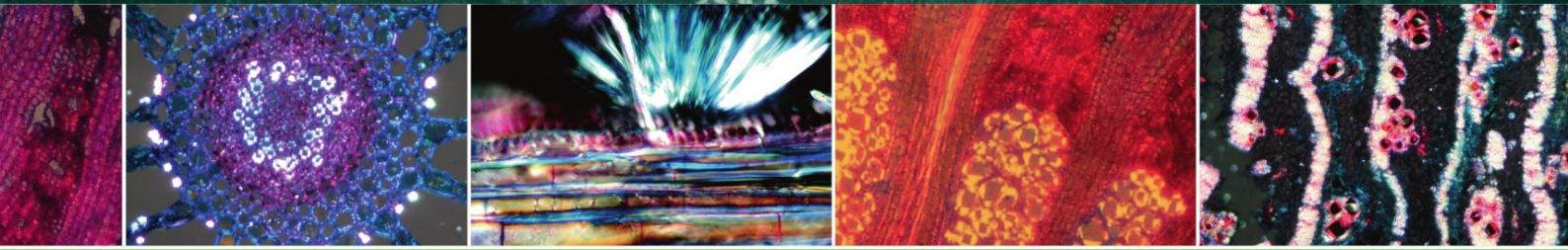


Volume 2



Fritz Hans Schweingruber · Annett Börner
Ernst-Detlef Schulze

2

Atlas of Stem Anatomy in Herbs, Shrubs and Trees

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Atlas of Stem Anatomy in Herbs, Shrubs and Trees

Volume II

F. H. Schweingruber

A. Börner

E.-D. Schulze

Atlas of Stem Anatomy

in Herbs, Shrubs and Trees

Volume II

With contributions by

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With over 1500 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 airconducting 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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Abbreviations

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

I. Introduction to Volume 2

I.1 Phylogeny and Taxonomy

Volume 2, as a continuation of Vol. 1, provides monographic descriptions for an additional 1295 species from 39 families. The major objectives, sampling design, sample preparation, and the anatomical characterizations are identical in both volumes. With the description of 2948 species within 124 families, Volumes 1 and 2 cover all dicotyledonous classes and plant orders, excluding monocotyledons, as indicated in **Fig. 1.1** on the next page.

The scientific limitations of the dataset are described in Vol.1 on p. 2.

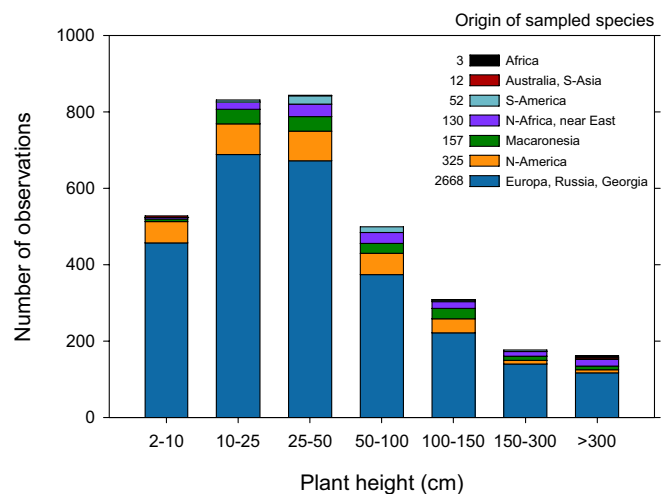
During the process of family characterization for Chapter 2, additional species have been collected, prepared and analyzed. Therefore, the statistical analyses in Chapters 3 and 4 are based on an extended dataset of 3347 species. An up-to-date table of all analyzed species can be found on the internet at <http://www.wsl.ch/dendro/xylemdb/index.php>.

I.2 Geographic and Climatic Origin

The majority of plants had been collected in Western Europe and Russia with fewer species collected in the Canary Islands (Macaronesia), northern Africa, the Americas and Australia (**Fig. 1.2**).

The dataset covers all vegetation zones although the tropics are represented by only a few species. The vegetation/climate zones are defined in Vol. 1 on p. 9.

Right: Fig. 1.2. Number of the analyzed species in relation to the geographic origin and plant height.



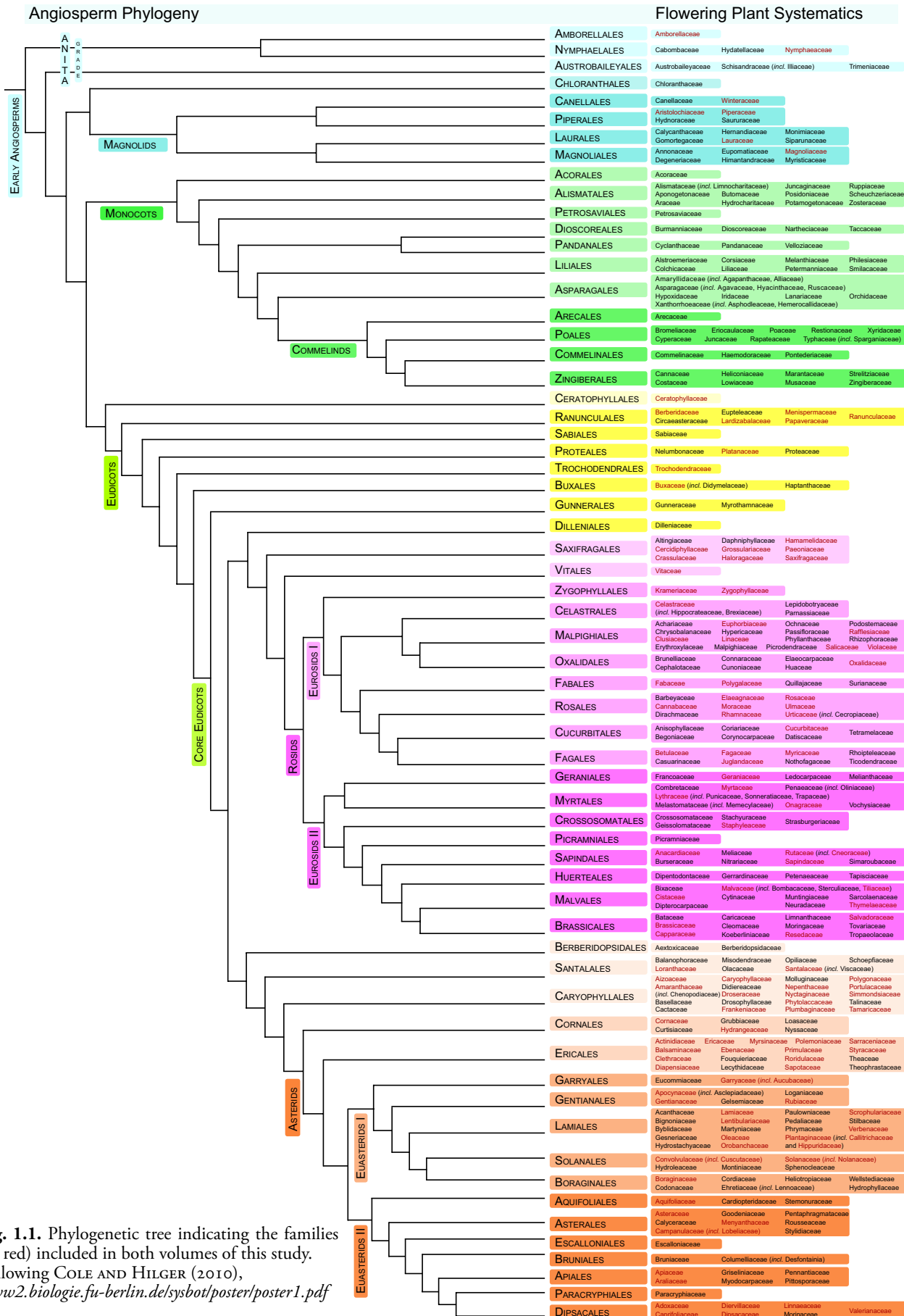


Fig. 1.1. Phylogenetic tree indicating the families (in red) included in both volumes of this study. Following COLE AND HILGER (2010), www2.biologie.fu-berlin.de/sysbot/poster/poster1.pdf

1.3 Life Forms

The dataset includes eleven life forms as described by Raunkiaer (Ellenberg et al. 1992).

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

Climbers: Plants climbing with adhesive roots growing over other plants or objects.

Hydrophyte: Water plants where most parts live and root below the water table.

Helophyte: Terrestrial plant rooting in wet ground.

Succulent: Plant with water-storing tissues.

1.4 Anatomical Features

All features as described in Vol. 1, pp. 13- 32 have been used for the characterization of the species described in Vol. 2. Two additional features (Features 60.1 and 70.3) are used for the characterization of species in Vol. 2 (**Figs. 1.3-1.6**).

60.1 Fibers absent.

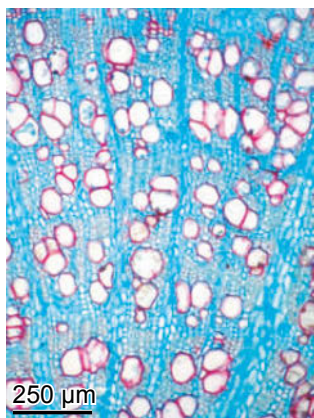


Fig. 1.3. *Euphorbia nicaensis*, Euphorbiaceae, herb.

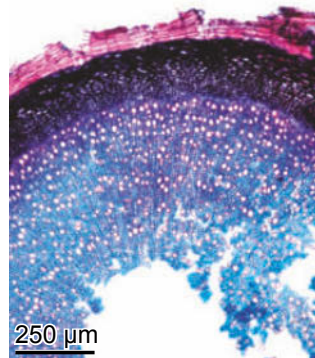


Fig. 1.4. *Arenaria ciliata*, Caryophyllaceae, herb.

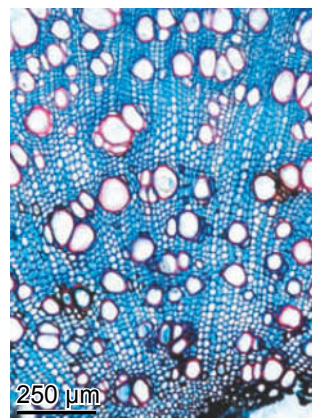


Fig. 1.5. *Nonea erecta*, Boraginaceae, herb.

70.3 Fibers absent in the stem center.

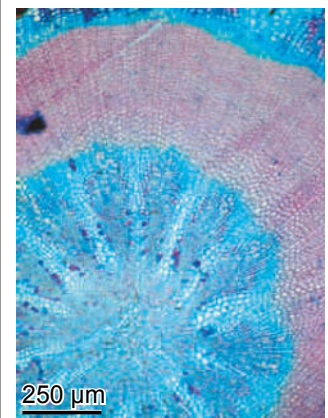


Fig. 1.6. *Jovibarba hirta*, Crassulaceae, succulent plant.

1.5 Morphological and Ecological Interpretation of Features

In Chapters 3 and 4 of the present volume we relate the stem anatomical features of the whole dataset to plant height, as it appears that static and hydraulic functions have been optimized in evolutionary processes, mainly in response to plant height. The actual APG III DNA-based taxonomic classification generally does not coincide with specific morphological or anatomical characteristics. The description of plant diversity in view of the differentiation in xylem structures remains a major problem. The “life-form” classification of RAUNKIAER (1904), which is still commonly used in vegetation science, does not treat stem features adequately. The Raunkiaer classification is based on the position of the regenerating bud in relation to the soil surface as a survival strategy in seasonal climates - an interpretation which has been questioned in the past (see SCHULZE 1982). Also, bud height may be quite different from plant height considering the flower stalks of herbaceous species. Lignification does not correspond with the Raunkiaer types of life forms (therophytes, hemicryptophyte, chamaephytes and phanerophytes). The xylem of small and large annual plants (e.g. *Arabidopsis thaliana* and *Helianthus annuus*) can be fully lignified, as in trees. In contrast, some small plants, such as *Silene acaulis* and water plants, consist primarily of un-lignified cells.

In contrast to Raunkiaer’s “life forms”, MONSI (1960) based a structural description on the economy of resource use during growth. He followed CLEMENTS (1920), who coined the words “herbaceous” and “woody” as descriptors for plant structures. MONSI (1960) distinguished evergreen and deciduous species within both herbaceous and woody plants. However, the classification of MONSI (1960) is questionable in an anatomical sense. LENS ET AL. (2011) describe all kinds of transitions between more and less lignified plant stems.

In all monographic descriptions (Vol. 1 Chapter 5 and Vol. 2 Chapter 2) we have used Raunkiaer’s life form classification because we were not aware that plant height correlates better with anatomical features than life forms (see Chapter 3 in this volume). Obviously, a more functional classification needs to include xylem anatomy.

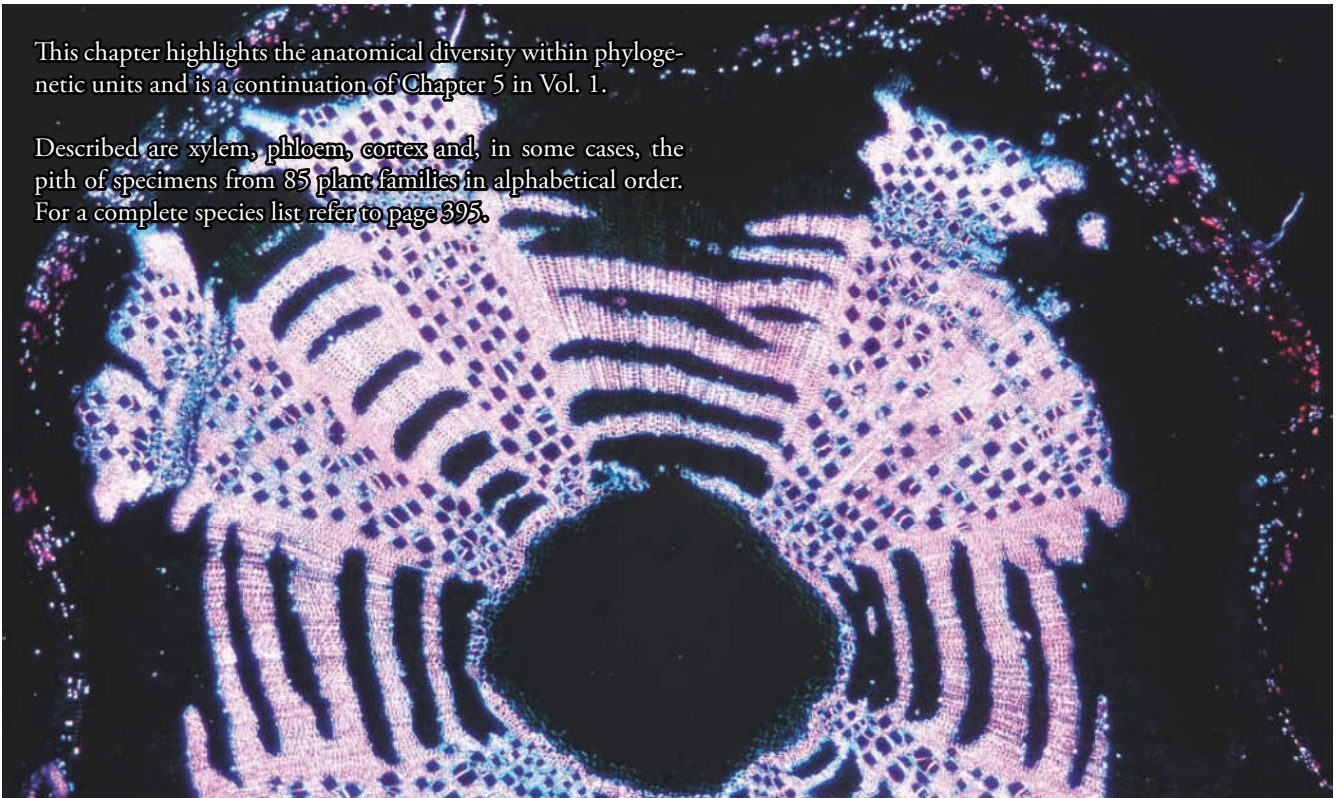
Lignification appears to be related to water, nutrient and phytohormone transport (NARDINI ET AL. 2011), which in turn is related to plant size and leaf area. The wood anatomy would also be affected by climate seasonality (drought or frost), which results in tree rings with early- and latewood. A seasonality of water demand with bud break and flushing leaves will cause a differentiation in the dimensions of vessels even during a single growing season. In seasonal climates, plants may avoid climatic stress by the shedding of leaves, short shoots (cladaptois), branches, or the whole above-ground canopy (hemicryptophytes), or they may endure the climatic stress and have evergreen foliage and perennial stems. This has major implications for the storage of reserves in seasonal climates, and on stem anatomy. Reserves could be stored in the leaves, stems, hypocotyl (including the root collar) or in the phloem and bark, and this will affect the presence of parenchyma. Large vessels, which are essential in deciduous species, would not be functional in evergreen trees occurring in seasonal climates (SCHULZE ET AL. 2005). Thus, all kinds of transitions will exist between these two adaptive techniques.

Following these considerations, the degree of “woodiness” or “herbaceousness” would be related to (1) plant size and height, (2) the seasonality of climate, and (3) the persistence of foliage. In the following we will maintain the terms “woody” and “herbaceous” because they are commonly used and easy to understand, but in our definition we imply a dynamic range of lignification, which could be species- or site-related. The degree of woodiness would be explained by the parameters of plant size/height, habitat seasonality, and the way reserves are stored in seasonal climates. Obviously, a more functional classification is needed to incorporate xylem anatomy.

2. Monographic Descriptions

This chapter highlights the anatomical diversity within phylogenetic units and is a continuation of Chapter 5 in Vol. 1.

Described are xylem, phloem, cortex and, in some cases, the pith of specimens from 85 plant families in alphabetical order. For a complete species list refer to page 395.



Actinidiaceae

Number of species, worldwide and in Europe

The north temperate Actinidiaceae family includes 3 genera with 355 species. Endemic species are absent in Europe. *Actinidia deliciosa* is frequently cultivated in Europe.

Analyzed material

The xylem and phloem of 1 genus with 2 species are analyzed here.

Life forms analyzed:	Studies from other authors:	
Lianas	2	3 genera
Plants analyzed from different vegetation zones:	Studies from other authors:	
Hill and mountain	2	

Analyzed species:

Actinidia deliciosa (A.Chev.) C.F.Liang & A.R.Ferguson

Actinidia kolomikta (Rupr. & Maxim.) Maxim.



Actinidia kolomikta (photo: Enking)



Actinidia deliciosa



Actinidia kolomikta (photo: Nicolas)

Characteristics of the xylem

Annual rings occur in both species (Figs. 1 and 2). Ring boundaries of the diffuse-porous species are represented by a zone of thicker-walled, flat latewood fibers. (Figs. 1 and 2). Vessel diameter varies from 150-300 μm (Figs. 1 and 2). Vessel walls are perforated by very distinct scalariform pits but no perforations were found (Fig. 3). Perforations of *Actinidia kolomikta* are scalariform with >15 bars and vessel walls have round pits. Vessel density varies from 50-80/mm² (Figs. 1 and 2). Intervessel pits are bordered, large and round. Vessel-ray pits are small, round

and arranged in horizontal lines (Fig. 4). Fibers are thin- to thick- or thick-walled (Figs. 1 and 2). Fibers are characterized by bordered pits with a diameter of 3-6 μm . Axial parenchyma is apotracheal in aggregates (Fig. 5).

Rays occur in two forms (ray-dimorphism): uniseriate and 3-5-seriate (Fig. 6). Rays are heterogeneous with 2 to >4 square or upright cells (Fig. 7).

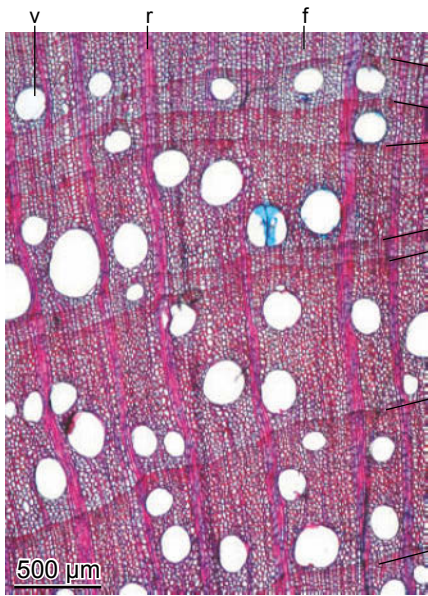


Fig. 1. Diffuse-porous wood with distinct rings. Ring boundaries are characterized by slightly flattened fibers. Stem of a 4 m-long liana, hill zone, temperate climate, Botanical Garden Zurich, Switzerland. *Actinidia deliciosa*, transverse section.

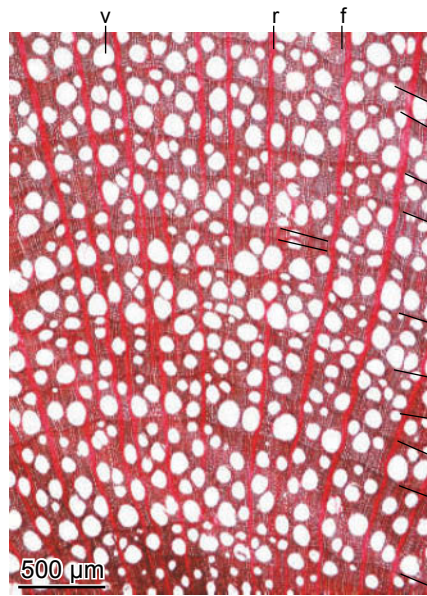
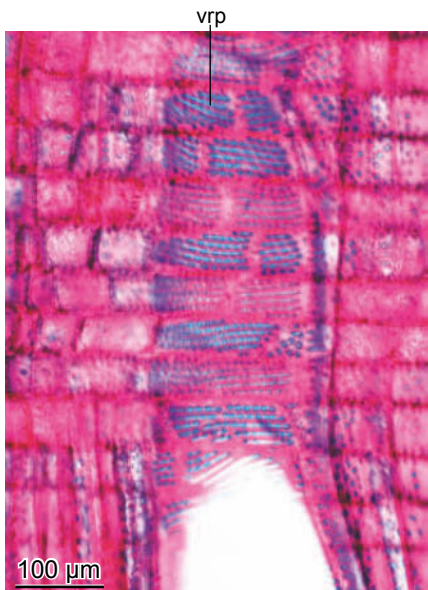


Fig. 2. Diffuse-porous wood with distinct rings. The ring-boundaries are characterized by a band of flattened fibers. Stem of a 4 m-long liana, boreal zone, temperate climate, Botanical Garden Chabarovsk, Russia. *Actinidia kolomikta*, transverse section.



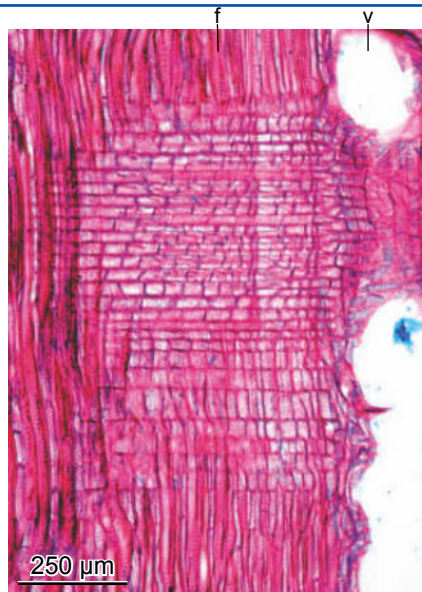
Fig. 3. Scalariform perforations all along the vessel. Perforations are absent. Origin as in Fig. 1. *Actinidia deliciosa*, radial section.



Left Fig. 4. Small ray-vessel pits arranged in horizontal lines. Origin as in Fig. 1. *Actinidia deliciosa*, radial section.



Right Fig. 5. Apotracheal parenchyma in aggregates. Origin as in Fig. 1. *Actinidia deliciosa*, transverse section.



Left Fig. 6. Rays of different sizes: uniseriate and 3-5-seriate. Origin as in **Fig. 1**. *Actinidia deliciosa*, tangential section.

Right Fig. 7. Heterogeneous ray with >4 rows of square and upright marginal cells. Origin as in **Fig. 1**. *Actinidia deliciosa*, radial section.

Characteristics of the phloem and the cortex

The phloem is fairly homogeneous in most cases. Parenchyma cells and sieve tubes are often/typically difficult to distinguish in cross-section. Irregularly distributed groups of sclereids, mucilage canals and very long, raphid-like prismatic crystals exist in the phloem of *Actinidia deliciosa* (**Figs. 8 and 9**).

Ecological trends and relations to life forms

Vessels with large diameters are characteristic of the liana life form.

Discussion in relation to previous studies

The genera *Actinidia* has been described in several previous studies (GREGORY 1994). The present observations of *Actinidia* correspond closely/for the most part with those from METCALFE AND CHALK (1957).

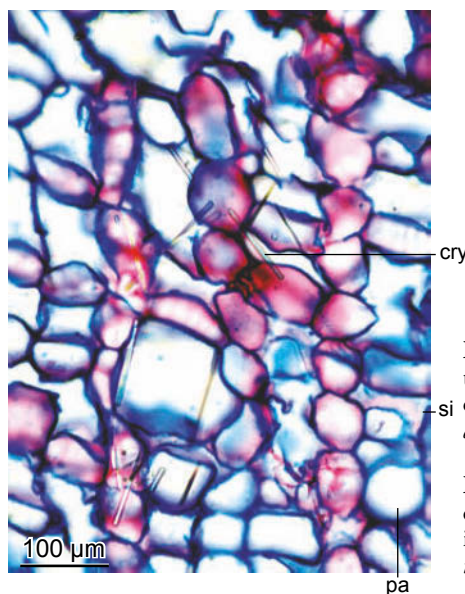
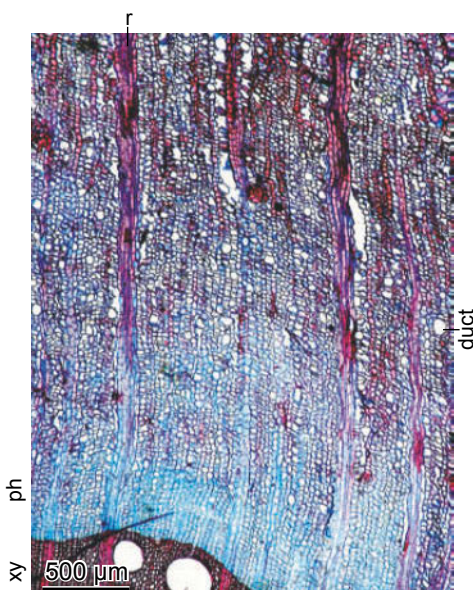


Fig. 8. Phloem with mucilage canals. Sieve tubes and parenchyma cells are difficult to differentiate. Origin as in **Fig. 1**. *Actinidia deliciosa*, transverse section.

Fig. 9. Phloem with roundish parenchyma cells and square sieve tubes. Crystals occur in raphid-like form. Origin as in **Fig. 1**. *Actinidia deliciosa*, transverse section.

Present features in relation to the number of analyzed species

IAWA code		frequency
	Total number of species	2
1	growth rings distinct and recognizable	2
5	diffuse-porous	2
9	vessels predominantly solitary	2
14	vessels with scalariform perforation plates	2
20	intervessel pits scalariform	1
22	intervessel pits alternate	2
42	earlywood vessels: tangential diameter 100-200 μm	2
50	<100 vessels per mm^2 in earlywood	2
56	tylosis with thin walls	2
62	fiber pits large and distinctly bordered ($>3 \mu\text{m}$ = fiber tracheids)	2
70	fibers thin- to thick-walled	2
76	parenchyma apotracheal, diffuse in aggregates	2
98	rays commonly 4-10-seriate	2
103	rays of two distinct sizes (tangential section)	2
107	ray: heterocellular with 2-4 upright cell rows (radial section)	2
108	ray: heterocellular with >4 upright cell rows (radial section)	2
R4	sclereids in phloem and cortex	1
R10	phloem not well structured	1
R11	with raphides	1
R12	with laticifers, oil ducts or mucilage ducts	1
R16	phellem consists of regularly arranged rectangular cells, Rosaceae type	1

Adoxaceae

Number of species, worldwide and in Europe

The cosmopolitan Adoxaceae family includes 5 genera with 200 species. Three *Sambucus* species, 3 *Viburnum* species and *Adoxa moschatellina* are endemic to Europe.

Analyzed material

The xylem and phloem of 3 genera with 14 species are analyzed here.

Life forms analyzed:		Studies from other authors:
Nanophanerophytes 0.5-4 m	2 genera with 12 species	11 genera
Hemicryptophytes	2	1
Plants analyzed from different vegetation zones:		Studies from other authors:
Boreal	2	
Hill and mountain	9	
Mediterranean	1	
Subtropical	2	



Adoxa moschatellina



Sambucus ebulus

Analyzed species:

Adoxa moschatellina L.
Sambucus callicarpa L.
Sambucus ebulus L.
Sambucus maderensis Lowe
Sambucus nigra L.
Sambucus racemosa L.
Sambucus sibirica Nakai
Viburnum edule Raf.
Viburnum lantana L.
Viburnum opulus L.
Viburnum orientale Pall.
Viburnum rigidum Vent.
Viburnum rhytidophyllum Grabner
Viburnum tinus L.



Viburnum rigidum



Viburnum opulus

Characteristics of the xylem and phloem

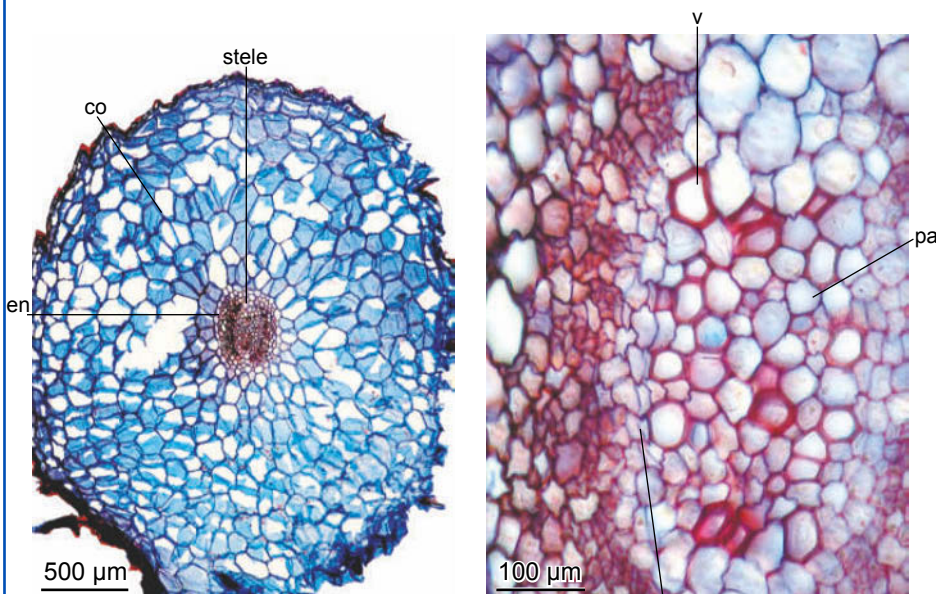
The anatomical structure of the hemicryptophyte *Adoxa moschatellina* is very different from all shrubs. Therefore, we characterize each type separately.

Adoxa moschatellina

Secondary and tertiary growth is absent (Fig. 1). A large cortex surrounds a central cylinder, which consists of a fiber- and rayless xylem, a phloem with groups of small sieve tubes, and large parenchyma cells (Fig. 2). The cylinder is surrounded by an endodermis (Fig. 1). Vessel diameter varies between 15-25 μm . Perforations are simple and intervessel pits are scalariform and reticulate (Fig. 3).

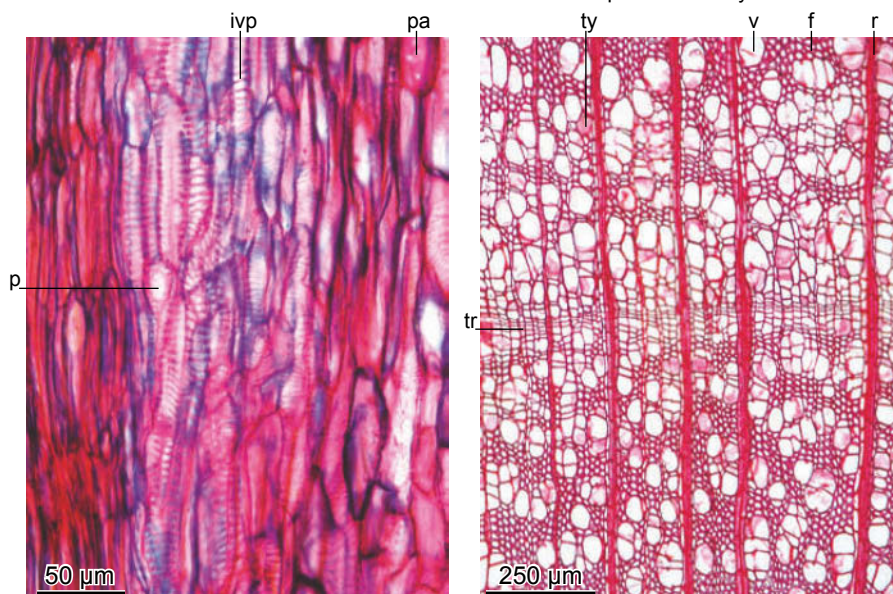
Sambucus and *Viburnum*; shrubs and trees

Annual rings occur in all species and are defined by radial, flat latewood fiber cells (Figs. 4-6). Thin-walled marginal fiber tracheids are typical for *Sambucus nigra* and *S. racemosa* (Fig. 4). All species are diffuse-porous (Figs. 4-6). Vessel diameter varies from 40-100 μm (Fig. 4) and vessel density varies from 200-250/mm². Perforations are simple in *Sambucus* (Fig. 7) and scalariform with >20 bars in *Viburnum* (Fig. 8). The occurrence of helical thickenings is typical for *Viburnum tinus*. Intervessel bordered pits are round. Vessel-ray pits are large and round in *Sambucus* (Fig. 7) but small and arranged in opposite positions in *Viburnum* (Fig. 9). Fibers are thin- to thick-walled (Figs. 4 and 6) and the radial walls are perforated by bordered pits 2-4 μm in diameter (Fig. 8). The axial parenchyma is usually absent (*Sambucus*, Fig. 9) but is apotracheal in aggregates in some cases, e.g. *Viburnum lantana* and *V. opulus* (Fig. 11).



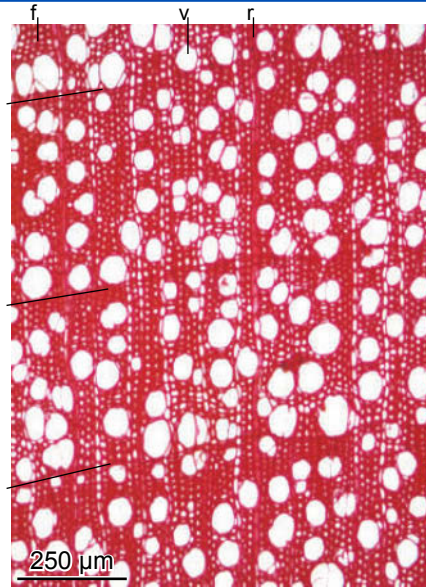
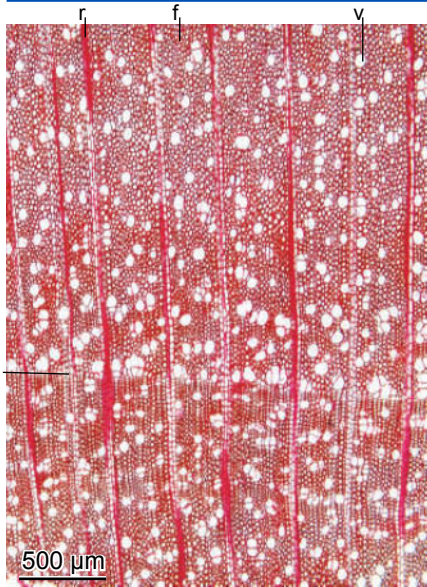
Left Fig. 1. A large cortex surrounds a small central cylinder. These two parts are separated by an endodermis. Root collar of a 5 cm-high hemicryptophyte, riparian, hill zone, temperate climate, Eglisau, Zurich, Switzerland. *Adoxa moschatellina*, transverse section.

Right Fig. 2. Fiber- and rayless xylem with a few vessels within a parenchymatic tissue. Phloem with groups of sieve tubes and parenchyma cells. Origin as in Fig. 1. *Adoxa moschatellina*, transverse section.



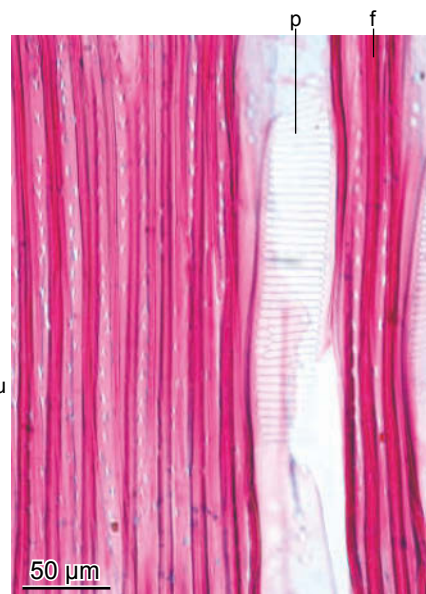
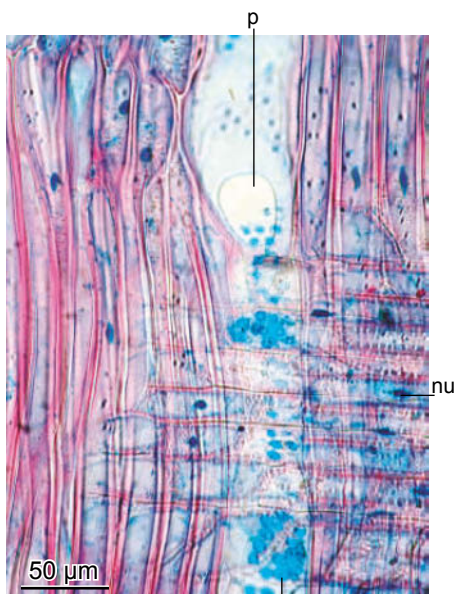
Left Fig. 3. Vessels with simple perforations and scalariform ray-vessel pits. Origin as in Fig. 1. *Adoxa moschatellina*, radial section.

Right Fig. 4. Distinct rings of a diffuse-porous wood with irregularly-formed vessel groups. Thin-walled fiber tracheids form the most recently produced latewood cells. Vessels contain tylosis. Stem of a 3 m-tall shrub, beech forest, hill zone, Birmensdorf, Zurich, Switzerland. *Sambucus nigra*, transverse section.



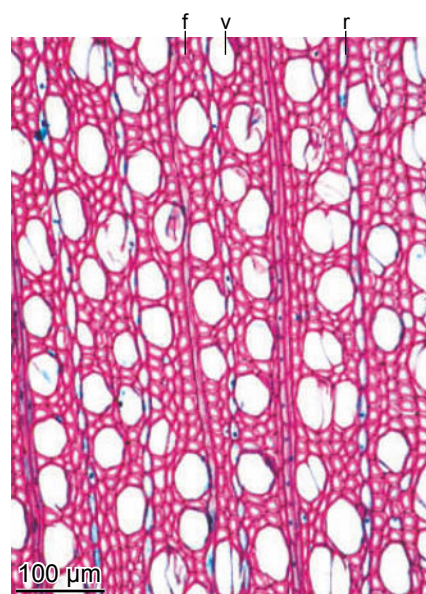
Left Fig. 5. Distinct rings of a diffuse-porous wood with solitary vessels. Stem of a 3 m-tall shrub, laurel forest, subtropical climate, Madeira, Macaronesia, Portugal. *Sambucus maderensis*, transverse section.

Right Fig. 6. Distinct rings of a diffuse-porous wood with solitary vessels. Stem of a 3 m-tall shrub, hedge, mountain zone, Zorten, Grisons, Switzerland. *Viburnum lantana*, transverse section.



Left Fig. 7. Vessel with a simple perforation, round intervessel pits and large, round vessel-ray pits. Rhizome of 3 m-tall shrub, hill zone, temperate climate, Coastal Range, Astoria, WA, USA. *Sambucus calli-carpa*, radial section.

Right Fig. 8. Vessel with a scalariform perforation with >40 bars. Fibers contain large bordered pits with slit-like apertures. Stem of a 3 m-tall shrub, cultivated, hill zone, temperate climate, Tbilisi, Georgia. *Viburnum orientale*, radial section.



Left Fig. 9. Small vessel-ray pits arranged in opposite positions. Stem of a 2 m-tall shrub, deciduous forest, southern boreal zone, Québec, Canada. *Viburnum edule*, radial section.

Right Fig. 10. Solitary vessels in a dense fiber tissue without parenchyma cells. Stem of a 3 m-tall shrub, cultivated, hill zone, temperate climate, Tbilisi, Georgia. *Viburnum orientale*, transverse section.

Ray width varies from 2-5-seriate in *Sambucus* (Fig. 12) and from 1-2-(3) in *Viburnum* (Fig. 13). All species have heterogeneous rays with 3-6 square and upright marginal cells (Fig. 14). The phloem of *Sambucus nigra* consists of tangential layers of small sieve tubes and larger parenchyma cells and sclerenchyma cells (Fig. 15).

Round groups of tangentially arranged sclerenchyma cells are characteristic of *Viburnum lantana* and *V. opulus* (Fig. 16), whereas sclerenchyma bands are typical of *V. tinus*. (Fig. 17). All *Viburnum* species contain crystal druses (Fig. 21).

Sambucus ebulus: hemicryptophyte

The anatomical structure of the rhizome of this species differs from that of *Sambucus* shrubs in that rings are indistinct (Fig. 18) and the parenchyma is paratracheal (Fig. 19). Rays are 1-5-seriate and homogeneous, consisting of upright cells and sheath cells (Fig. 20). Laticifers are located in the inner part of the cortex (Fig. 21).

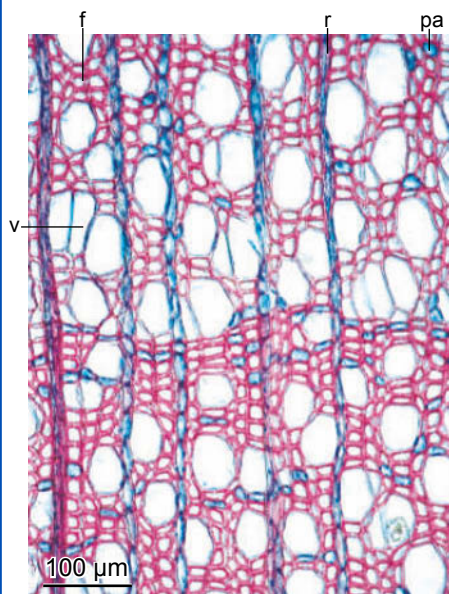


Fig. 11. Solitary and grouped vessels in a thin- to thick-walled tissue with parenchyma cells arranged in aggregates. Stem of a 3 m-tall shrub, hedge, hill zone, Birmensdorf, Zurich, Switzerland. *Viburnum opulus*, transverse section.

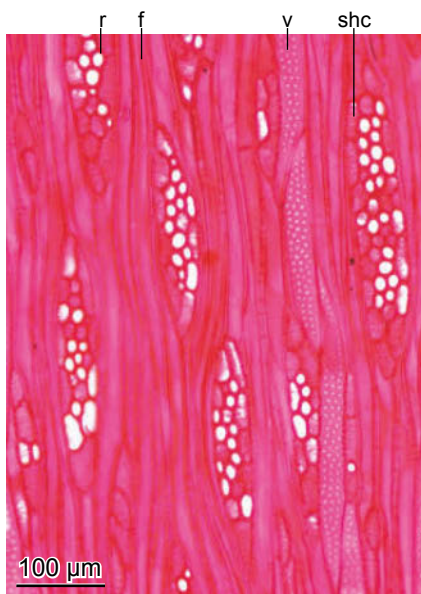


Fig. 12. 3-5-seriate rays containing sheath cells. Stem of a 3 m-tall shrub, beech forest, hill zone, Birmensdorf, Zurich, Switzerland. *Sambucus nigra*, tangential section.

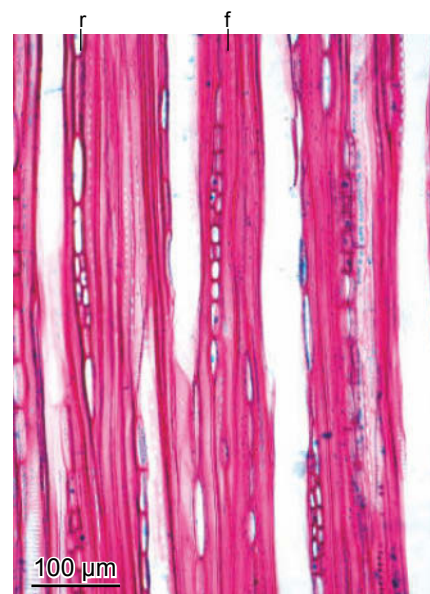
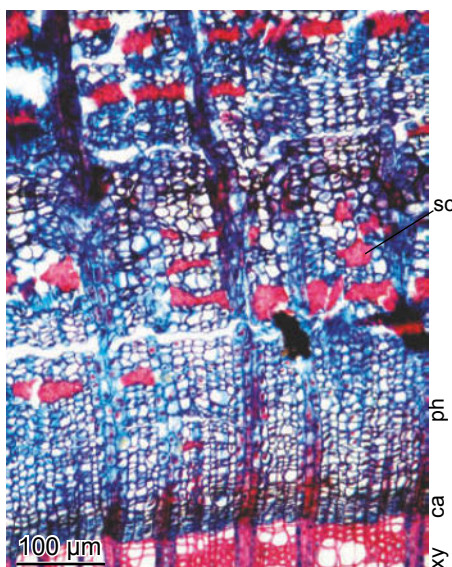
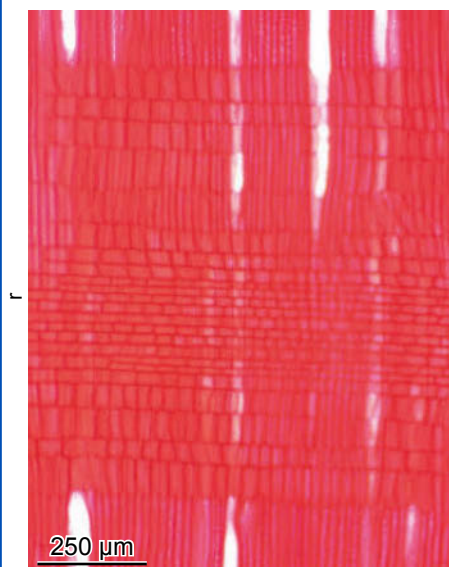
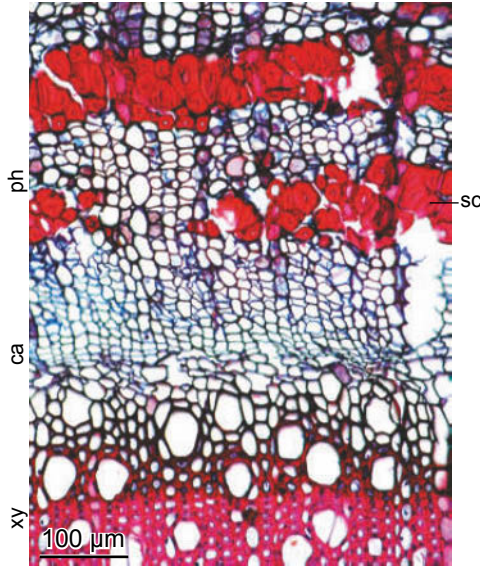
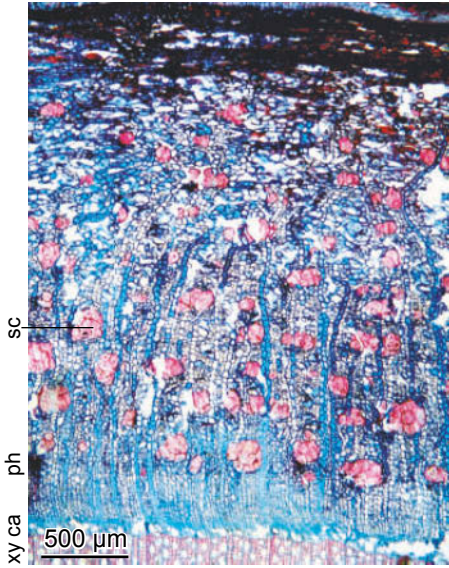


Fig. 13. Uni- and biseriate heterogeneous rays. Stem of a 3 m-tall shrub, cultivated, hill zone, temperate climate, Tbilisi, Georgia. *Viburnum orientale*, tangential section.



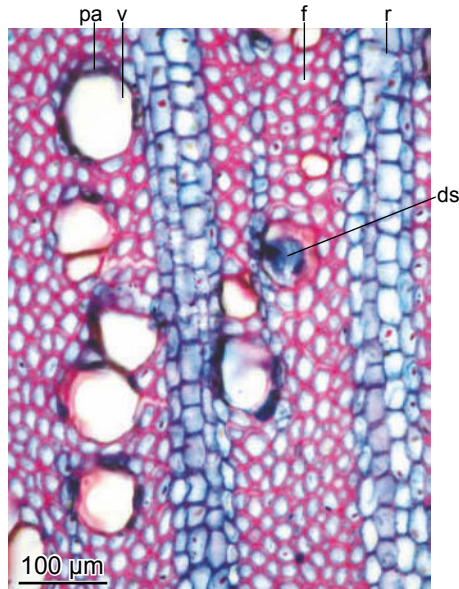
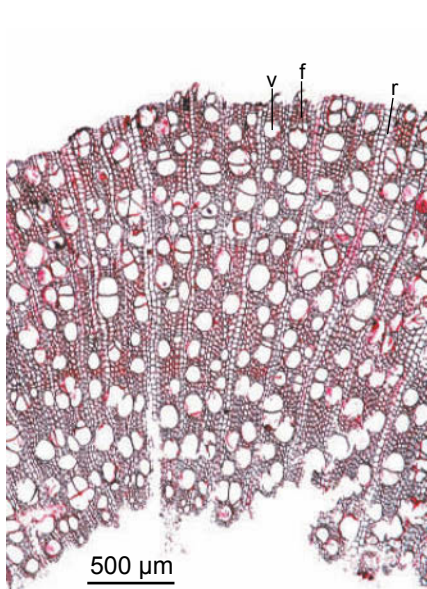
Left Fig. 14. Heterogeneous ray with 4-6 marginal cells (square and upright). Stem of a 3 m-tall shrub, hedge, hill zone, Birmensdorf, Zurich, Switzerland. *Viburnum opulus*, tangential section.

Right Fig. 15. Phloem with horizontal layers of small sieve tubes and large parenchyma cells. Groups of sclerenchyma cells are oriented in tangential lines. Stem of a 3 m-tall shrub, beech forest, hill zone, Birmensdorf, Zurich, Switzerland. *Sambucus nigra*, transverse section.



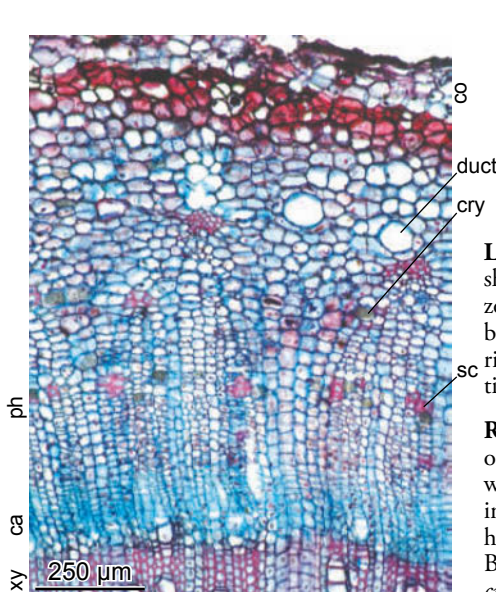
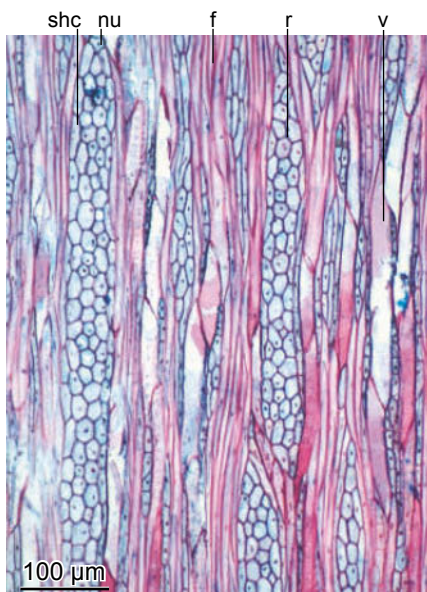
Left Fig. 16. Phloem with round groups of sclerenchyma cells oriented in tangential lines. Stem of a 3 m-tall shrub, hedge, hill zone, Birmensdorf, Zurich, Switzerland. *Viburnum opulus*, transverse section.

Right Fig. 17. Phloem with tangential bands of sclerenchyma cells. The xylem is in formation therefore the cell walls are not fully developed. Stem of a 2 m-tall shrub, laurel forest, subtropical zone, Tenerife, Macaronesia, Spain. *Viburnum tinus*, transverse section.



Left Fig. 18. Diffuse porous xylem with solitary vessels and indistinct ring boundaries. Rhizome of a 1.5 m-tall hemicryptophyte, beech forest, hill zone, Hausen, Zurich, Switzerland. *Sambucus ebulus*, transverse section.

Right Fig. 19. Paratracheal parenchyma containing dark-stained substances in a thin- to thick-walled tissue. Rhizome of a 1.5 m-tall hemicryptophyte, beech forest, hill zone, Birmensdorf, Zurich, Switzerland. *Sambucus ebulus*, transverse section.



Left Fig. 20. 1-5-seriate rays containing sheath cells. Ray cells contain nuclei. Rhizome of a 1.5 m-tall hemicryptophyte, beech forest, hill zone, Birmensdorf, Zurich, Switzerland. *Sambucus ebulus*, tangential section.

Right Fig. 21. Phloem with small groups of sclereids. Some parenchyma are filled with crystal druses. Laticifers are located in the cortex. Rhizome of a 1.5 m-tall hemicryptophyte, beech forest, hill zone, Birmensdorf, Zurich, Switzerland. *Sambucus ebulus*, transverse section.

Discussion in relation to previous studies

STÜRM (1910) studied the anatomy of *Adoxa moschatellina* in detail. The anatomy of *Adoxa moschatellina* is very different to the two other genera (*Sambucus* and *Viburnum*).

The genera *Sambucus* and *Viburnum* have been described often but studies have mostly been confined to the Caprifoliaceae family, e.g. BRAZIER AND FRANKLIN (1961), GREGUSS (1945), GROSSER (1977), and SCHWEINGRUBER (1990). HUBER AND ROUSCHAL (1954) described *Viburnum tinus*. HOLDHEIDE (1951) described the bark of *Sambucus nigra* in detail. Our results are in accordance with those of previous authors.

Present features in relation to the number of analyzed species

IAWA code	frequency
Total number of species	14
1 growth rings distinct and recognizable	13
2.2 without secondary growth	1
4 semi-ring-porous	1
5 diffuse-porous	13
9 vessels predominantly solitary	11
10 vessels in radial multiples of 4 or more common	1
11 vessels predominantly in clusters	4
13 vessels with simple perforation plates	7
14 vessels with scalariform perforation plates	7
20.1 intervessel pits pseudoscalariform to reticulate	1
22 intervessel pits alternate	13
31 vessel-ray pits with large apertures, <i>Salix/Laurus</i> type	6
36 helical thickenings present	1
40.1 earlywood vessels: tangential diameter <20 µm	1
40.2 earlywood vessels: tangential diameter 20-50 µm	4
41 earlywood vessels: tangential diameter 50-100 µm	8
42 earlywood vessels: tangential diameter 100-200 µm	2
50 <100 vessels per mm ² in earlywood	2
50.1 100-200 vessels per mm ² in earlywood	11
50.2 200-1000 vessels per mm ² in earlywood	2
56 tylosis with thin walls	2
60.1 fibers absent	1
61 fiber pits small and simple to minutely bordered (<3 µm = libriform fibers)	11
62 fiber pits large and distinctly bordered (>3 µm = fiber tracheids)	11
68 fibers thin-walled	1
69 fibers thick-walled	1
70 fibers thin- to thick-walled	12
75 parenchyma absent or unrecognizable	8
76 parenchyma apotracheal, diffuse and in aggregates	4
79 parenchyma paratracheal	1
79.1 parenchyma pervasive	1
97 ray width predominantly 1-3 cells	8
98 rays commonly 4-10-seriate	6
105 ray: all cells upright or square	1
106 ray: heterocellular with 1 upright cell row (radial section)	1
107 ray: heterocellular with 2-4 upright cell rows (radial section)	10
108 ray: heterocellular with >4 upright cell rows (radial section)	6
110 rays with sheath cells (tangential section)	3
117 rayless	1
R1 groups of sieve tubes present	6
R4 sclereids in phloem and cortex	7
R6 sclereids in radial rows	2
R6.1 sclereids in tangential rows	3
R6.2 sclereids in tangentially arranged groups, <i>Rhamnus</i> type	5
R7 with prismatic crystals	2
R8 with crystal druses	3
R9 with crystal sand	3
R12 with laticifers, oil ducts or mucilage ducts	2
R16 phellem consists of regularly arranged rectangular cells, Rosaceae type	4

Apiaceae

Number of species, worldwide and in Europe

The cosmopolitan Apiaceae family includes 434 genera with 3780 species. There are 415 species endemic to Europe. Many species exist in the genera *Bupleurum* (39), *Seseli* (34) and *Peucedanum* (29).

Analyzed material

111 species are analyzed here.

Life forms analyzed:	Studies from other authors:	
Nanophanerophytes 0.5-4 m	3	ca. 5
Woody chamaephytes	5	ca. 4
Semi-woody chamaephytes	2	
Hemicryptophytes	73	ca. 11
Therophytes	26	
Helophytes	2	

Plants analyzed from different vegetation zones:	
Alpine and arctic	19
Hill and mountain	47
Mediterranean	33
Arid	4
Subtropical	8



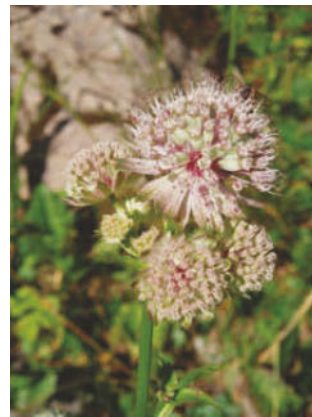
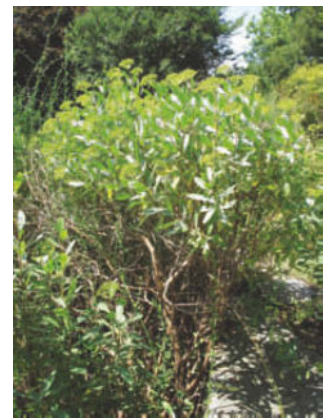
Laserpitium siler

Analyzed species:

Aegopodium podagraria L.
Aethusa cynapium L.
Ammi majus L.
Angelica sylvestris L.
Anthriscus sylvestris (L.) Hofmann
Apium nodiflorum (L.) Laq.
Apium repens Lag.
Astericum glaucum Hieron. et Wolff
Astrantia major L.
Astrantia maxima Pall.
Astrantia minor L.
Astydamia latifolia Baill.
Athamanta cretensis L.
Azorella compacta Phil.
Berula erecta (Huds.) Coville
Bifora radians Bieb.
Bupleurum baldense Turra
Bupleurum exaltatum M. Bieb.
Bupleurum falcatum D.C.
Bupleurum foliosum Salm. ex D.C.
Bupleurum frutescens L.
Bupleurum fruticosum L.
Bupleurum gracile D'Urv
Bupleurum longifolium L.
Bupleurum petraeum L.
Bupleurum ranunculoides L.
Bupleurum rotundifolium L.
Bupleurum salicifolium Sol. ex Lowe
Bupleurum spinosum Gouan
Bupleurum stellatum L.
Carum carvi L.
Caucalis platycarpus L.
Chaerophyllum aureum L.
Chaerophyllum bulbosum L.
Chaerophyllum hirsutum L.
Chaerophyllum villarsii Koch
Conium maculatum L.
Crithmum maritimum L.
Cryptotaenia elegans Webb. ex Bolle
Daucus carota L.
Drusa glandulosa Bornm.
Eryngium alpinum L.
Eryngium campestre L.
Eryngium giganteum M. Bieb.
Eryngium maritimum L.
Eryngium spinalba L.
Falcaria vulgaris Bernh.
Ferula communis L.
Ferula linkii Webb.
Foeniculum vulgare Mill.
Gymnophyton polycephalum Clos
Hacquetia epipactis D.C.
Heracleum mantegazzianum Sommier et Levier
Heracleum sphondylium L.
Lagoecia cuminoides L.

Laserpitium gallicum L.
Laserpitium latifolium L.
Laserpitium peucedanooides L.
Laserpitium siler L.
Ligusticum alpinum L.
Ligusticum lucidum Miller
Ligusticum mutellina (L.) Crantz
Ligusticum mutellinoides (Crantz) Vill.
Melanoselinum decipiens Hoffm.
Meum athamanticum Jacq.
Myrrhis odorata (L.) Scop.
Oenanthe pimpinelloides L.
Olymposciadium caespitosum (S.M) Wolff
Oreoxis alpina J.M. Coult. & Rose
Osmorhiza depauperata Phil.
Pastinaca sativa L.
Petroselinum crispum (Mill.) Fuss
Peucedanum austriacum W.D.J. Koch
Peucedanum officinale L.
Peucedanum oreoselinum (L.) Moench
Peucedanum ostruthium (L.) Koch
Peucedanum venetum (Sprengel) Koch
Peucedanum verticillare (L.) Koch
Pimpinella alpina Host.
Pimpinella cretica Poirlet
Pimpinella dendrotragium Webb.
Pimpinella major (L.) Hudson
Pimpinella nigra Miller

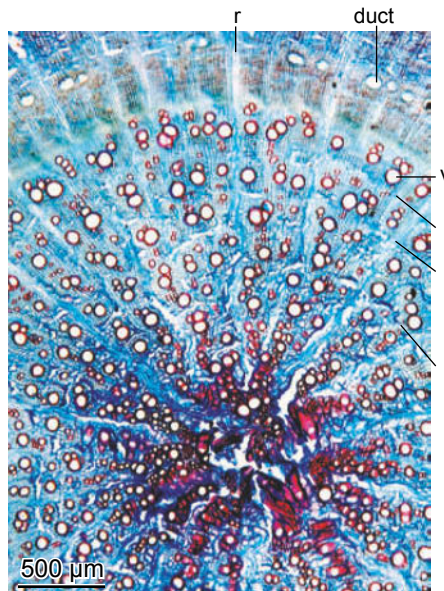
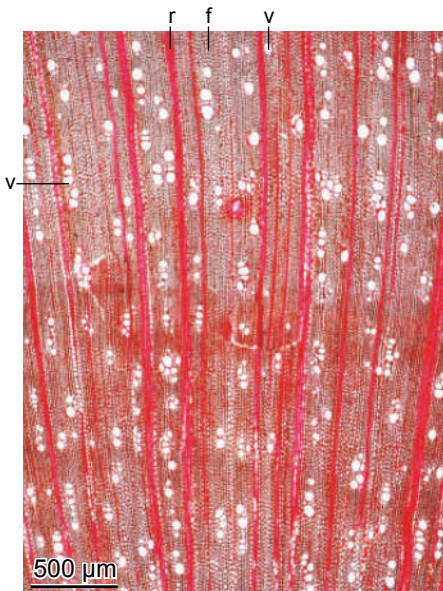
Pituranthos chloranthus Bent. et Hook
Pituranthos scoparius Bent. ex Hook
Pleurospermum austriacum (L.) Hoffm.
Pseudorlaya pumila (L.) Grunler
Rouya polygama (Desf.) Coincy
Sanicula europaea L.
Scaligeria napiformis Will. ex Sprengel, Grande
Scandix pecten-veneris L.
Seseli annuum L.
Seseli annuum ssp. *carvifolium* (Vill.) P. Fourn.
Seseli hippomarathrum Jacq.
Seseli libanotis (L.) Koch
Seseli montanum L.
Seseli osseum Crantz
Seseli rupicola Woronow
Sison amomum L.
Sium sisarum L.
Smyrniium perfoliatum L.
Taenidia integerrima Drude
Thapsia garganica L.
Thapsia villosa L.
Tinguarra montana Bent. et Hook f.
Todaroa aurea Parl.
Tordylium apulum L.
Tordylium officinale L.
Torilis arvensis (Hudson) Link
Torilis japonica (Houtt.) DC.
Torilis leptophylla (L.) Reichenb. fil.

*Ferula communis**Astrantia major**Eryngium campestre**Aegopodium podagraria**Bupleurum fruticosum*

Characteristics of the xylem and phloem

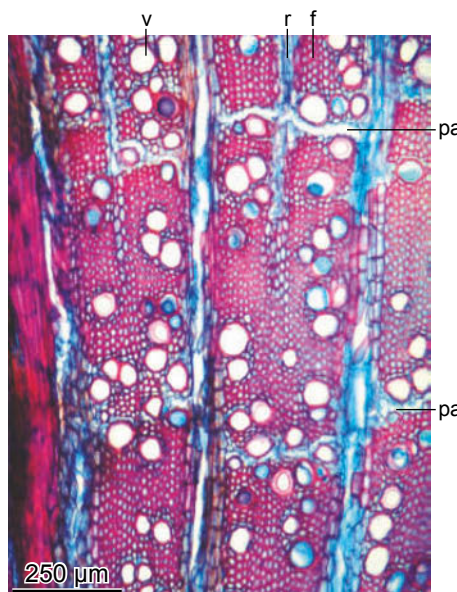
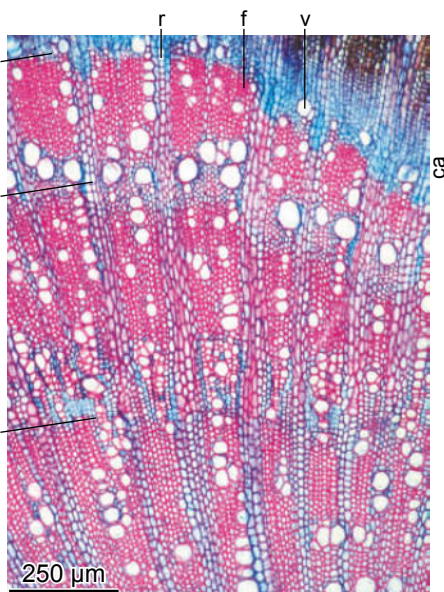
Simple perforations, the absence of crystals, and the presence of rays are common to all species. Ring distinctness varies. Rings are absent or barely recognizable in two thirds of the perennial species analyzed here (54 species; **Figs. 1-5**) but are distinct in the remaining 30 species (**Figs. 8** and **9**). Ring distinctness varies greatly within individual species and depends on growth conditions (**Fig. 3**). 24 therophytes have only one ring (**Figs. 7** and **16**). All perennial species with annual rings are diffuse-porous (17 species; **Fig. 4**) or semi-ring-porous (41 species; **Figs. 2, 5, and 8**). Vessels are either solitary (72 species; **Figs. 2** and **4**), in short and long radial multiples (59 species; **Figs. 1, 6** and **7**), or in groups (30 species; **Figs. 8** and **9**). Transitions

between all vessel distribution types are very frequent, even within individuals. A diagonal pattern occurs only in shrubs (*Bupleurum* and *Pituranthos*; **Fig. 8**). Earlywood diameter generally varies from 30-70 μm . However, earlywood diameter is smaller than 20 μm in 11 species, mostly in small individuals. Vessel diameter only exceeds 100 μm in 6 large species, e.g. *Ferula communis*, *Bupleurum fruticosum* and *Foeniculum vulgare*. Vessel density varies between 100-200 mm^2 in most species but is higher (300-400 mm^2) in a small number of small species (e.g. *Azorella*, *Haquetia* and *Oreoxis*) and lower (50-80 mm^2) in a small number of large species (e.g. in *Ferula communis*, *Heracleum mantegazzianum* and *Melanoselinum decipiens*).



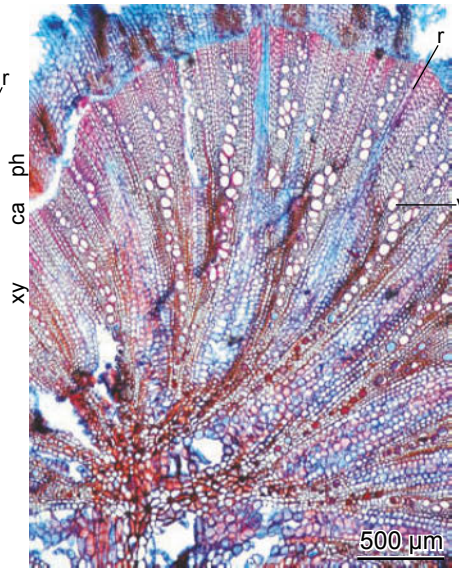
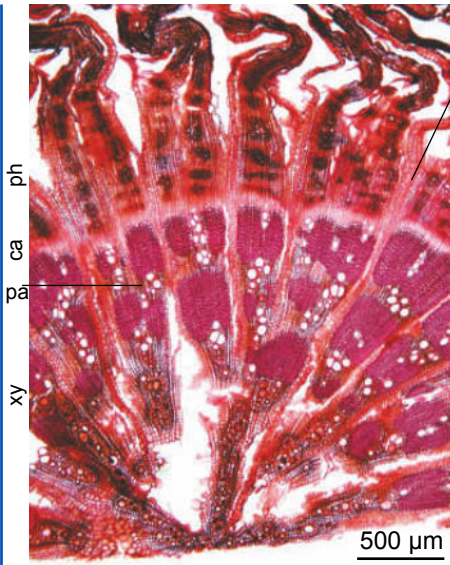
Left Fig. 1. Indistinct rings. Vessels are solitary and in short radial multiples. Both types are partially arranged in tangential rows. Stem of a 1.5 m-tall shrub, laurel forest, subtropical zone, Madeira, Macaronesia, Portugal. *Melanoselinum decipiens*, transverse section.

Right Fig. 2. Indistinct rings in the center and distinct rings at the periphery. Fibers are absent. Root collar of a 60 cm-tall hemicryptophyte, dry meadow, mountain zone, Briançon, France. *Laserpitium gallicum*, transverse section.



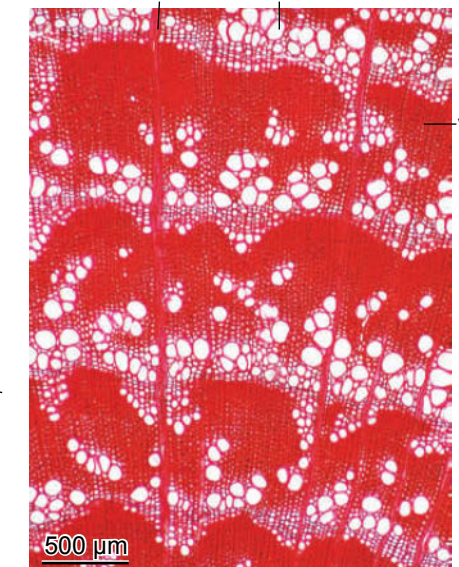
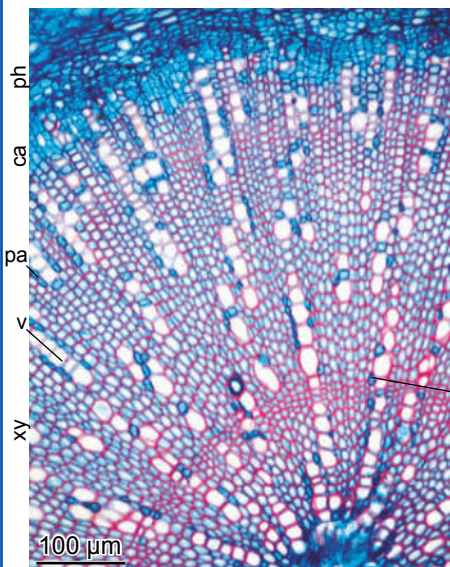
Left Fig. 3. Indistinct and distinct ring boundaries. Stem of a 60 cm-tall upright dwarf shrub, dry meadow, arid climate, Valle della Luna, Argentina. *Astericum glaucum*, transverse section.

Right Fig. 4. Unicellular marginal parenchyma zones indicate ring boundaries in a diffuse-porous xylem. Root collar of a 40 cm-tall hemicryptophyte, dry, saline coastal zone, coast Los Silos, Tenerife, Macaronesia, Spain. *Crithmum maritimum*, transverse section.



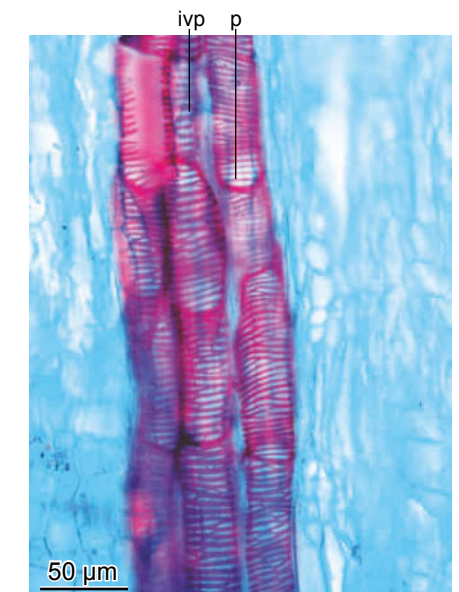
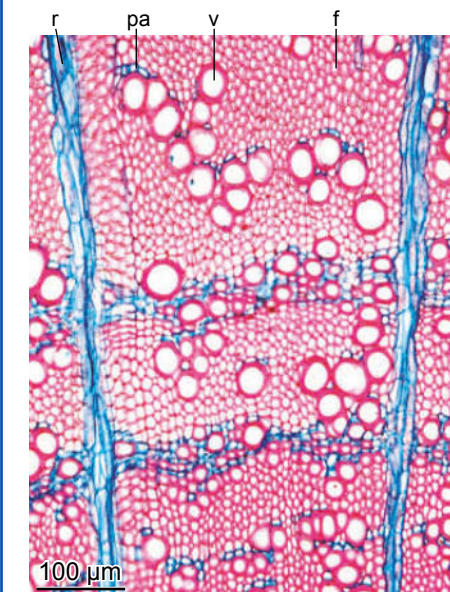
Left Fig. 5. Distinct rings due to semi-ring-porosity and marginal parenchyma bands. Root collar of a 50 cm-tall hemicryptophyte, megaherb, subalpine zone, Davos, Grisons, Switzerland. *Chaerophyllum aureum*, transverse section.

Right Fig. 6. Vessels in long, irregular radial multiples. Root collar of an 80 cm-tall hemicryptophyte, moist meadow, hill zone, Rottenschwil, Aargau, Switzerland. *Angelica silvestris*, transverse section.



Left Fig. 7. Bi-annual plant. Vessels are arranged in long, radial multiples. Root collar of a 20 cm-tall therophyte, dry rock, botanical garden, hill zone, Austria. *Bupleurum baldense*, transverse section.

Right Fig. 8. Semi-ring-porous xylem with vessels in groups and in irregular diagonal patterns. Stem of a 1 m-tall shrub, dry site, Mediterranean, Lerida, Zaragoza, Spain. *Bupleurum frutescens*, transverse section.



Left Fig. 9. Groups of thick-walled vessels within a thin- to thick-walled fiber tissue. Parenchyma is paratracheal and marginal. Rays are unligified. Stem of a 50 cm-tall shrub, dry rock, Mediterranean, Sitges, Catalonia, Spain. *Bupleurum frutescens*, transverse section.

Right Fig. 10. Vessels with simple perforations and scalariform intervessel pits are surrounded by an unligified parenchyma tissue. Rhizome of a 1.5 m-tall hemicryptophyte, dry meadow, Mediterranean, Crete, Greece. *Ferula communis*, tangential section.

Thick-walled vessels are characteristic of many fiberless species with pervasive parenchyma (68 species; **Figs. 9, 13, 15 and 18**). Vessels with scalariform intervessel pits occur in combination with the pervasive parenchyma (68 species; **Fig. 10**). In species or zones within species containing fibers, intervessel pits are horizontally enlarged or round and arranged in alternating positions (**Fig. 11**). Thin-walled tylosis were observed in all *Chaerophyllum* species, in *Myrrhis odorata* and in *Heracleum sphondylium*. Dark-staining substances of the heartwood occur in a few species, e.g. in *Crithmum maritimum* (**Fig. 4**) and in *Bupleurum fruticosum*. Fibers are often absent (**Fig. 2**). Fiber-wall thickness varies but is thin- to thick-walled in most cases (47 species; **Fig. 12**). Fiber walls in shrubs are occasionally thick-walled, e.g. in *Bupleurum* (**Fig. 8**). In herbaceous species, variable fiber

wall thickness occurs occasionally in intra-annual bands and in patches (**Figs. 13-15**). Thin-walled fibers occur in root collars of a small number of small herbs, e.g. *Caucalis platycarpus* and *Torilis japonica* (**Figs. 6 and 16**).

The axial parenchyma is paratracheal in all species that contain fibers (64 species; **Figs. 7, 9, 16 and 17**). Parenchyma is pervasive in all species without fibers (60 species; **Figs. 2 and 18**). Pervasive and paratracheal parenchyma often occur within one individual. Parenchyma is often pervasive in the center and paratracheal at the periphery (**Figs. 19 and 20**). Marginal parenchyma is especially frequent in *Bupleurum* (**Figs. 8 and 9**) but also occurs in other species, e.g. *Seseli annuum* and *Todaroa aurea*.

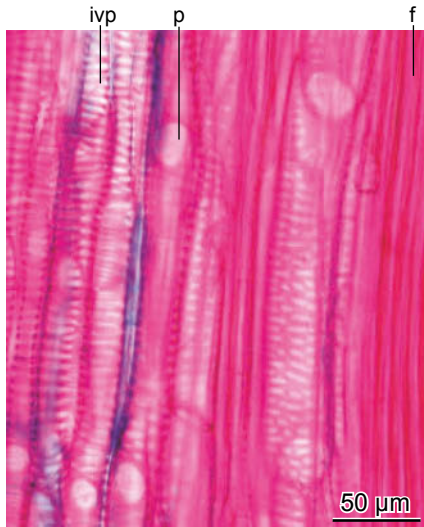


Fig. 11. Vessels with simple perforations and scalariform and rounded intervessel pits. Root collar of a 40 cm-tall hemicryptophyte, field, Mediterranean, Crete, Greece. *Smyrnum perfoliatum*, tangential section.

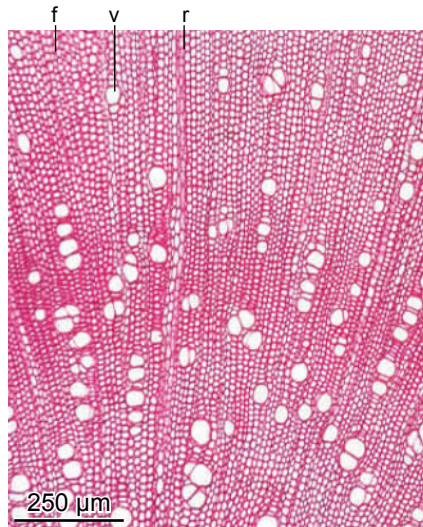


Fig. 12. Thin- to thick-walled fibers. Root collar of a 60 cm-tall hemicryptophyte, hedge, hill zone, Tirano, Valtellina, Italy. *Torilis japonica*, transverse section.

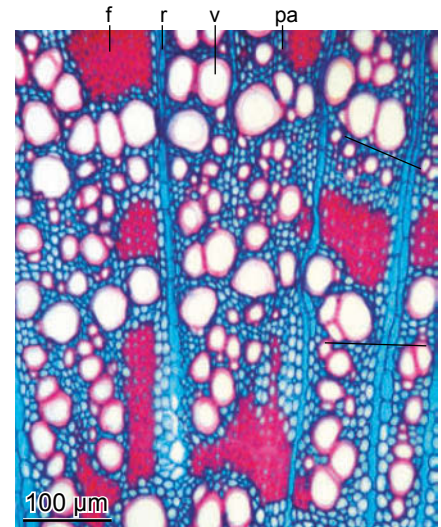
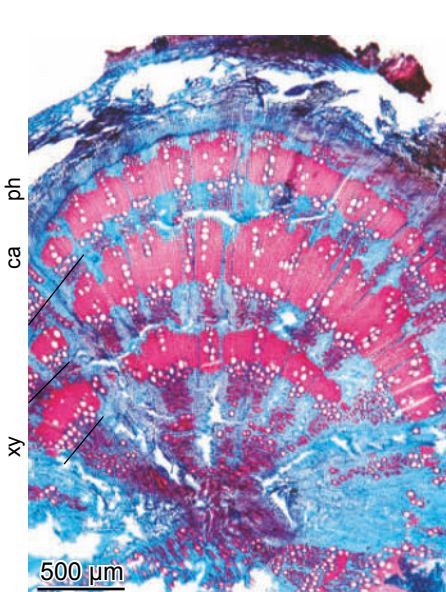
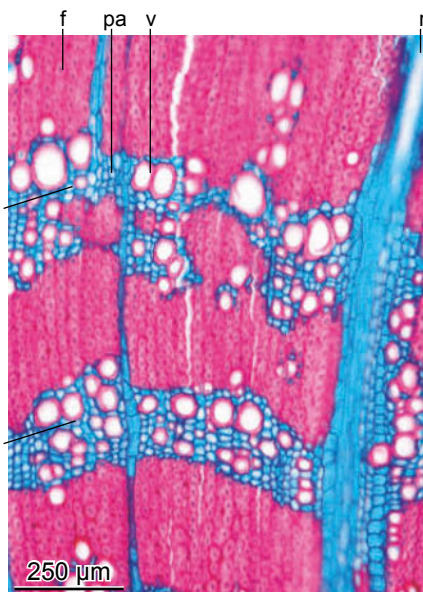


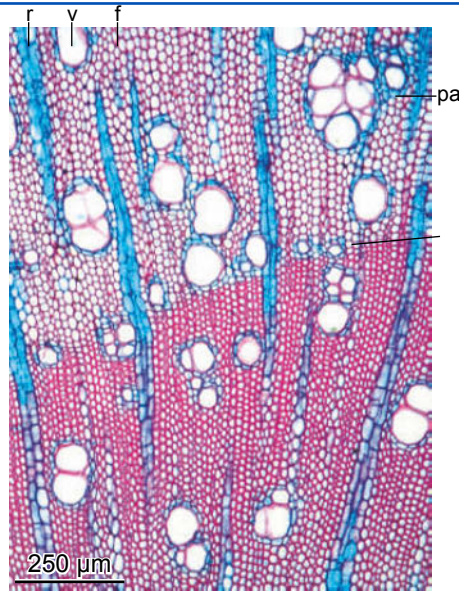
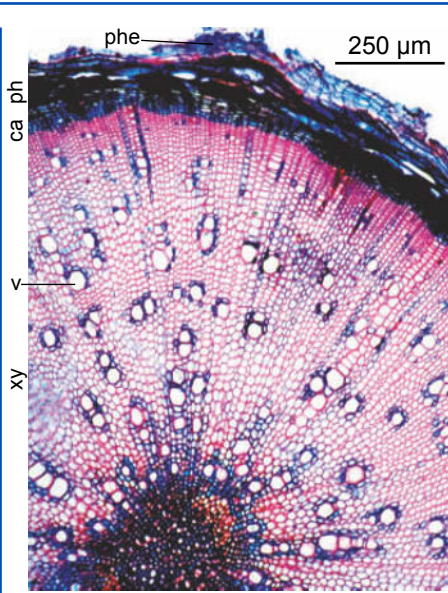
Fig. 13. Patches of thick-walled fibers within an unligified pervasive parenchyma. Root collar of a 40 cm-tall hemicryptophyte, dry meadow, hill zone, Hainburg, Burgenland, Austria. *Seseli hippomarathrum*, transverse section.



Left Fig. 14. Intra-annual tangential bands of thick-walled fibers in the earlywood and thin-walled, unligified parenchyma in the latewood. Root collar of a 40 cm-tall hemicryptophyte, dry meadow, hill zone, Breitenbrunn, Burgenland, Austria. *Bupleurum falcatum*, transverse section.

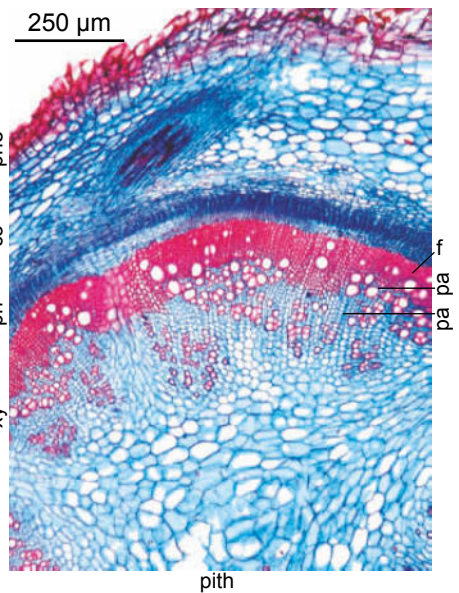
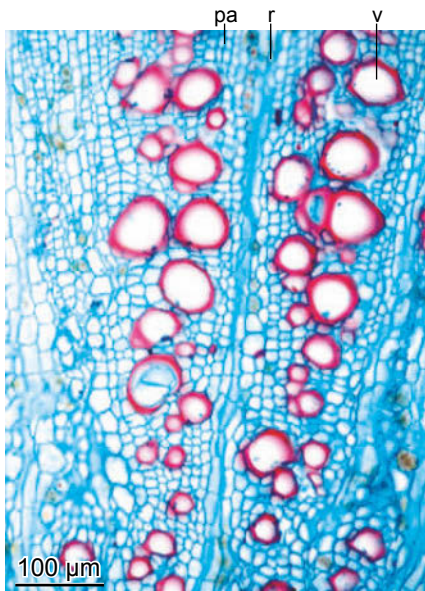


Right Fig. 15. A few vessels in tangential bands of thick-walled fibers and many thick-walled vessels within a parenchymatic tissue. Root collar of a 40 cm-tall hemicryptophyte, dry meadow, Mediterranean, Ax les Thermes, Andorra, France. *Seseli annuum* ssp. *carvifolium*, transverse section.



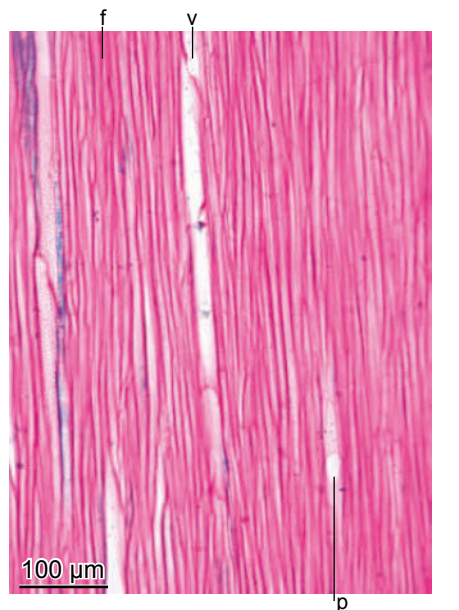
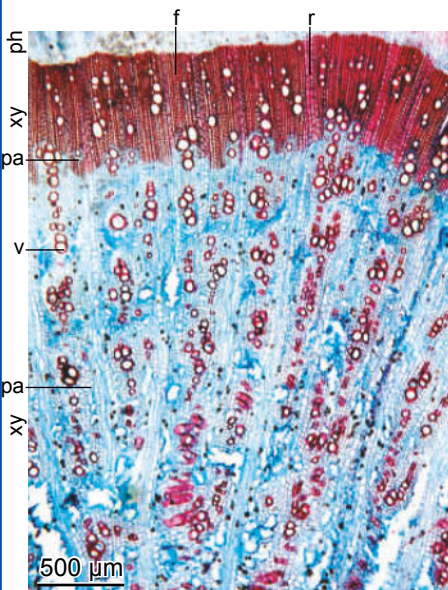
Left Fig. 16. Paratracheal parenchyma within a tissue of thin-walled fibers. Root collar of a 25 cm-tall therophyte, dry meadow, Mediterranean, Berjules, Andalusia, Spain. *Caulocalis platycarpus*, transverse section.

Right Fig. 17. Paratracheal parenchyma within a tissue of thin- to thick-walled fibers. Rhizome of a 100 cm-tall hemicryptophyte, meadow, thermophile zone, subtropical zone, Gomera, Macaronesia, Spain. *Ferula linkii*, transverse section.



Left Fig. 18. Pervasive parenchyma surrounds thick-walled vessels. Root collar of a 40 cm-tall hemicryptophyte, dry meadow, hill zone, Masun, Slovenia. *Eryngium campestri*, transverse section.

Right Fig. 19. Pervasive parenchyma surrounding the pith and paratracheal parenchyma in the fiber zone at the periphery. Root collar of a 15 cm-tall therophyte, field, Mediterranean, Spili, Crete, Greece. *Scandix pecten-veneris*, transverse section.



Left Fig. 20. Pervasive parenchyma in the center and paratracheal parenchyma in the fiber zone at the periphery. Root collar of a 80 cm-tall therophyte, dry meadow, subalpine zone, Aldigeni district, Georgia. *Eryngium giganteum*, transverse section.

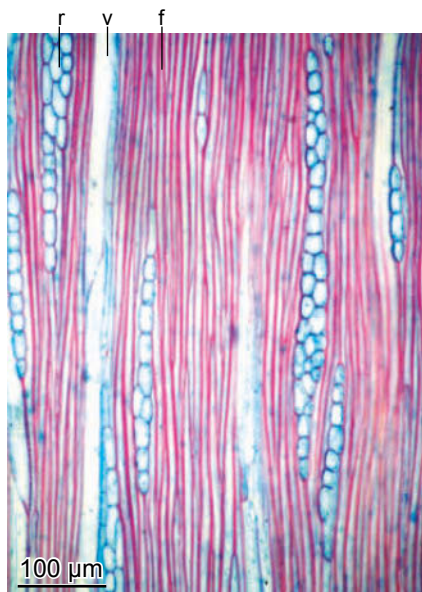
Right Fig. 21. Absence of rays. Root collar of a 20 cm-tall therophyte, dry meadow, Mediterranean, Spili, Crete, Greece. *Tordylium apulum*, tangential section.

Ray width varies greatly. Rays are absent in small annual species (10 species), e.g. *Scandix pecten-veneris* and *Sanicula europaea* (Fig. 21). Rays are occasionally uniseriate, e.g. in a small number of *Bupleurum* species and in *Caucalis platycarpus* (Fig. 22). Rays are exclusively 2-3-seriate in several genera (17 species), e.g. *Athamanta* and *Aethusa* (Fig. 23), 3-5-seriate in 20 species, e.g. *Bupleurum foliosum* and *Laserpitium gallicum* (Fig. 24), and 4-8-seriate in 52 species, e.g. *Melanoselinum* and *Bupleurum fruticosum* (Fig. 25). Large rays are often confluent with the axial tissue (Figs. 25 and 26). Rays are larger than 10-seriate in species where vascular bundles or enlarging vessel-fiber zones remain for a long time, e.g. in *Astrantia* species and *Heracleum mantegazzianum* (Figs. 27-29). In addition, ray composition greatly varies between homocellular with square and upright marginal cells, to heterocellular with procumbent central and marginal square and upright cells, to homocellular with exclusively procumbent cells (Figs. 30-32). Within the xylem, axial

oil canals have been observed in the parenchymatic tissue between vascular bundles in all *Astrantia* species, in *Pleurospermum austriacum* and in *Apium nodiflorum*. Canals occasionally occur in rays, e.g. in *Bupleurum spinosum*, in *Peucedanum austriacum* and in *Seseli libanotis* (Fig. 33).

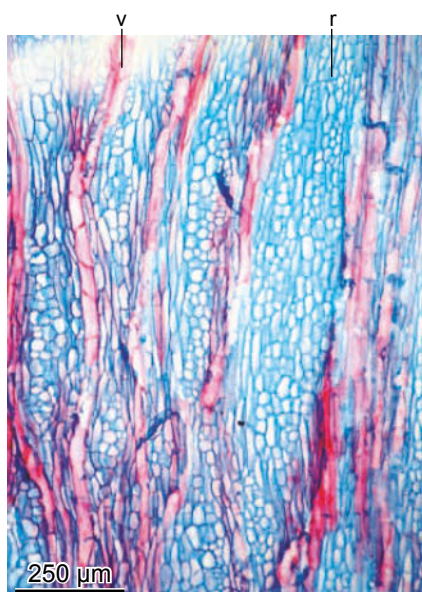
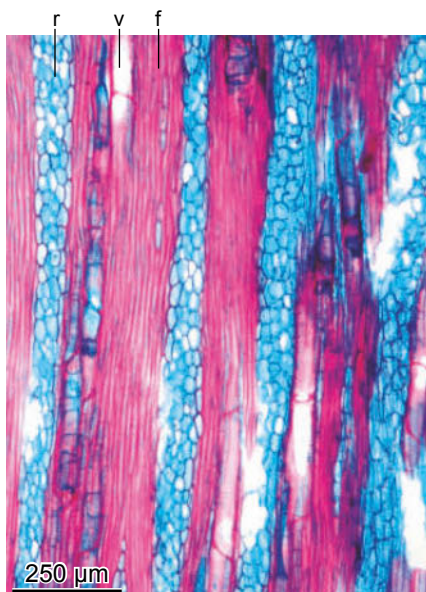
Axial secretory canals in the pith occur frequently in a variety of forms and diameters (Figs. 33-36). Not all species contain such ducts (Fig. 37), but we cannot quantify the frequency of occurrence because the pith was not included in some of our slides.

Crystals can occur in different forms in the xylem but are generally rare within the family (14 species). Crystal druses are characteristic of all *Eryngium* species but also occur in *Ammi majus*, *Falcaria vulgaris*, *Astydamia latifolia* and *Aethusa cynapium*. Crystal sand has been observed in *Ferula* species, *Foeniculum vulgare* and *Lagoecia cuminoides*.



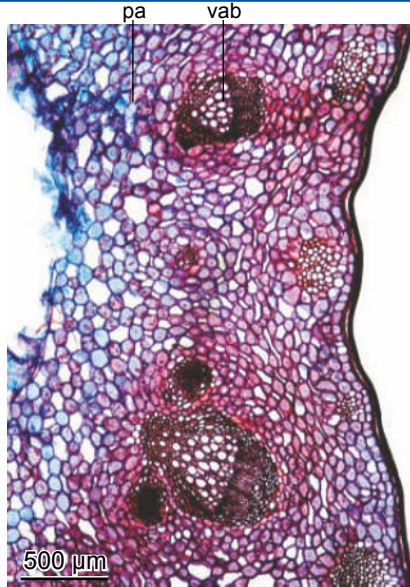
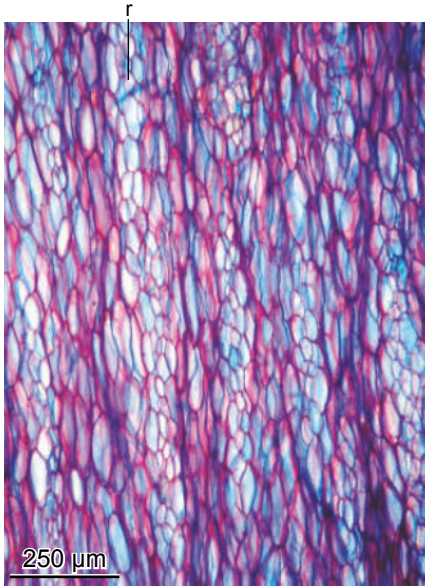
Left Fig. 22. Uniseriate rays. Root collar of a 30 cm-tall therophyte, field, Mediterranean, Castellane, Provence, France. *Bifora radians*, tangential section.

Right Fig. 23. Rays 1-3-seriate. Root collar of a 60 cm-tall therophyte, cultivated, Botanical Garden Zurich, Switzerland. *Ammi majus*, tangential section.



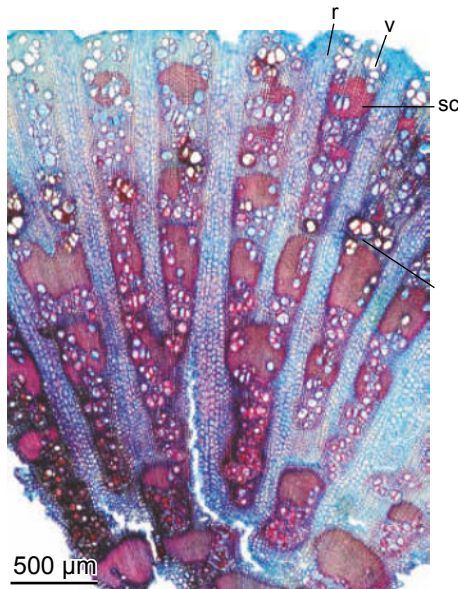
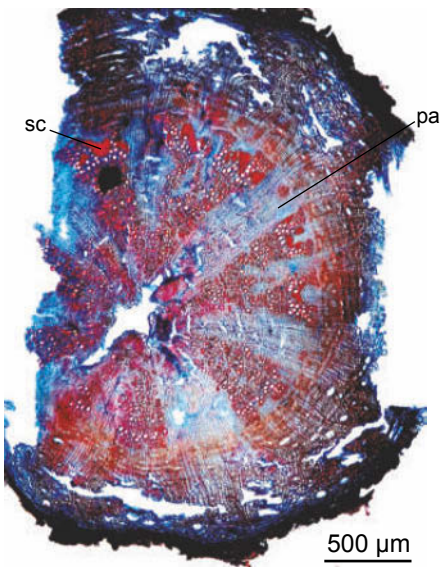
Left Fig. 24. Rays 3-5-seriate. Root collar of a 40 cm-tall hemicryptophyte, saline coastal zone, coast Los Silos, Tenerife, Macaronesia, Spain. *Critbium maritimum*, tangential section.

Right Fig. 25. Rays 4-10-seriate. Root collar of a 40 cm-tall therophyte, cultivated, garden, Birmensdorf, Zurich, Switzerland. *Petroselinum crispum*, tangential section.



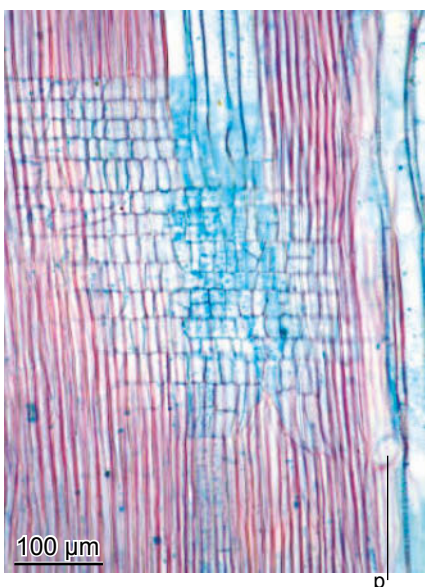
Left Fig. 26. Rays confluent with the axial tissue. Rhizome of a 40 cm-tall hemicryptophyte, canyon near coast, San Andres, Gran Canaria, Macaronesia, Spain. *Astydamia latifolia*, tangential section.

Right Fig. 27. Single vascular bundles laterally separated by large parenchyma zones. Rhizome of a 40 cm-tall hemicryptophyte, moist riverbed, Mediterranean, Rethymno, Crete, Greece. *Apium nodiflorum*, transverse section.



Left Fig. 28. Vessel-fiber zones laterally separated by large, unlignified parenchyma zones (rays). Root collar of a 40 cm-tall chamaephyte, dry rock, Grasse, Provence, France. *Bupleurum petraeum*, transverse section.

Right Fig. 29. Radial, long vessel-fiber strips laterally separated by large, unlignified parenchyma zones (rays). Rhizome of a 40 cm-tall hemicryptophyte, meadow, subalpine zone, Klewenalp, Obwalden, Switzerland. *Chaerophyllum hirsutum*, transverse section.



Left Fig. 30. Homocellular ray with square and upright cells. Root collar of a 60 cm-tall therophyte, cultivated, Botanical Garden Zurich, Switzerland. *Ammi majus*, radial section.

Right Fig. 31. Heterocellular ray with procumbent and upright cells. Rhizome of a 1 m-tall hemicryptophyte, field, thermophile subtropical zone, Gomera, Macaronesia, Spain. *Tinguarra montana*, radial section.