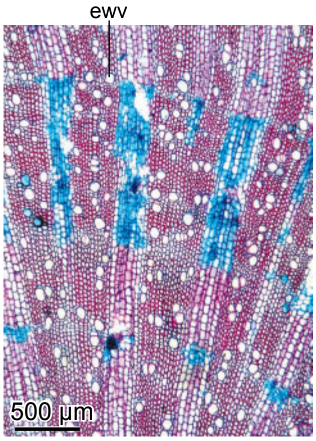


Fig. 72. *Kleinia neriifolia*, Asteraceae, succulent.

41 Earlywood vessels: tangential diameter 50-100 µm. See also **Figs. 47** and **48**.

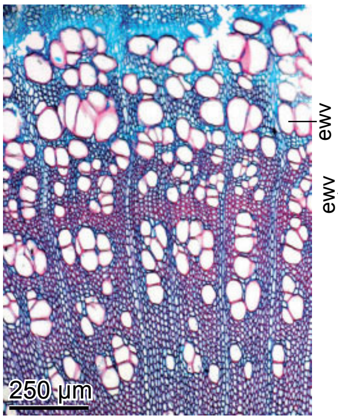


Fig. 73. *Cakile maritima*, Brassicaceae, herb.

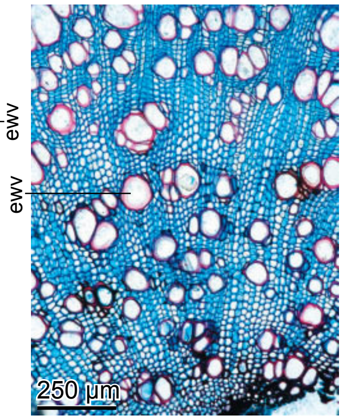


Fig. 74. *Nonea erecta*, Boraginaceae, herb.

42 Earlywood vessels: tangential diameter 100-200 µm.

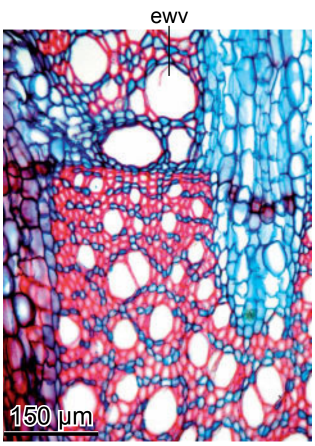


Fig. 75. *Aristolochia macrophylla*, Aristolochiaceae, liana.

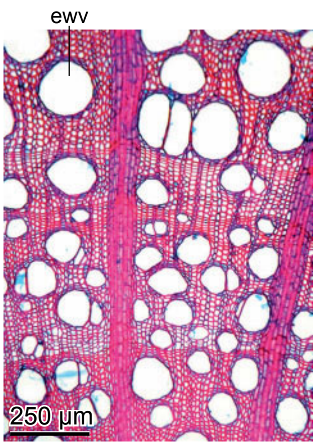


Fig. 76. *Sinofranchetia chinensis*, Lardizabalaceae, liana.

50 <100 vessels per mm^2 in earlywood.
Vessel counting is unambiguous in structures with a more or less regular vessel distribution e.g. **Figs. 71** and 77. Problems arise in types with isolated vascular bundles e.g. **Figs. 23** and **24**. In such cases the vessels within the vascular bundle are counted. Vessel numbers are also difficult to determine in ring porous woods (**Fig. 28**) or types with irregular vessel distribution (**Figs. 40** and **85**).

50.1 100-200 vessels per mm^2 in earlywood.
See **Figs. 95** and **96**.

50.2 200-1000 vessels per mm^2 in earlywood.
See **Figs. 30** and **41**.

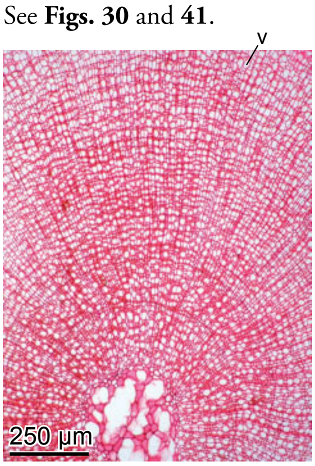


Fig. 77. *Andromeda polifolia*, Ericaceae, dwarf shrub.

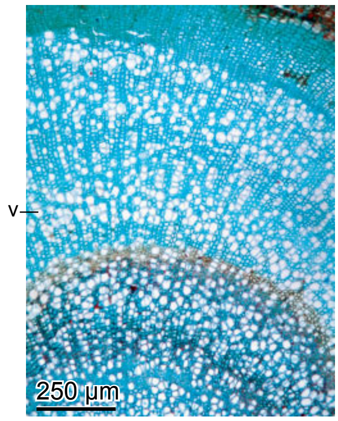


Fig. 78. *Castilleja arctica*, Orobanchaceae, hemicryptophyte.

56 Tylosis with thin walls common.
They are mostly unlignified and blue-stained.

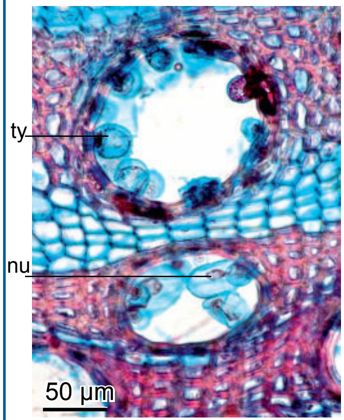


Fig. 79. *Cissus quadrangularis*, Vitaceae, succulent liana.

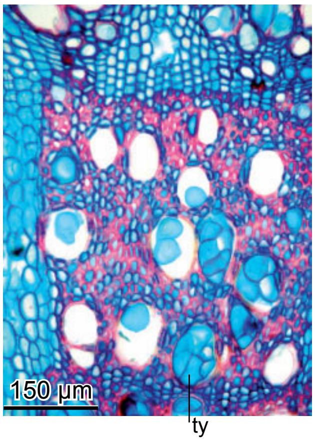


Fig. 80. *Aristolochia clematitis*, Aristolochiaceae, herb.

58 Dark-stained substances in vessels and/or fibers present (gum, tannins).

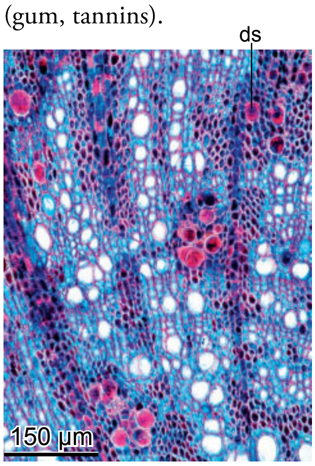


Fig. 81. *Eriogonum ovalifolium*, Polygonaceae, herb.

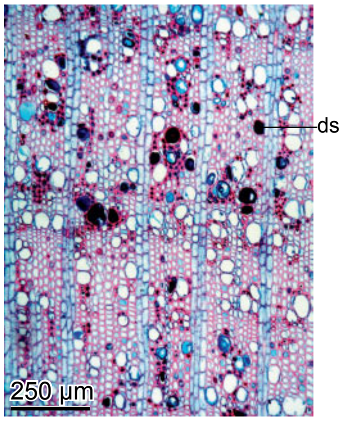


Fig. 82. *Arbutus canariensis*, Ericaceae, tree.

59 Vessels absent or indistinguishable from fibers. Xylem without vessels composed of only imperforate tracheary elements (**Fig. 83**) or vessels absent in the fiber zone of the latewood (**Fig. 84**).

Fig. 83. *Trochodendron aralioides*, Trochodendraceae, tree.

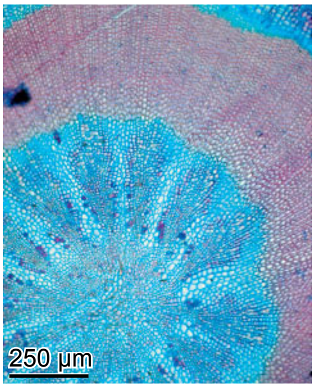


Fig. 84. *Jovibarba hirta*, Crassulaceae, succulent plant.

60 Vascular/vasicentric tracheids, *Daphne* type. Vessels are surrounded by tracheids.

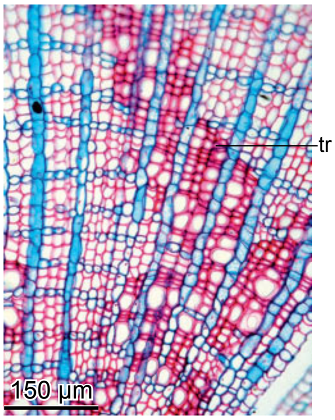


Fig. 85. *Daphne striata*, Thymelaeaceae, dwarf shrub.

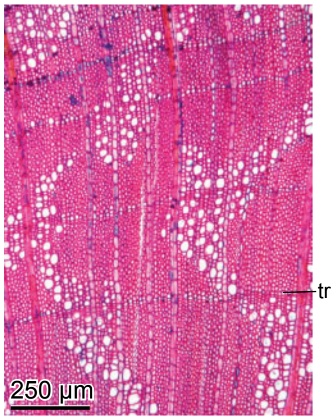


Fig. 86. *Osmanthus decorus*, Oleaceae, shrub.

60.1 Fibers absent. Xylem without fibers; composed of only parenchyma and vessels. See **Figs. 67** and **68**.

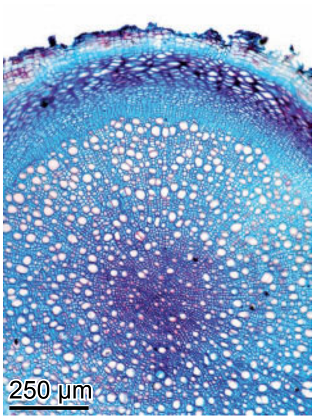


Fig. 87. *Cerastium arvense*, Caryophyllaceae, herb.

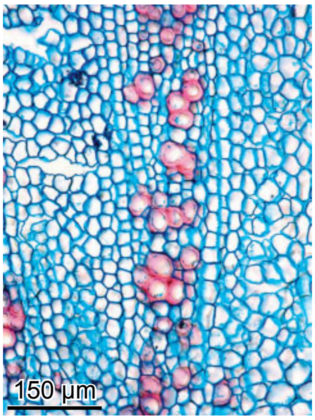


Fig. 88. *Campanula beckiana*, Campanulaceae, herb.

61 Fiber pits small and simple to minutely bordered (<3 µm = libriform fibers).

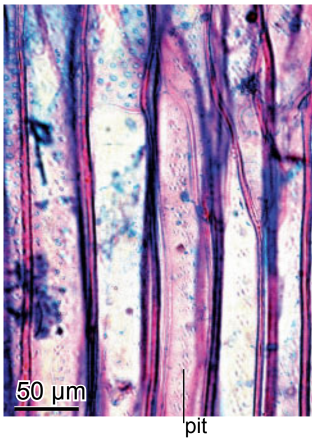


Fig. 89. *Fumaria officinalis*, Papaveraceae, herb.

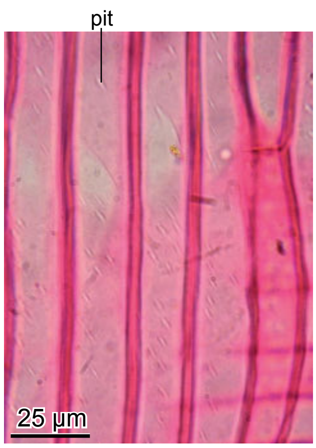


Fig. 90. *Betula glandulosa*, Betulaceae, shrub.

62 Fiber pits large and distinctly bordered (>3 µm = fiber tracheids). See also **Fig. 58**.

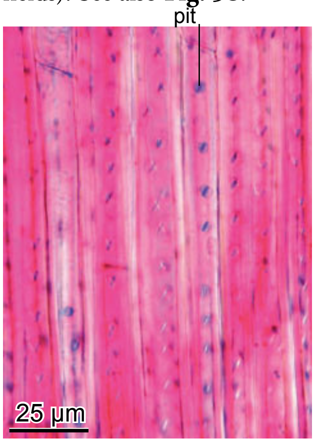


Fig. 91. *Sarcococca hookeriana*, Buxaceae, small shrub.

Fig. 92. *Gaultheria shalon*, Ericaceae, shrub.

65 Septate fibers present. Fibers with thin, mostly unlignified, transverse walls.

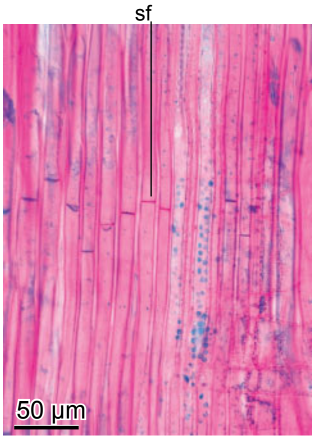


Fig. 93. *Hypericum inodorum*, Clusiaceae, shrub.

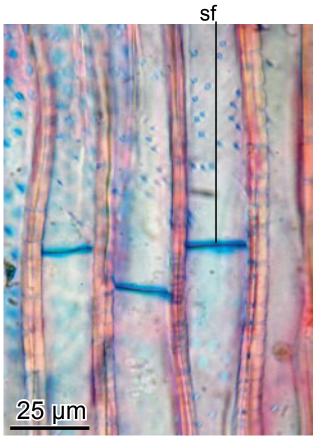


Fig. 94. *Berberis julianae*, Berberidaceae, shrub.

67 Thick- and thin-walled fiber bands, *Acer* type.

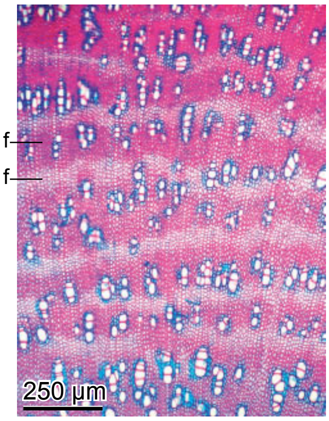


Fig. 95. *Lepidium campestre*, Brassicaceae, herb.

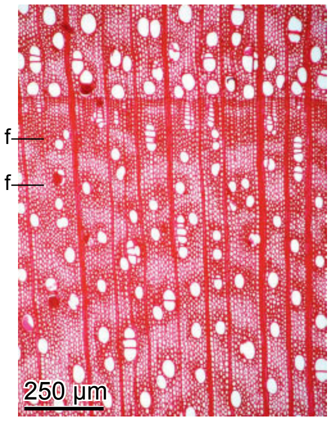


Fig. 96. *Acer tataricum*, Sapindaceae, tree.

68 Fibers thin-walled. Fiber lumina 3 or more times wider than the double wall thickness.

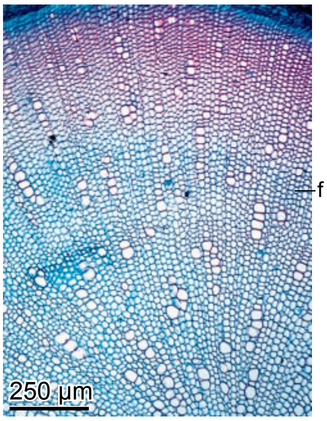


Fig. 97. *Rhinanthus glacialis*, Orobanchaceae, parasite.

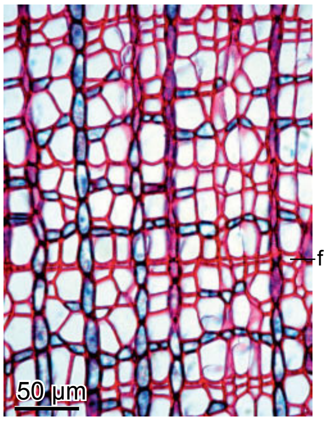


Fig. 98. *Ledum decumbens*, Ericaceae, dwarf shrub.

69 Fibers thick-walled. Fiber lumina almost completely closed. See also **Figs. 4** and **119**.

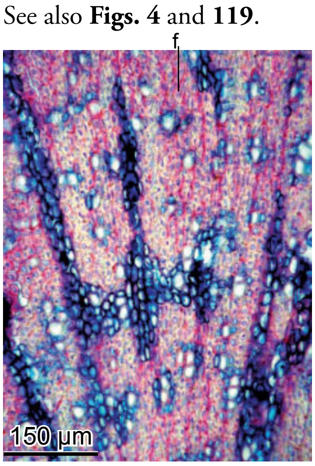


Fig. 99. *Limonium pectinatum*, Plumbaginaceae, herb.

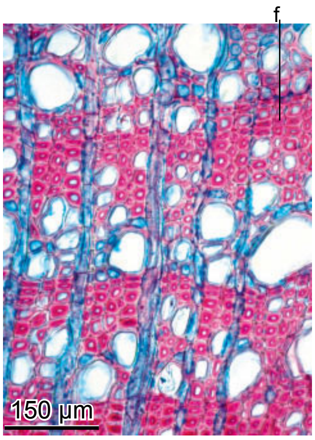


Fig. 100. *Syringa vulgaris*, Oleaceae, shrub.

70 Fibers thin- to thick-walled. Fiber lumina less than 3 times the double wall thickness, distinct lumina. See **Figs. 109** and **115**.

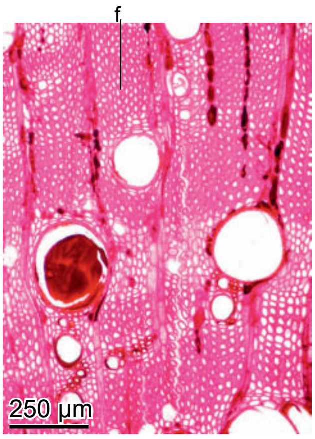


Fig. 101. *Calligonum comosum*, Polygonaceae, shrub.

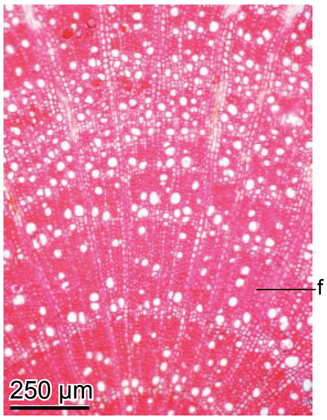


Fig. 102. *Thesium bavarum*, Santalaceae, herb.

70.1 Intra-annual thick-walled tangential fiber bands. Fiber bands (red) are located between fiber-less zones (blue).

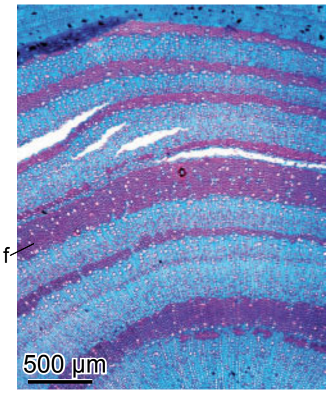


Fig. 103. *Dianthus seguieri*, Caryophyllaceae, herb. With continuous bands.

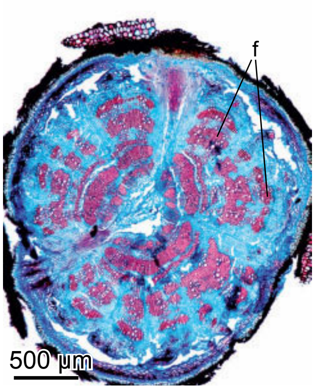


Fig. 104. *Matthiola fruticulosa*, Brassicaceae, herb. With lateral interrupted bands.

70.2 Fibers contain tension wood. Gelatinous, unlignified, blue secondary walls in fibers.

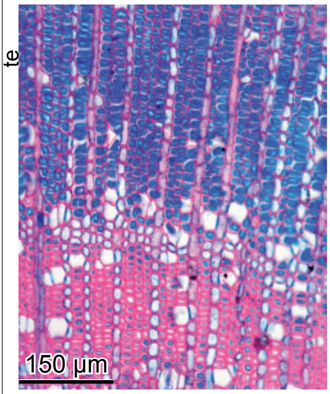


Fig. 105. *Sycopsis sinensis*, Hamamelidaceae, shrub.

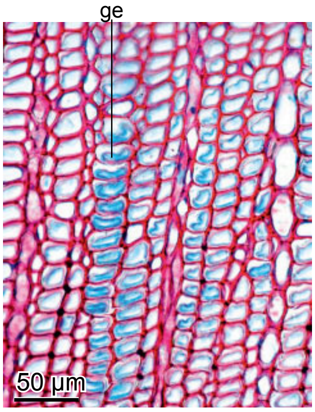


Fig. 106. *Trochodendron aralioides*, Trochodendraceae, small tree.

75 Parenchyma absent or unrecognizable. Parenchyma cells unrecognizable in Safranin/Astrablue stained slides.

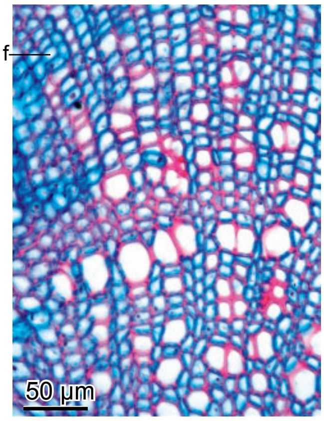


Fig. 107. *Viola elatior*, Violaceae, herb. Unlignified fibers.

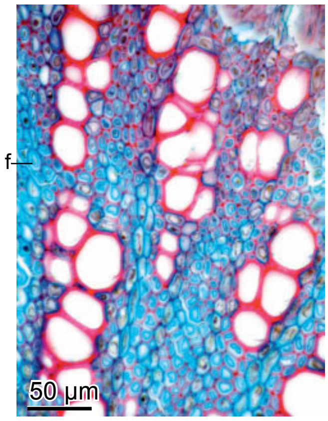


Fig. 108. *Euphorbia maculata*, Euphorbiaceae, herb.

76 Parenchyma apotracheal, diffuse in aggregates. Parenchyma cells single or grouped into short discontinuous tangential or oblique lines. See also **Fig. 75**.

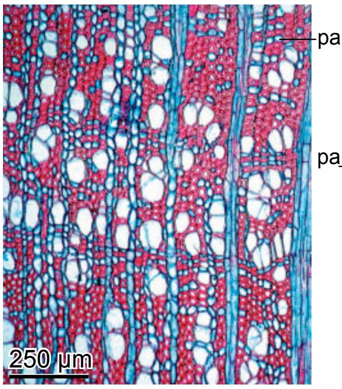


Fig. 109. *Apollonias barbujana*, Lauraceae, tree.

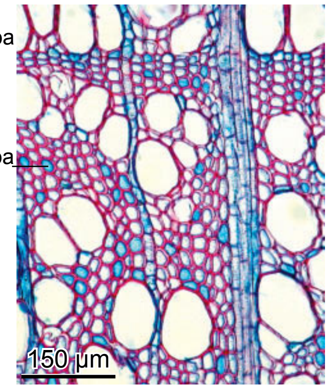


Fig. 110. *Hedera helix*, Araliaceae, climber.

79 Parenchyma paratracheal. Axial parenchyma associated with vessels.

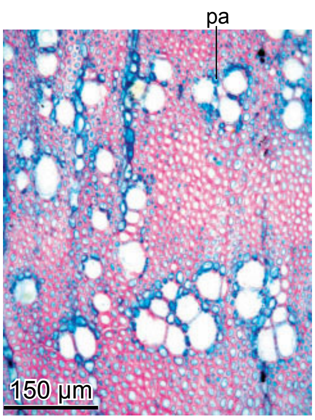


Fig. 111. *Eriogonum trichopes*, Polygonaceae, herb. Parenchyma vasicentric.

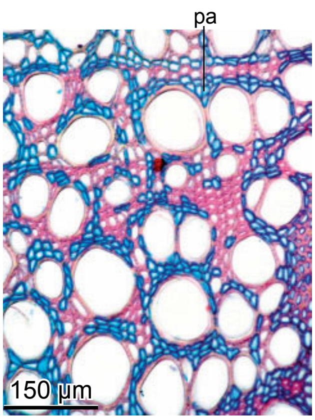


Fig. 112. *Clematis flammula*, Ranunculaceae, herb. Parenchyma vasicentric in groups.

79.1 Parenchyma pervasive. The ground tissue consists exclusively of thin-walled, unlignified parenchyma. See also **Figs. 67** and **68**.

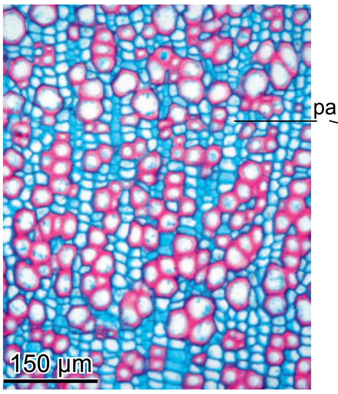


Fig. 113. *Pulsatilla montana*, Ranunculaceae, herb.

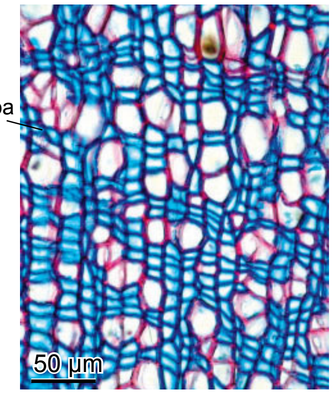


Fig. 114. *Polemonium coerulea*, Polemoniaceae, herb.

79.2 Parenchyma intervascular, Crassulaceae type. Isolated groups of vessels are surrounded by parenchyma and occur in a dense fiber tissue (Carlquist 2001).

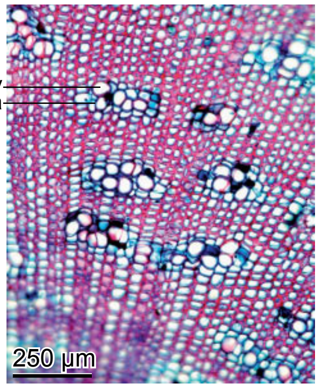


Fig. 115. *Aeonium viscatum*, Crassulaceae, dwarf shrub.

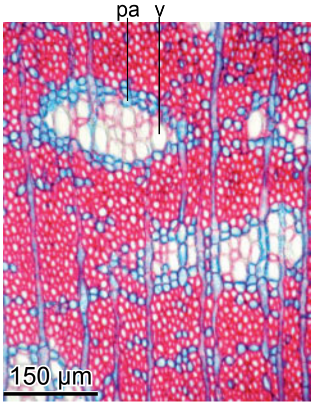


Fig. 116. *Thymelaea hirsuta*, Thymelaeaceae, shrub.

85 Axial parenchyma bands more than three cells wide, *Ficus/Urtica* type.

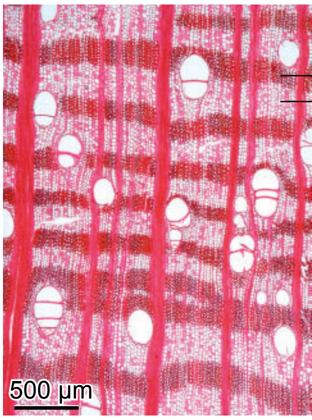


Fig. 117. *Ficus sycomorus*, Moraceae, tree.

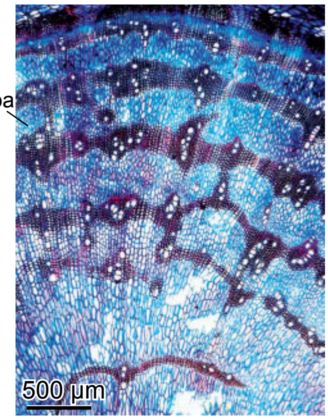


Fig. 118. *Urtica urens*, Urticaceae, herb.

89 Parenchyma marginal. Parenchyma bands form continuous layer in late- or earlywood. Cell walls can be lignified or unlignified.

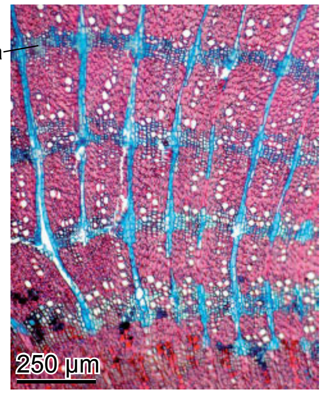


Fig. 119. *Vella spinosa* ssp. *lucentina*, Brassicaceae, dwarf shrub. Marginal terminal.

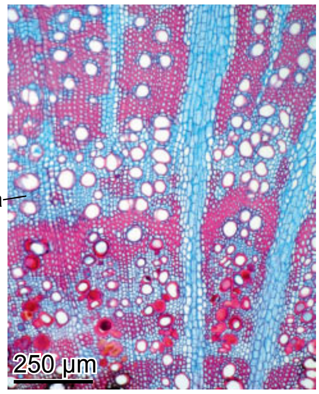


Fig. 120. *Diplotaxis tenuifolia*, Brassicaceae, herb. Marginal initial.

89.1 Parenchyma marginal thin-walled; dark in polarized light. Parenchyma cells without secondary walls do not reflect polarized light and appear as dark zones.

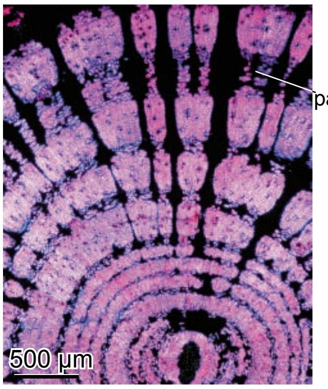


Fig. 121. *Alyssum argenteum*, Brassicaceae, herb.

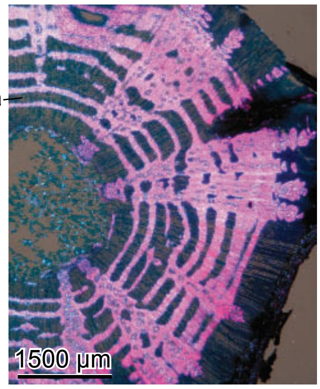


Fig. 122. *Urtica dioica*, Urticaceae, herb.

89.2 Ring shake, *Saxifraga* type. During mechanical stress, drought or preparation procedure rings or compartments of rings fall apart.

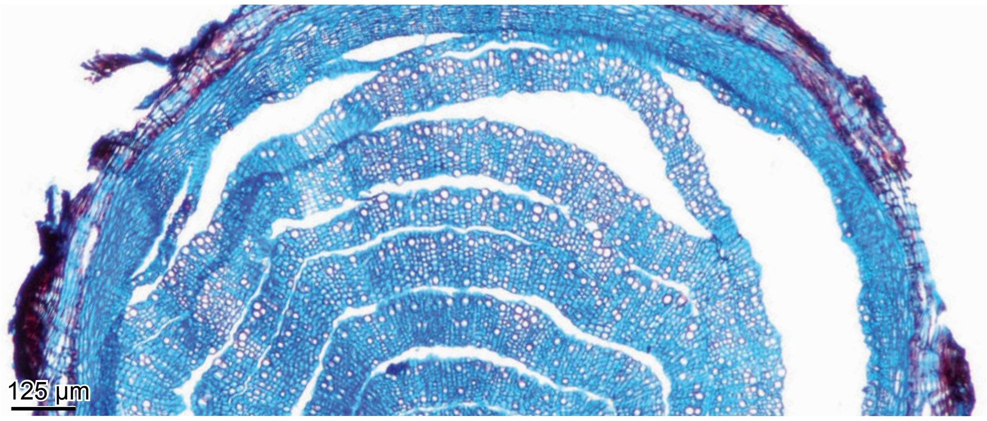


Fig. 123. *Saxifraga moschata*, Saxifragaceae, herb.

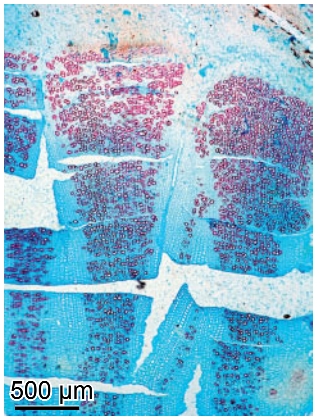


Fig. 124. *Geum glaciale*, Rosaceae, herb.

96 Rays exclusively uniseriate.

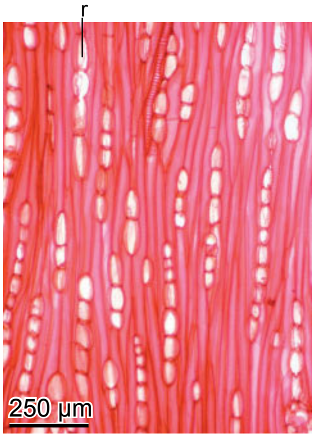


Fig. 125. *Euphorbia echinus*, Euphorbiaceae, shrub.

97 Rays width 1-3 cells.

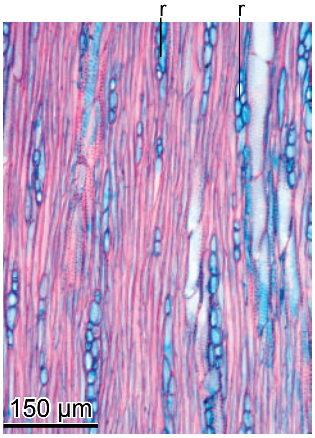


Fig. 126. *Eriogonum inflatum*, Polygonaceae, herb.

98 Rays commonly 4-10-seriate.

Fig. 127. *Parthenocissus inserta*, Vitaceae, liana.

99 Rays commonly >10-seriate.

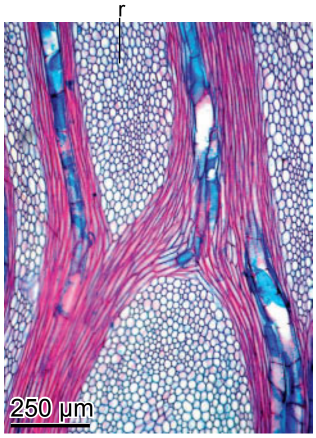


Fig. 128. *Brassica nigra*, Brassicaceae, herb.

99.1 Vascular-bundle form remaining. Vascular bundles are separated by pith-like parenchyma cells. It lacks a continuous fiber/vessel zone. See also **Figs. 8** and **29**.

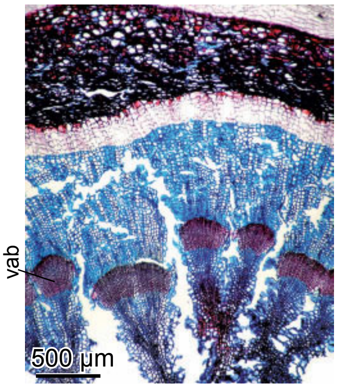


Fig. 129. *Sempervivum tectorum*, Crassulaceae, herb.

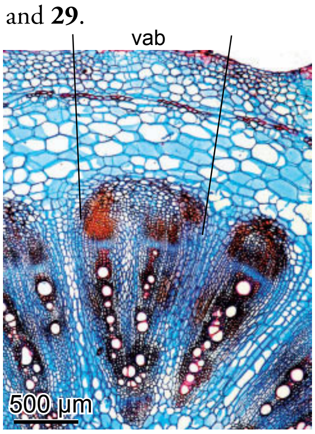


Fig. 130. *Ecballium elaterinum*, Cucurbitaceae, creeping liana.

99.2 Stem fluted.

Fig. 131. *Eriogonum jamesii*, Polygonaceae, chamaephyte.

Fig. 132. *Satureja montana*, Lamiaceae, chamaephyte.

100.1 Rays confluent with ground tissue. Lateral borders of rays merge with axial tissue.

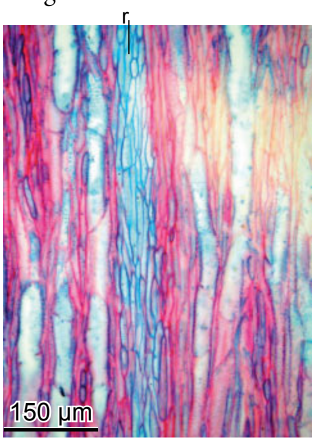


Fig. 133. *Geranium columbinum*, Geraniaceae, herb.

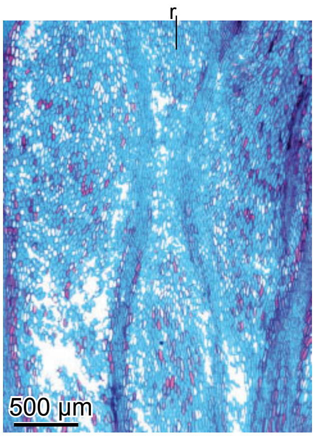


Fig. 134. *Sedum anopetalum*, Crassulaceae, herb.

100.2 Rays not visible in polarized light.

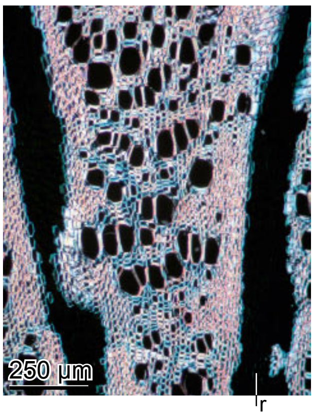


Fig. 135. *Clematis recta*, Ranunculaceae, herb. Dark strips represent thin-walled parenchymatic ray tissue.

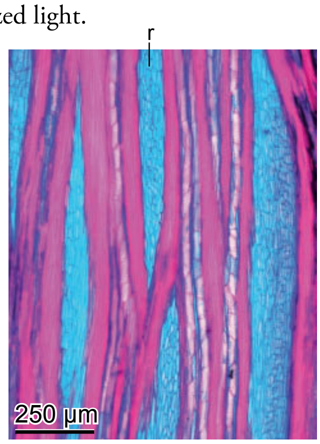


Fig. 136. *Sisymbrium austriacum*, Brassicaceae, herb. Thin-walled, unlignified ray cells do not reflect polarized light.