

Anatomy of fruit stalks

Fritz H. Schweingruber, Urs Max Weber, Norbert Kessel

Impressum

Prof. em. Fritz H. Schweingruber
Wood anatomist, dendrochronologist
Swiss Federal Institute for Forest, Snow
and Landscape Research, WSL
Birmensdorf, Switzerland

Dr. Urs Max Weber
Forest biologist, dendrochronologist
Fehraltorf, Switzerland
e-mail: uramax.weber@bluewin.ch

Dr. Norbert Kessel
Forest scientist, publisher
Kessel Publishing House
Remagen-Oberwinter, Germany
e-mail: webmaster@forstbuch.de

Fritz H. Schweingruber: all microscopic content and
descriptions
Urs Max Weber: all macroscopic content and text
revision
Norbert Kessel: editing and layout

Image sources:
all microscopic photos by Fritz H. Schweingruber
all macroscopic photos by Urs Max Weber, except:
cover by Fritz H. Schweingruber
p. 38 top left by Fritz H. Schweingruber
p. 62 top left by Fritz H. Schweingruber
p. 141 top left by Fritz H. Schweingruber
p. 144 top left by Fritz H. Schweingruber

Captions front cover:
Top right: *Rubus fruticosus*, cross section (100x)
Center left: *Malva moschata*, cross section (400x)
Center right: *Mahonia aquifolium*, cross section (100x)
Bottom left: *Laburnum anagyroides*, cross section
(100x)
Bottom center: *Berberis vulgaris*, cross section (400x)
Bottom right: *Malus sylvestris*, cross section (100x)

© 2020
Kessel Publishing House
Eifelweg 37
53424 Remagen-Oberwinter
Germany

Tel: +49-2228-493
Fax: +49-3212-1024877

e-mail: webmaster@forstbuch.de

Internet:
www.forestrybooks.com
www.forstbuch.de

Printed in Germany
www.business-copy.com

ISBN: 978-3-945941-58-4

Contents

Foreword	v	<i>Fragaria vesca</i> L.	69
Introduction into fruit stalks.	1	<i>Frangula alnus</i> Mill.	70
Definition and explanation of fruit stalk features	10	<i>Geum reptans</i> L.	71
Monographic presentation		<i>Gleditsia triacanthos</i> L.	72
of 127 species	29	<i>Gossypium herbaceum</i> L.	73
<i>Acer campestre</i> L.	30	<i>Hedera helix</i> L.	74
<i>Acer pseudoplatanus</i> L.	31	<i>Heracleum sphondylium</i> L.	75
<i>Aesculus hippocastanum</i> L.	32	<i>Hibiscus syriacus</i> L.	76
<i>Akebia quinata</i> (Houtt.) Decne.	33	<i>Hippocrepis emerus</i> L. Lassen.	77
<i>Alnus alnobetula</i> (Ehrh.) K. Koch,		<i>Hippophae rhamnoides</i> L.	78
syn. <i>Alnus viridis</i> (Chaix) DC.	34	<i>Ilex aquifolium</i> L.	79
<i>Alnus glutinosa</i> L. Gaertner(L.)	35	<i>Juglans regia</i> L.	80
<i>Arbutus andrachne</i> L.	36	<i>Juniperus communis</i> , var. <i>saxatilis</i> Pall.	81
<i>Arbutus unedo</i> L.	37	<i>Koelertheria paniculata</i> Laxm.	82
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	38	<i>Laburnum anagyroides</i> Medik.	83
<i>Atropa belladonna</i> L.	39	<i>Ligustrum vulgare</i> L.	84
<i>Berberis vulgaris</i> L.	40	<i>Lilium martagon</i> L.	85
<i>Betula pendula</i> Roth.	41	<i>Liriodendron tulipifera</i> L.	86
<i>Buddleia davidii</i> Franch.	42	<i>Loiseleuria procumbens</i> (L.) Desv.	87
<i>Bupleurum fruticosum</i> L.	43	<i>Lonicera xylosteum</i> L.	88
<i>Capparis spinosa</i> L.	44	<i>Mahonia aquifolium</i> (Pursh) Nutt.	89
<i>Carpinus betulus</i> L.	45	<i>Malus baccata</i> (L.) Borkh.	90
<i>Castanea sativa</i> Miller	46	<i>Malus domestica</i> Borkh. var. 'Boskoop'	91
<i>Celtis australis</i> L.	47	<i>Malus sylvestris</i> (L.) Mill. original species ..	92
<i>Cephalotaxus harringtonii</i> (Forb.) K. Koch.	48	<i>Malva moschata</i> L.	93
<i>Ceratonia siliqua</i> L.	49	<i>Medicago sativa</i> L.	94
<i>Chaenomeles japonica</i> (Thunb.) Lindl.	50	<i>Mespilus germanica</i> L.	95
<i>Chamaecyparis lawsoniana</i> (A. Murr.) Parl.	51	<i>Myrtus communis</i> L.	96
<i>Citrus sinensis</i> (not determined)	52	<i>Nerium oleander</i> L.	97
<i>Clematis vitalba</i> L.	53	<i>Olea europaea</i> L.	98
<i>Cornus mas</i> L.	54	<i>Ostrya carpinifolia</i> Scop.	99
<i>Corylus avellana</i> L.	55	<i>Paeonia officinalis</i> L.	100
<i>Cotinus coggygria</i> Scop.	56	<i>Parthenocissus quinquefolia</i> (L.) Planch.	101
<i>Crataegus monogyna</i> Jacq.	57	<i>Parthenocissus tricuspidata</i>	
<i>Cucumis melo</i> L.	58	(Sieb. et Zucc.) Planch.	102
<i>Cucurbita pepo</i> L.	59	<i>Pastinaca sativa</i> L.	103
<i>Cydonia oblonga</i> Mill.	60	<i>Phaseolus vulgaris</i> L.	104
<i>Daucus carota</i>	61	<i>Phytolacca americana</i> L.	105
<i>Diospyros lotus</i> L.	62	<i>Pinus mugo</i> Turra.	106
<i>Elaeagnus angustifolia</i> L.	63	<i>Pistacia lentiscus</i> L.	107
<i>Eucalyptus</i> sp.	64	<i>Plantago lanceolata</i> L.	108
<i>Euonymus europaeus</i> L.	65	<i>Platanus x acerifolia</i> syn.	
<i>Euonymus latifolius</i> (L.) Mill.	66	<i>Platanus x hispanica</i>	109
<i>Fagus sylvatica</i> L.	67	<i>Prunus avium</i> L.	110
<i>Ficus carica</i> L.	68	<i>Prunus domestica</i> L.	111
		<i>Prunus laurocerasus</i> L.	112
		<i>Prunus padus</i> L.	113
		<i>Punica granatum</i> L.	114

<i>Pyrus communis</i> L.	115	<i>Solanum lycopersicum</i> L.	137
<i>Quercus ilex</i> L.	116	<i>Solanum tuberosum</i> L.	138
<i>Quercus robur</i> L.	117	<i>Sorbus aria</i> (L.) Crantz.	139
<i>Quercus rubra</i> L.	118	<i>Sorbus aucuparia</i> L.	140
<i>Quercus suber</i> L.	119	<i>Sorbus domestica</i> L.	141
<i>Rhamnus alpina</i> L.	120	<i>Sorbus mougeotii</i> Soy.-Will & Goor.	142
<i>Rhamnus cathartica</i> L.	121	<i>Staphyllea pinnata</i> L.	143
<i>Rhododendron ferrugineum</i> L.	122	<i>Styrax officinalis</i> L.	144
<i>Rhus typhina</i> L.	123	<i>Syringa vulgaris</i> L.	145
<i>Ribes nigrum</i> L.	124	<i>Thuja occidentalis</i> L.	146
<i>Ribes rubrum</i> L.	125	<i>Tilia cordata</i> Mill.	147
<i>Robinia pseudoacacia</i> L.	126	<i>Tilia platyphyllos</i> Scop.	148
<i>Rosa arvensis</i> Huds.	127	<i>Tilia tomentosa</i> Moench.	149
<i>Rosa spinosissima</i> L., syn. <i>pimpinellifolia</i> .	128	<i>Trochodendron aralioides</i> Sieb. & Zucc. .	150
<i>Rubus caesius</i> L.	129	<i>Viburnum lantana</i> L.	151
<i>Rubus fruticosus</i> L.	130	<i>Viburnum opulus</i> L.	152
<i>Rubus idaeus</i> L.	131	<i>Viburnum rhytidophyllum</i> Hemsl.	153
<i>Salix helvetica</i> Vill.	132	<i>Viburnum tinus</i> L.	154
<i>Sambucus ebulus</i> L.	133	<i>Vitex agnus-castus</i> L.	155
<i>Sambucus nigra</i> L.	134	<i>Vitis vinifera</i> L.	156
<i>Securigera varia</i> (L.) Lassen	135	Acknowledgements	157
<i>Solanum dulcamara</i> L.	136		

Foreword and commemoration

All plants on earth have developed fruit stalks of one form or another. The main reason why they did or had to do so has still not been fully answered. One plausible explanation is that fruits (or leaves) with stalks can break off the plant body more easily than if fruits (or leaves) were directly attached to twigs or branches (broader adhesion area). Be that as it may, the anatomy of fruit stalks so far has rarely been studied. With this book, we have tried to fill this gap by presenting a microscopical approach to mainly (but not only) central European angiosperm species. We are well aware of the fact that describing 127 out of worldwide 240,000 to 400,000 plant species (depending on source) is not much more than a first step. At least the species selected cover a relatively wide range of the plant world.

This volume completes the first author's book series on microscopic plant anatomy (stem, branch, leaf stalk, fruit stalk). The overall conclusion is that all above-ground plant parts are principally constructed of the same fundamental tissues: pith, xylem, cambium, phloem, cortex and periderm. However, from a holistic point of view, an in-depth analysis of one essential part of the plant is still missing: the roots. We gladly leave the exploration of this largely unknown field in plant anatomy to coming generations, since we all know that it is hardly possible to answer all questions in one lifetime.

Fritz Schweingruber died in January 2020 at the age of 83. His contribution to advances in dendroecology and plant anatomy was passionate and unparalleled. Even during his last weeks of life he was an active scientist and, whenever his physical handicaps allowed, he went to the WSL to cut and stain microsections and have discussions with colleagues. Apart from numerous scientific articles, he wrote dozens of books, a fact that stands for itself.

Fritz Schweingruber was not only an outstanding, dedicated researcher, but also an inspiring, gifted teacher and fatherly supervisor. He knew how to awake enthusiasm for nature and science in many Master and Ph.D. students and helped them to widen their views, create new ideas and discover the world. For this we will always be grateful to him.

Fritz told me he'd had a good life and therefore couldn't complain that he would soon die. May he now be discovering a new, even more interesting and better world. In silent memory,

Urs Max Weber



Introduction into fruit stalks

Introduction

Fruit stalks are part of the inflorescence (Blütenstand). The morphology of inflorescences is classified in detail by Troll (1964, 1969) and Weberling (1981). Very few inflorescences of single species (e.g. *Arabidopsis thaliana*) have been described (Chang 2007).

The following study presents the anatomy of adult female inflorescences of trees, shrubs and herbs from mainly Central Europe, but also from other parts of the world. In focus are parts with adult fruits. We call them fruit stalks.

Principally, a few basic types of inflorescences exist. Monopodial types with the dominance of one principal shoot and sympodial types with several dominant shoots. Both types can be subdivided in many sub-forms e.g., spikes, racemes, panicles, umbels and many others.

Since the classification has already been described for single species (Chan Liu et al. 2007) and extensively for the whole form of appearance (Troll 1964, 1969, Weberling 1981), we do not enter in this discussion. From wood, bark, twig and petiole anatomy it is well known that environmental factors modify each part of plants. Mentioned here are major studies which demonstrate the ecologically relevant modification in wood (Schweingruber 1990) and in growing points (Troll 1967). Therefore it is not astonishing that inflorescences as extensions of shoots are anatomically different from them. However, the anatomy of fruit stalks so far has hardly been a scientific topic. The extremely variable ramification of female, male and hermaphrodite flowers and fruit stalks is extended by the length and the position of flowers and fruit stalks and finally the weight of fruits. In any case inflorescences are metamorphosed shoots.

Therefore we ask the following questions:

1. What is the anatomical aspect of growing points within buds?
2. What are the anatomical differences between three products of growing points? (1) Shoots as primary, vegetative and (2) fruit stalks and (3) petioles as generative products of primary and secondary tissues.
3. What are the characteristic features of fruit stalks in a broad range of fruits types?
4. What are the characteristic features of fruit stalks of morphologically different inflorescences in general?

The microscopic origin of all inflorescences and leaves are tips of growing zones. In very early differentiation processes the shoot, the leaf and inflorescence are determined.

Anatomical aspects of growing points in buds

The principal construction of early shoot development can be recognized in macroscopic longitudinal sections (Fig. 1a). The terminal bud with bud scales is accompanied by buds of lateral shoots which are initiated in the axil of dropped leaves (leaf scar). Leaves are initiated in the cortex. Behind the growing point lies an undifferentiated primary pith zone which already separates the undeveloped xylem from the pith and cortex zone. The final differentiation of primary tissues (pith and cortex) and secondary tissues (xylem and phloem) is fully developed in the bud (Fig. 1a). Similar to macroscopic sections are double-stained microsections. In addition, they show un lignified parts like growing point, cortex and initial leaves. Behind this zone extends a belt of cambium which differentiates phloem and xylem (Fig. 1b). Lateral shoot-initials are absent or cannot be recognized.

The construction of scale-less bud tips of herbs and a few shrubs (e.g. *Viburnum lantana*) is similar, but initial lateral shoots and flowers are already present. The lignification process did not start in this stage (Figs. 1b and d). However, secondary cambia develop in shoots, leaves and fruit stalks and get active as soon as buds break, but the final form varies. The cambial cells of all three parts differentiate in all possible phloem and xylem elements (Fig. 2 a-c).

However, the longevity of cambial cells differs. In shoots they remain active for an undefined period. In fruit stalks and in petioles they are active for very few weeks at the beginning of the vegetation period. Cell-wall thickening and differentiation to sclereids lasts until the fruit is ripe.

Differentiation processes are determined by the final form of shoots, fruit stalks or leaves. With a few characteristics of 17 species we try to find common and different developments. The following species are compared:

- *Acer campestre*
- *Alnus glutinosa*
- *Castanea sativa*
- *Clematis vitalba*
- *Fagus sylvatica*

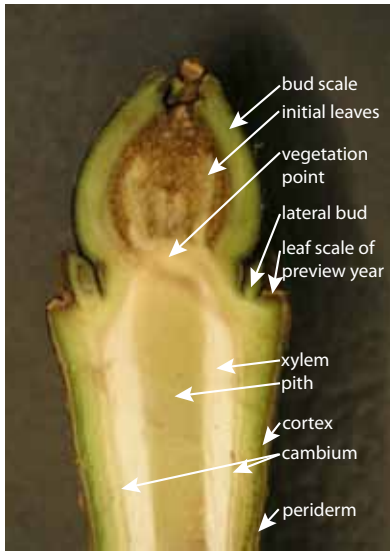


Fig. 1a Macroscopic longitudinal section through a tip of an annual twig of *Fraxinus excelsior*.

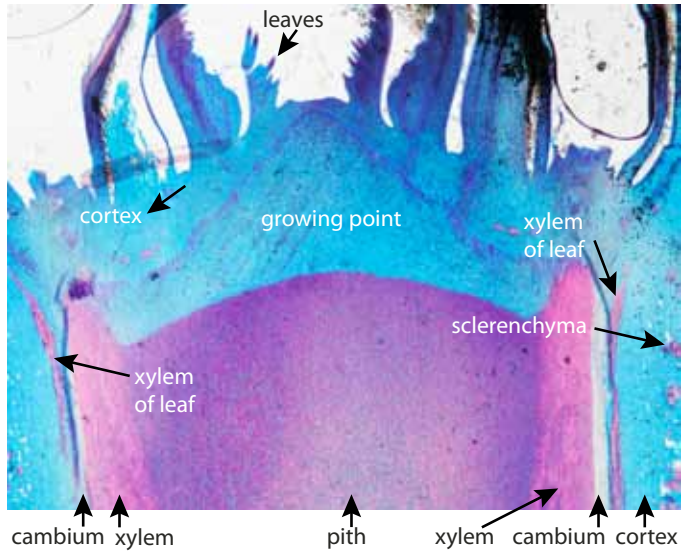


Fig. 1b Microscopic longitudinal section through a tip of an annual twig of *Fraxinus excelsior*. Leaves and the cortex are not lignified (100x).



Fig. 1c Macroscopic aspect of tips of the annual herb of *Euphorbia chamaecyparis*.

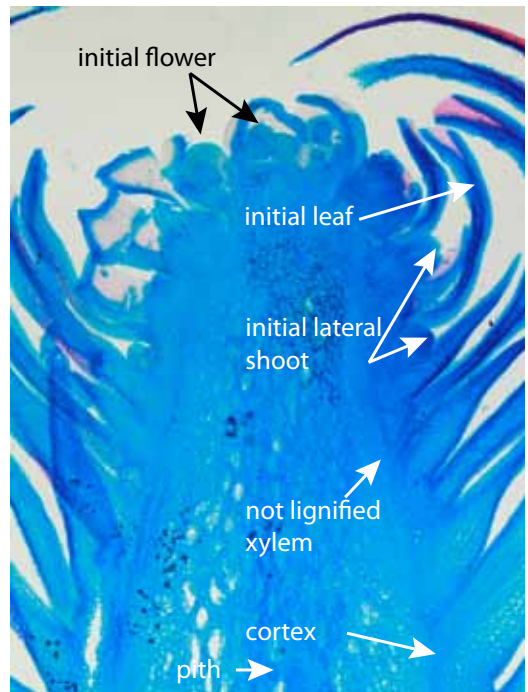


Fig. 1d Microscopic longitudinal section through a tip of the annual herb *Euphorbia chamaecyparis*. Lignification is absent in the whole initial shoot (100x).



Fig. 2a Young shoot (twig). *Crataegus laevigata*.

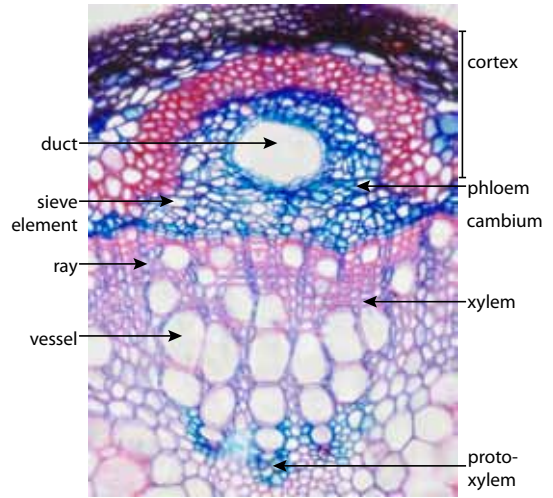


Fig. 2b Fruit stalk. *Rhus typhina*.

Fig. 2. Cambia in shoots, fruit stalks and petioles. Cambia differentiate into a xylem with vessels, fibers, parenchyma cells and rays, and into a phloem with sieve elements, parenchyma cells and rays, ducts and a tertiary cambium (phellogen).

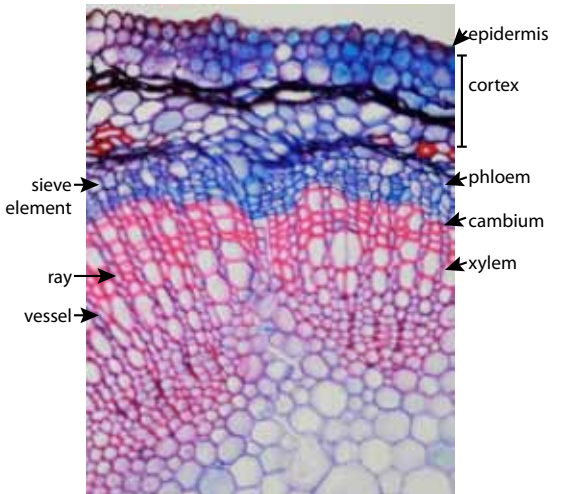


Fig. 2c Petiole. *Stayphyllea pinnata* (400x).

- *Frangula alnus*
- *Ilex aquifolium*
- *Myrtus communis* (presence of ducts)
- *Pistacia lentiscus* (presence of ducts)
- *Populus alba*
- *Prunus domestica*
- *Pyrus communis*
- *Rhus typhina* (presence of ducts)
- *Solanum tuberosum* (presence of medullary phloem)
- *Quercus robur*
- *Rubus idaeus*
- *Tilia platyphyllos*

The following features were compared in annual or biannual parts of the shoots and the middle part of fruit stalks and petioles:

- Diameter of the shoot
- External form
- Pith shape
- Vascular bundle arrangement, solitary or continuous after the first year in shoots or the stage after fruit ripening and the stage after full development of leaves
- Tangential vessel diameter in the first stage of secondary growth close to the pith
- Vessel arrangement in the first ring

- Presence or absence of fibers in the xylem of the first ring
- Presence or absence of rays in the xylem of the first ring
- Presence or absence of sclerenchyma zones in the cortex
- Presence or absence of the periderm
- Presence or absence of sclereids in the pith
- Presence or absence of ducts in the phloem or cortex
- Presence or absence of medullary sheath
- Presence or absence of medullary phloem

The following differences and similarities occur between the long shoot, fruit stalks and petioles:

- Diameter of the shoot. **Shoots** are often thicker than the other parts. However, thickness is not a special characteristic for one of the tree parts.
- External form. Most shoots, fruit stalks or petioles have a circular cross-section as in *Hedera helix* (Fig. 3a). In a few cases the cortex either expresses warts, or it is polygonal (Fig. 3b), e.g. in *Paeonia fruticosa*, or a vertical extension, e.g. in *Populus sp.* (Fig. 3c).

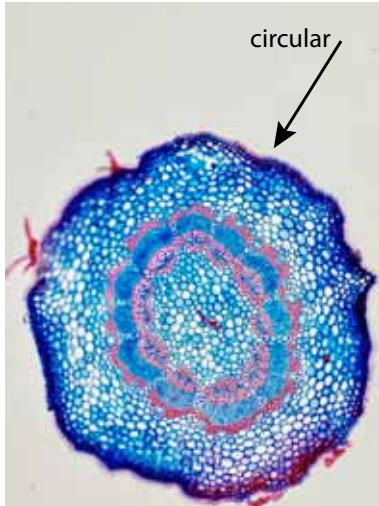


Fig. 3a Circular is the most frequent form in shoots and fruit stalks, *Hedera helix* (100x).



Fig. 3b Very few species with isolated vascular bundles have a polygonal external form, *Paeonia officinalis* (100x).

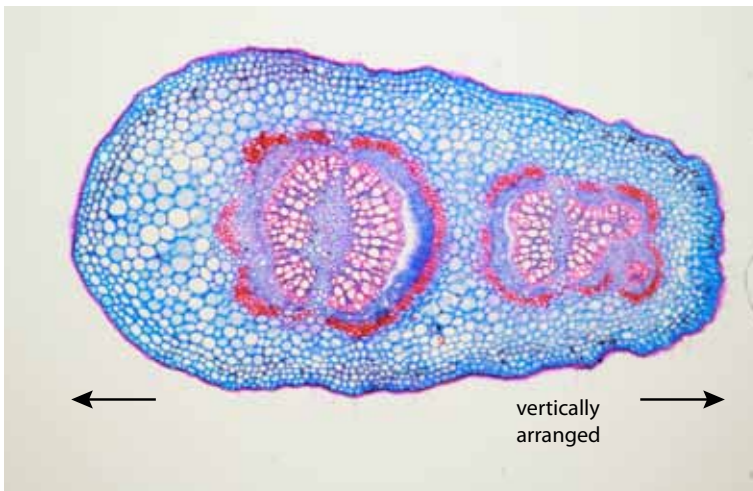


Fig. 3c Vertical extensions with several vascular bundles have a vertical form, *Populus sp.* (100x).

Pith shape varies in relation to the part of plant and between species. The variability is little in long shoots and fruit stalks. Circular and slightly polygonal forms are most frequent (Fig. 4a). If vascular bundles are large in the initial stage, the forms tend to be round, if they are small, they are rather polygonal. All fruit stalks in our dataset have a circular cross-section (Fig. 4a).

Special for shoots is the triangular pith of *Alnus* sp. and the slightly triangular form for *Fagus sylvatica* (Fig. 4c).

In petioles, the pith shape is mainly crescent (Fig. 4b). In a few cases, the pith in petioles is circular and not really different from those in shoots and fruit stalks.

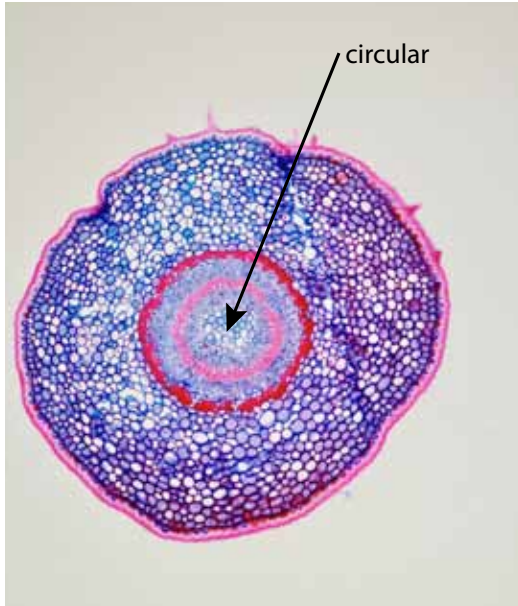


Fig. 4a Circular pith forms are most frequent in shoots. *Ilex aquifolium*, fruit stalk (100x).

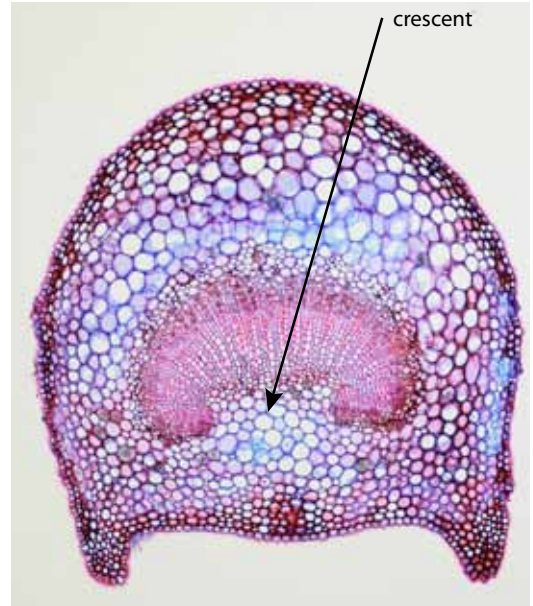


Fig. 4b Crescent pith forms are most frequent in petioles. *Euonymus europaeus* (100x).

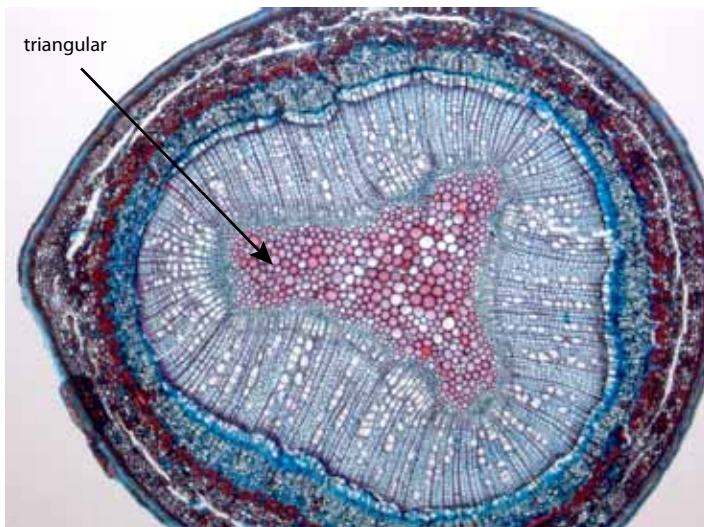


Fig. 4c Triangular forms exist only in shoots of *Alnus* sp. (100x).

The **arrangement and development of vascular bundles** vary up to the end of the vegetation period. Two types exist: (a) Solitary vascular bundles which persist, e.g. *Rubus fruticosus*, *Clematis alpina* (Fig. 5a,b). Most species with a circle of primarily isolated vascular bundles will be connected in later development stages (Fig. 5c). (b) Some few petioles contain vascular bundles within the pith, e.g. *Quercus sp.* (Fig. 5e). The central bundles can be round or radially elongated.

Connected vascular bundles with a lateral continuous latewood zone are present in most

shoots, fruit stalks and petioles of most species (Fig. 5c).

Isolated vascular bundles are mostly absent in shoots, e.g. in *Acer sp.* If present, they remain isolated in shoots of *Acer sp.* This type exists in fruit stalks and petioles with the exceptions of *Clematis vitalba*, *Rubus sp.* and *Rosa sp.*

Special types are petioles with round or crescent vascular bundles in the pith, e.g. *Aesculus sp.*, *Platanus sp.* and *Quercus sp.* (Fig. 5d,e).

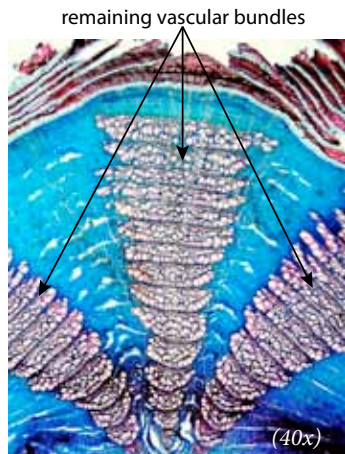


Fig. 5a

Fig. 5a,b Remaining vascular bundles occur in a few shoots and fruit stalks. They can be laterally separated by rays (*Clematis alpina*) (Fig. 5a) or form solitary internal bundles (*Rubus fruticosus*) (Fig. 5b).



Fig. 5b

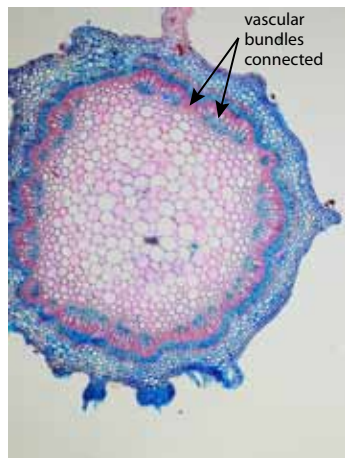


Fig. 5c Laterally connected vascular bundles are most frequent in shoots and fruit stalks. *Buddleya davidii* (100x).

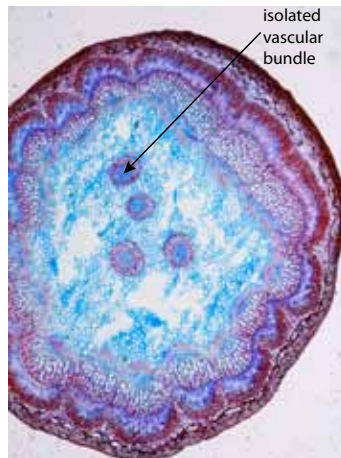


Fig. 5d Circular vascular bundles in the pith occur in petioles of a few species. *Aesculus hippocastanum* (100x).



Fig. 5e Crescent vascular bundles in the pith occur in petioles of a few species. *Quercus sp.* (100x).

Vessel diameter and probably also the size of the conductive area are related to shoots, fruit stalks and petioles. Most conductive are shoots (vessel diameter 20-40 μm). Vessels have to supply the whole assimilating system. Smaller are vessels in the petioles (vessel diameter 8-30 μm) because only the leaf area has to be supplied with water. Even smaller are vessels in fruit stalks (vessel diameter 8-15 μm) because the transpiration is reduced on fruits. Water is probably used mostly for fruit formation.

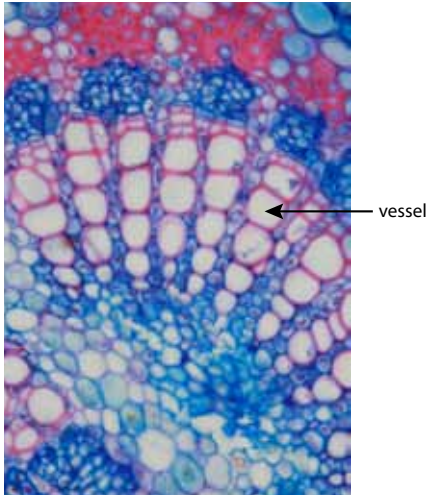


Fig. 6a Radially arranged vascular bundles occur in most shoots, fruit stalks and petioles. *Tilia tomentosa* (400x).

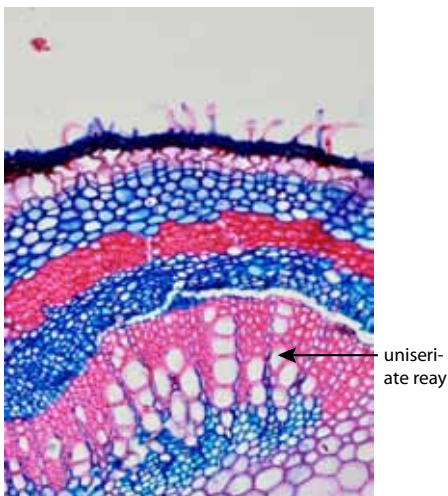


Fig. 7a Uniseriate rays are most common in shoots, fruit stalks and petioles. *Vitex agnus-castus* (400x).

Vessels in the primary stage of secondary growth in shoots, fruit stalks and petioles are mostly in radial rows (Fig. 6a), or they are indistinct (Fig. 6b) or rarely arranged.

Uniseriate rays are present in all shoots and petioles (Fig. 7a). They are missing only in fruit stalks of *Fagus sylvatica* and *Ilex aquifolium*. Multiseriate rays are present in those species where vascular bundles are not laterally connected (Fig. 7b).

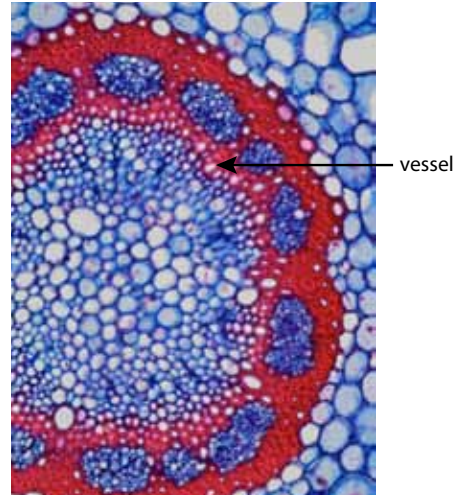


Fig. 6b Absent or irregularly distributed first vessels occur in a few species. *Fragaria vesca* (400x).

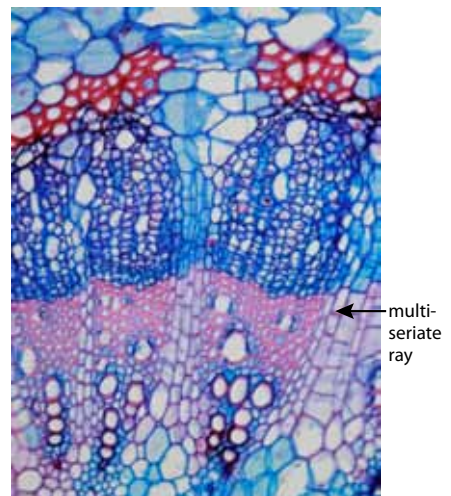


Fig. 7b Multiseriate rays occur in species with isolated vascular bundles. *Vitis vinifera* (400x).

Sclerenchymatic zones in the cortex occur in shoots, fruit stalks and petioles of most species of the whole taxonomic system. The omnipresent feature lets assume that sclerenchyma are in peduncles (annual shoot, fruit stalk, petiole) the major stabilization element.

The feature appears in continuous or discontinuous bands with different thickness and cellular composition (fibers, sclereids). Sclerenchyma in the cortex is missing only in petioles of *Ilex*

aquifolium. It is mostly difficult to locate the sclerenchyma. Most of it is located in the cortex and only few in the phloem (e.g. *Castanea sativa* and *Citrus sinensis*). Relationships between upright, horizontal and hanging fruits are not to recognize.

Here we present the variability in fruit stalks (Figs. 8a-d).

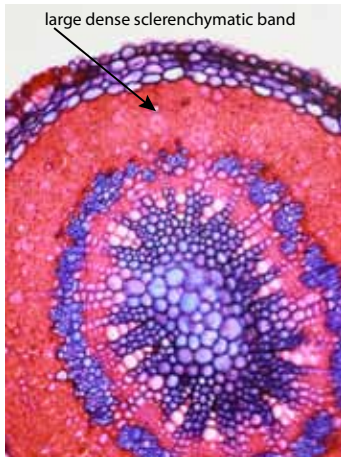


Fig. 8a Very large and dense, continuous sclerenchymatic belt in a vertically positioned fruit of *Celtis australis* (400x).

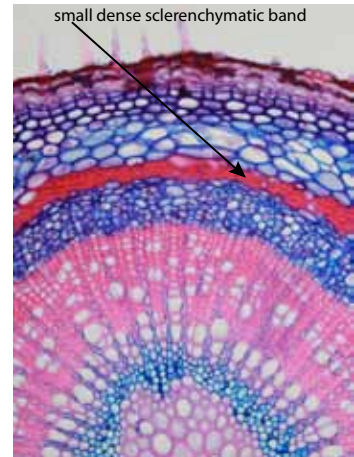


Fig. 8b Small dense, continuous sclerenchymatic belt in a hanging inflorescence with winged fruits of *Carpinus betulus* (400x).

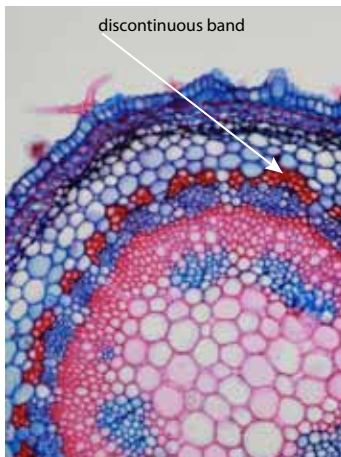


Fig. 8c Discontinuous sclerenchymatic belt in an upright fruit stalk of the herb *Malva moschata* (400x).

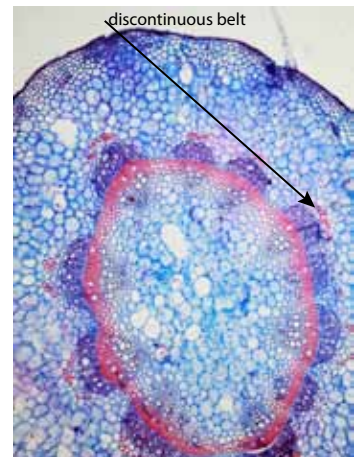


Fig. 8d Very small discontinuous sclerenchymatic belt in a hanging inflorescence of *Parthenocissus quinquefolius* (400x).

The **periderm** occurs in all shoots. Its occurrence is unpredictable in fruit stalks and petioles. It can be expected mainly in fruit stalks and petioles with larger diameters. Some species have a periderm around the fruit stalk or the petiole, some others only partially (Fig. 9).

Ducts are a taxonomically important feature. They are present in shoots, fruit stalks and petioles of *Cotinus coggygria*, *Eucalyptus* sp., *Myrtus communis*, *Pistacia lentiscus* and *Rhus typhina*. See monographic presentation.

Sclereids in the pith are rare. In our dataset they are present only in fruit stalks, e.g. in *Eucalyptus* sp. (Fig. 10).

Fibers in the xylem are mostly present in shoots, fruit stalks and petioles. It is often difficult to distinguish fibers from small vessels. Therefore we did not classify this feature.

Medullary phloem is a typical feature for Solanaceae. In our dataset is present in shoots, fruit stalks and petioles of *Solanum tuberosum*. See monographic presentation.

Medullary sheaths are difficult to define. It is clear when the cells differ in form from those in the pith and the initial zones of vascular bundles, e.g. in fruit stalks of *Alnus glutinosa*. The feature

is almost omnipresent if the term includes also un lignified zones. See Definition of fruit stalks.

Gelatinous fibers occur only in fruit stalks of *Frangula alnus*. See definition of fruit stalks.

Collenchyma: see definition of fruit stalks.

References

- Troll W (1964): Die Infloreszenzen; Band 1. Gustav Fischer, Stuttgart
- Troll W (1969): Die Infloreszenzen; Band 2, Teil 1. Gustav Fischer, Stuttgart
- Weberling F (1981): Morphologie der Blüten und Blütenstände. Ulmer Stuttgart
- Chang Liu, Jing Zhou, Keren Bracha-Drori, Shaul Yalovsky, Toshiro Ito, Hao Yu (2007): Development 134: 1901-1910; doi:10.1242/dev.003103

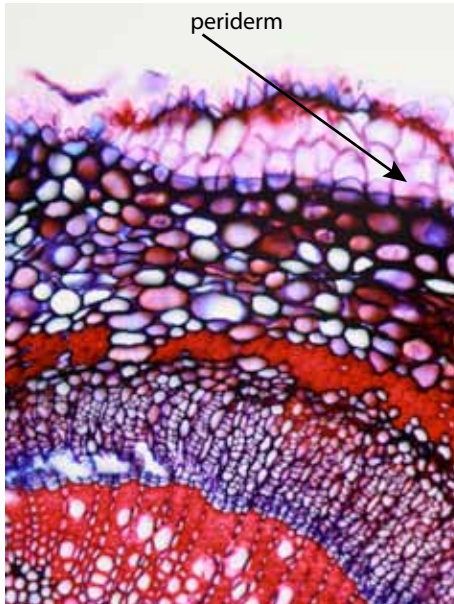


Fig. 9 Partial periderm in a fruit stalk of *Olea europaea* (400x).

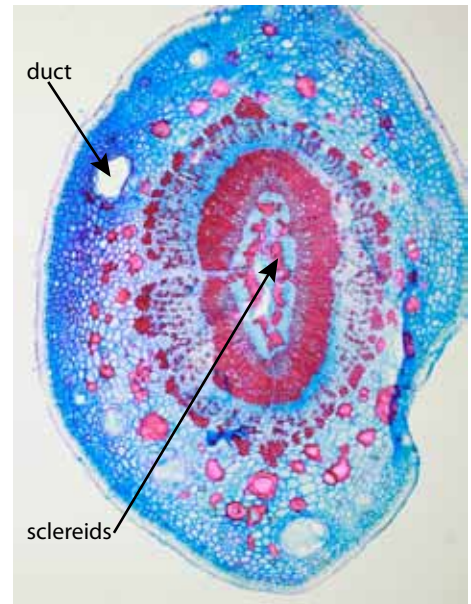


Fig. 10 Sclereids in the pith. Pith and cortex sclereids are products of primary growth (100x).

Definition and explanation of fruit stalk features

In the following, we describe fruit stalks by the morphological features of pith, xylem, phloem, cortex and periderm (see also Crivellaro and Schweingruber 2015). We concentrate on the proportions between these elements by which each species can be anatomically characterized.

External form and relations to morphology

The variability of external forms is minimal. Most fruit stalks are circular to slightly oval (e.g. *Fagus sylvatica*, Fig. 11). Some of the species have ribs which are mostly extensions of the cortex by parenchyma (e.g. *Buddleia davidii*, Fig. 12a) or collenchyma (e.g. *Daucus carota*, Fig. 12b). The form of xylem and phloem is normally not related to the external form (Fig. 11). The external form is usually typical for single species (*Sambucus nigra*, Fig. 13; *Berberis vulgaris*, Fig. 14; *Viburnum opulus*, Fig. 15). The circular form can be explained by the fact that inflorescences, in this case fruit stalks, are axial elongations of circular twigs.

Inflorescences show a great variability, which is also expressed in various characters of fruit stalks. The dimensions of stalks greatly vary (Weberling 1981). The diameters of the analyzed species are documented in the monographic

chapter. Dominant are diameters of 1 to 2 mm. Very thin stalks with diameters between 0.5 and 0.8 mm (e.g. *Berberis vulgaris*) or very thick stalks with diameters between 4 and 5 mm (e.g. *Aesculus sp.*, *Castanea sp.*) rarely occur.

The length of stalks varies between 20 cm (e.g. *Platanus sp.*) and 1 mm (e.g. *Cydonia sp.*, *Castanea sp.*). Extremely variable are the positions on twigs. Some are upright, some hanging, and many are in a horizontal position. Also variable is the weight of the fruits, from below 1 g (e.g. *Loiseleuria sp.*, *Berberis sp.*) to above 100 g (e.g. *Prunus domestica*, *Malus sylvestris*). Not less variable are the forms of fruits and their distribution mechanisms, e.g. heavy fruits (*Olea sp.*) or light, winged fruits (*Acer sp.*, *Tilia sp.*).

Many taxonomically different plants have exactly the same external characters. Therefore it is impossible to relate the morphology to anatomical characteristics that are relevant for stability, conduction or storage. However, in contrast to purely morphological features, the present material suggests that most anatomical fruit stalk features are taxonomically significant.



Fig. 11 *Fagus sylvatica*, circular (100x).

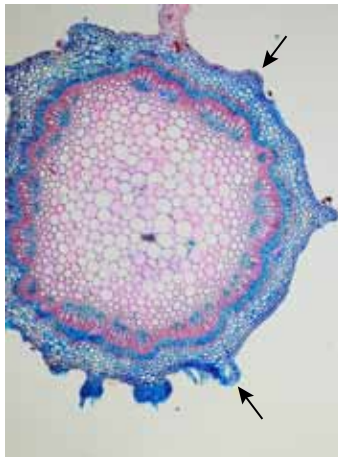


Fig. 12a *Buddleia davidii*, circular, wavy (100x).

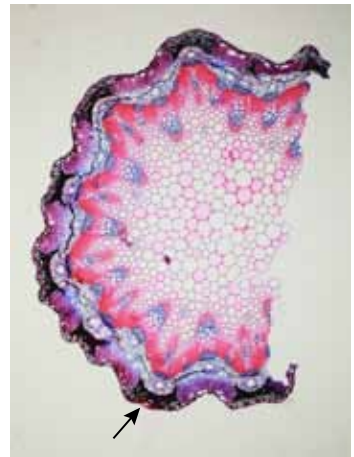


Fig. 12b *Daucus carota*, circular, wavy (100x).

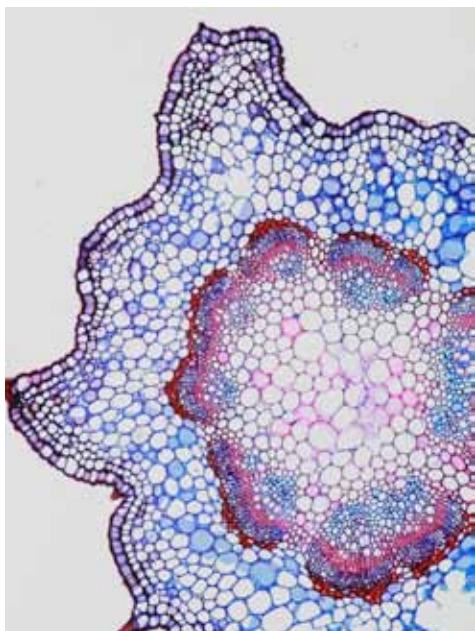


Fig. 13 *Sambucus nigra*, polygonal (100x).

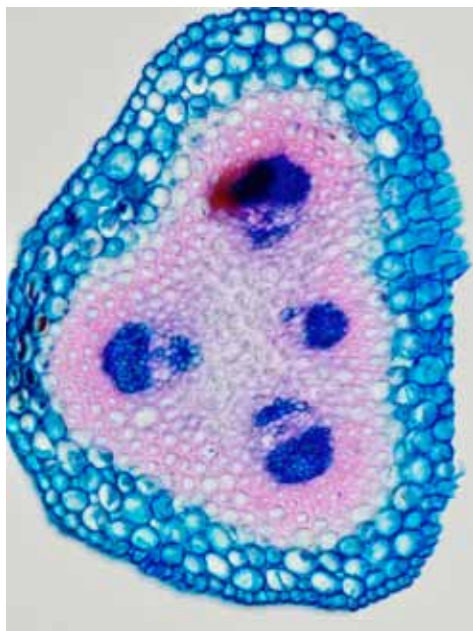


Fig. 14 *Berberis vulgaris*, triangular, (400x).

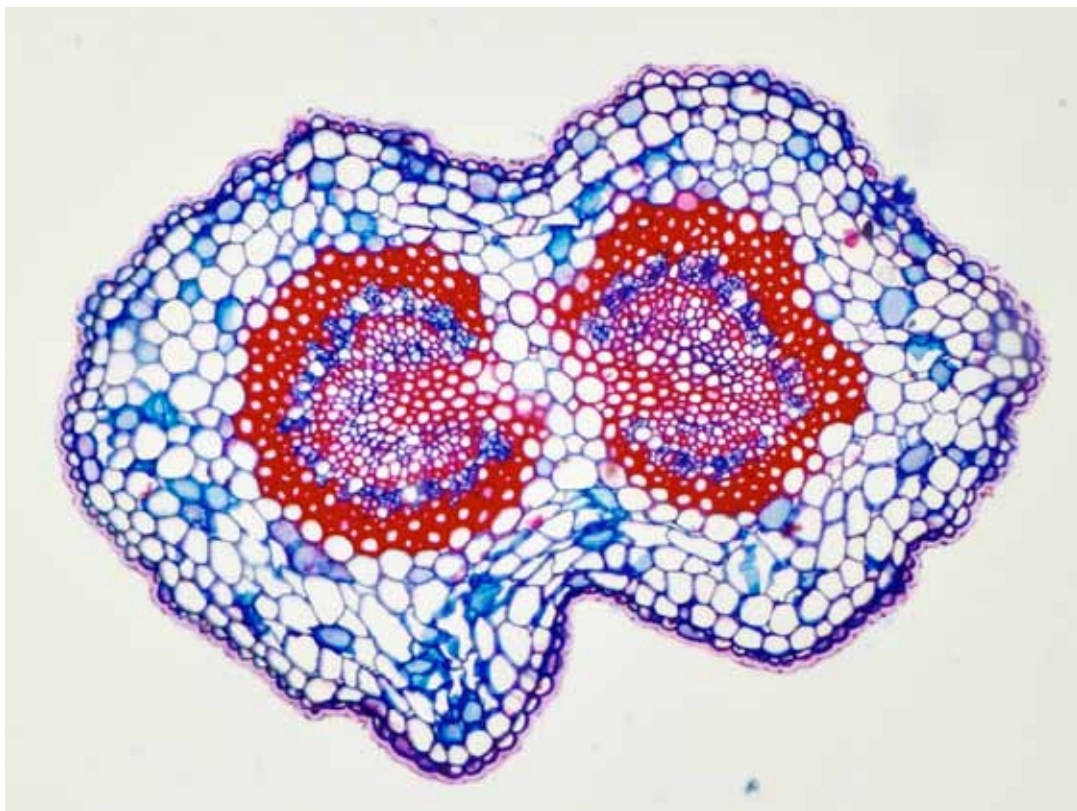


Fig. 15 *Viburnum opulus*, vertical combination of stems (100x).

Pith shape

External pith borders are mainly determined by the proto- and metaxylem arrangement of vascular bundles. If the bundles are large and flat, the pith is rather round, if they are small, triangular and/or separated from each other, the pith is rather polygonal.

Dominant are round (e.g. *Ilex aquifolium*, Fig. 16) or oval and polygonal forms (e.g. *Laburnum anagyroides*, Fig. 17). Polygonality can be expressed by wave-like structures or, as another

extreme, by a star-like form (e.g. *Chamaecyparis* sp.). Triagonal is only *Koelreutheria* sp. (Fig. 18).

The round pith of some few species is surrounded by a medullary sheath, which is a lignified or unlignified fiber-less parenchymatic zone (e.g. *Alnus glutinosa*, *Capparis orientalis*, Figs. 19,20).

Medullary phloem surrounds the pith of Solanaceae (Fig. 21).

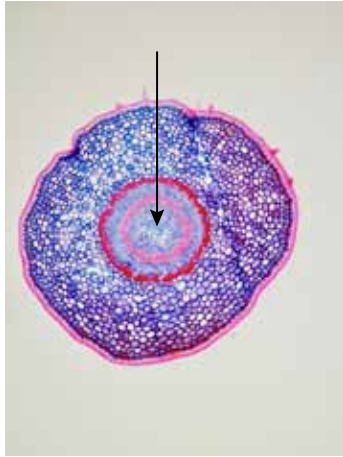


Fig. 16 *Ilex aquifolium*, circular (100x).

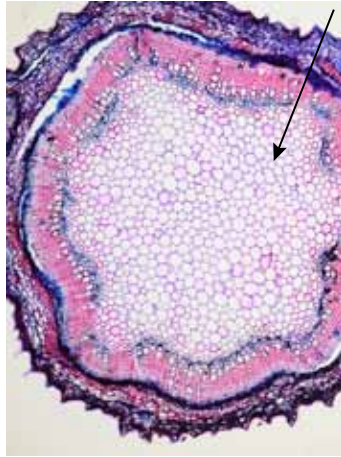


Fig. 17 *Laburnum anagyroides*, polygonal (100x).

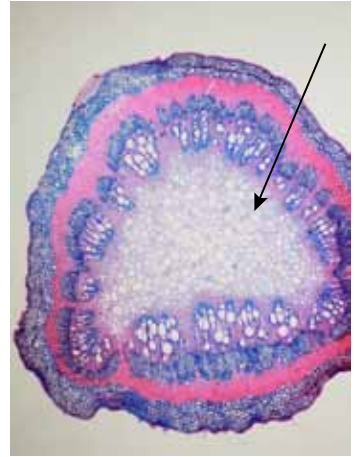


Fig. 18 *Koelreutheria paniculata*, triagonal (100x).



Fig. 19 *Alnus glutinosa*, medullary sheath lignified (400x).

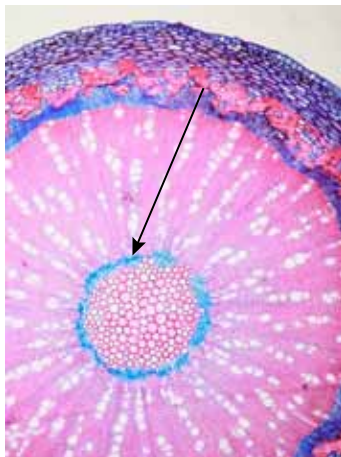


Fig. 20 *Capparis orientalis*, medullary sheath unlignified (100x).

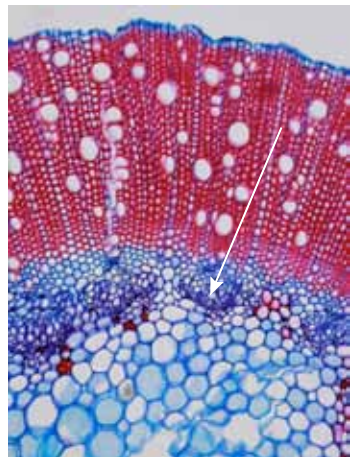


Fig. 21 *Solanum lycopersicum*, medullary phloem.

Pith cavity

The central part of the fruit stalks of very few species is empty (e.g. *Mahonia aquifolium*, *Coronilla* sp., Fig. 22). During the radial expansion of the stalk, cell wall growth of the central parts cannot follow the expansion. Thus, these cells burst and the pith empties out.

Cell composition of the pith can be homocellular, with only uniform parenchyma cells of equal

size and small intercellulares (e.g. *Malva moschata*, Fig. 23).

Cell composition of the pith can be heterocellular, with parenchyma cells of different size. Between large cells, small and mostly round cells occur (e.g. *Rubus* sp., *Rosa* sp., Fig. 24). This feature seems to be characteristic for these two genera.



Fig. 22 *Mahonia aquifolium*, central pith cavy (100x).

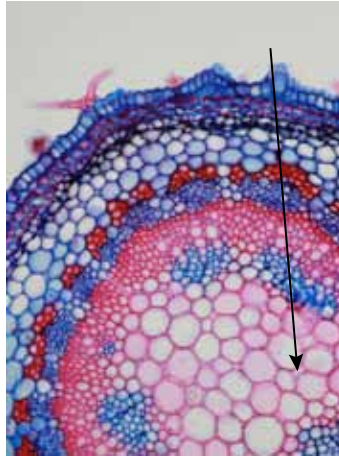


Fig. 23 *Malva moschata*, small intercellulares (400x).

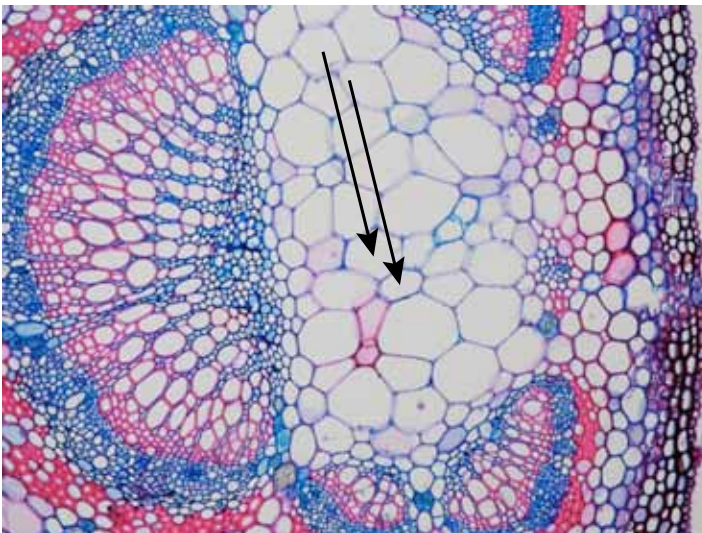


Fig. 24 *Rubus fruticosus*, small and large pith cells (400x).

Pith cell composition heterocellular, with different cell types

Fig. 25 shows a heterocellular pith which contains groups of sclereids (*Eucalyptus* sp.). They get formed when pith cells are still living and the plant gets under mechanical stress. This feature has been observed only in *Eucalyptus* sp., *Malus* sp. and *Pyrus* sp.

Fig. 26 shows a heterocellular pith which contains fibers. This feature occurs only in *Viburnum opulus*.

Fig. 27 shows a heterocellular pith and cells with some contents (*Tilia platyphyllos*). The heter-

ogenous features show dark staining substances as tannins or gums which are formed mostly after injuring. It is probably an expression of stress without taxonomic significance.

Fig. 28 shows a heterocellular pith with ducts, laticifers or just mucilage. Ducts are characterized by surrounding cells (Apiaceae, e.g. *Bupleurum* sp., *Daucus* sp. and others). Types with laticifers (ducts without surrounding excretion cells) have not been observed, but we expect them in some Euphorbiaceae. Species with mucilage exist here only in *Tilia* sp.

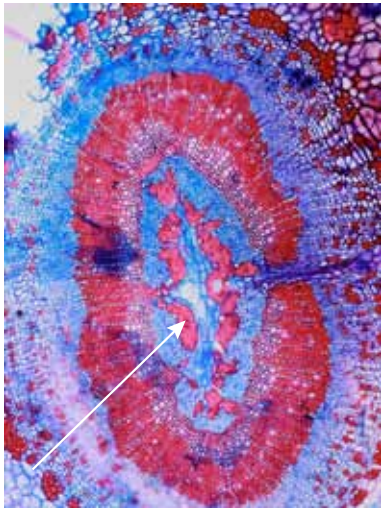


Fig. 25 *Eucalyptus* sp., sclerenchyma (200x).

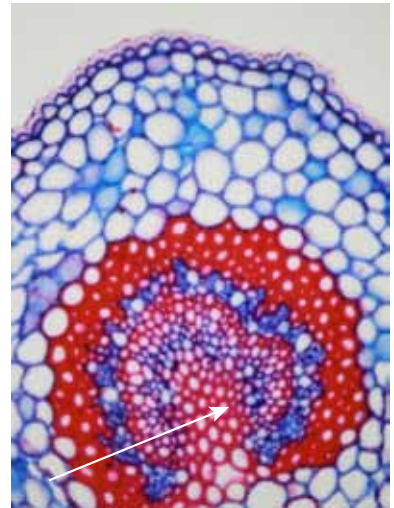


Fig. 26 *Viburnum opulus*, fibers (400x).

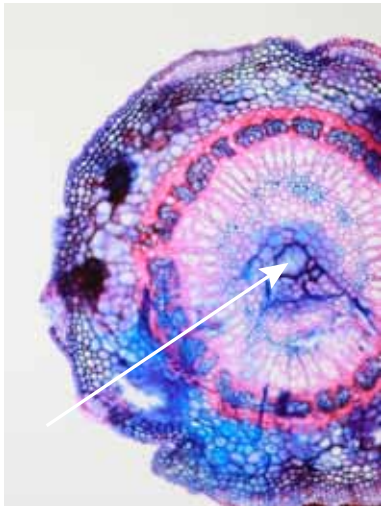


Fig. 27 *Tilia platyphyllos*, laticifer (100x).

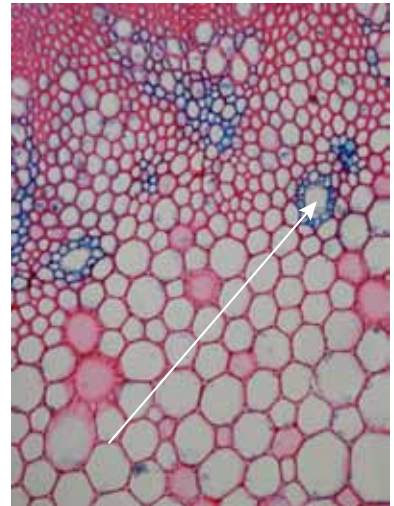


Fig. 28 *Bupleurum fruticosum*, duct (400x).

Pith with vascular bundles

This feature is characteristic for a few species. Collateral closed vascular bundles are common in monocots (e.g. *Lilium martagon*, Fig. 29). Collateral open vascular bundles are characteristic for *Platanus* sp. (Fig. 30). Collateral open and concentric vascular bundles occur in *Tilia* sp. (Fig. 31).

Pith with mineral inclusions (see cortex)

The presence of crystals in the pith is rarely species-specific. In the present dataset, prismatic crystals occur always in *Tilia* sp. Since crystals are very frequent in the cortex, the phloem and the pith, we refer to crystals just by the cortex.

Pith cell arrangement

Species with a homocellular pith (only with parenchyma cells) can principally be divided into types with a uniform cell size from the center to the xylem/phloem complex (e.g. *Rubus caesius*, Fig. 32) and into types with gradually smaller cells from the center to periphery (e.g. *Vitex agnus-castus*, Fig. 33). Since the transition between the two types is confluent, the feature is not easy to recognize and classify. It is not clearly related to taxonomy.

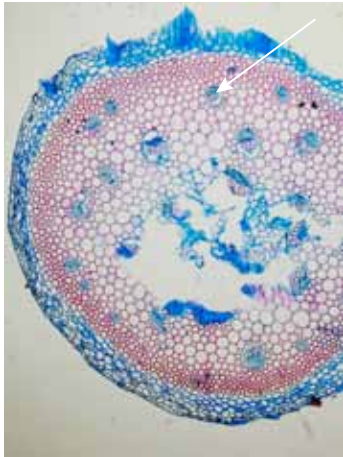


Fig. 29 *Lilium martagon*, closed vascular bundle (100x).

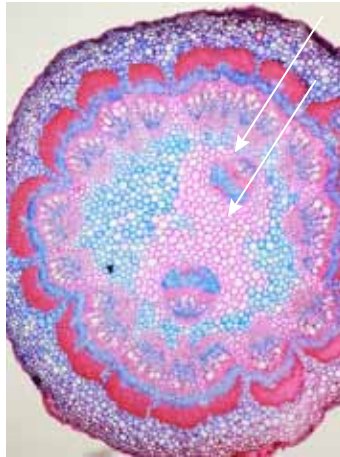


Fig. 30 *Platanus* sp., collateral open vascular bundle (100x).

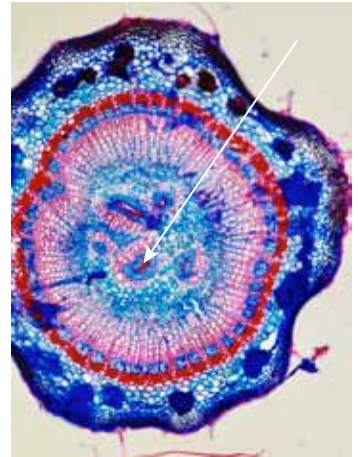


Fig. 31 *Tilia platyphyllos*, collateral open vascular bundle (100x).

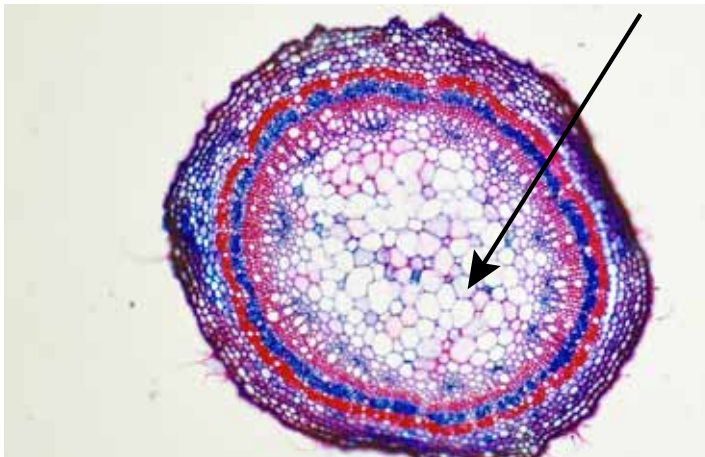


Fig. 32 *Rubus caesius*, uniform cells from center to periphery (100x).

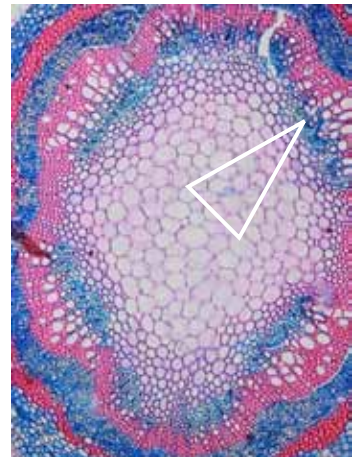


Fig. 33 *Vitex agnus-castus*, gradually smaller cells from center to periphery (200x).

Intercellulars

Intercellulars are very frequent in fruit stalks. Small triangular intercellulars occur mainly in piths with round parenchyma cells (e.g. *Medicago sativa*, Fig. 34). In a few species, larger irregular forms occur (e.g. *Trochodendron aralioides*, Fig. 35). The taxonomic and ecological significance is not clear.

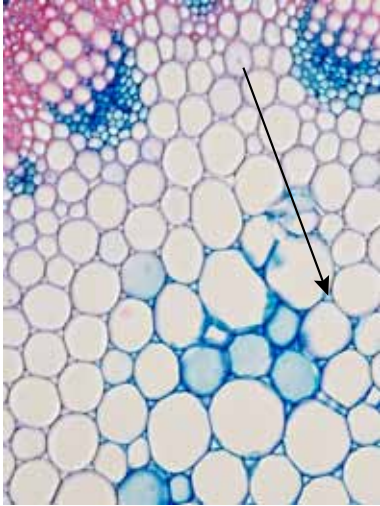


Fig. 34 *Medicago sativa*, small intercellulars (400x).

Parenchyma cell shape

Circular forms are most frequent (e.g. *Malva moschata*, Fig. 36). The form is mostly related to fairly thick-walled cells. Angular forms (e.g. *Rubus idaeus*, Fig. 37) are also frequent but mainly related to types with thin-walled cells.

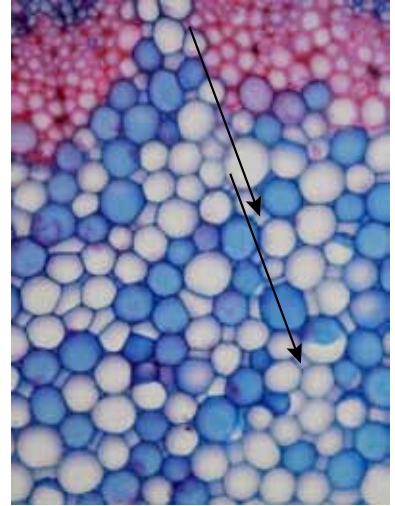


Fig. 35 *Trochodendron aralioides*, large intercellulars (400x).

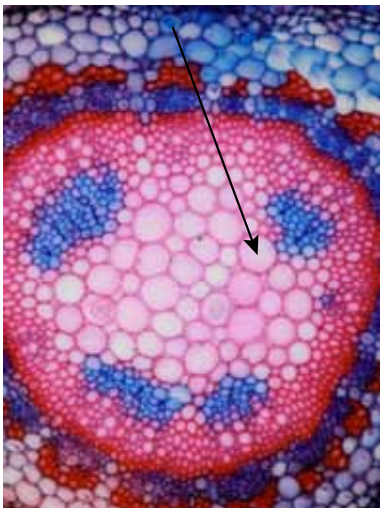


Fig. 36 *Malva moschata*, round parenchyma cells (400x).

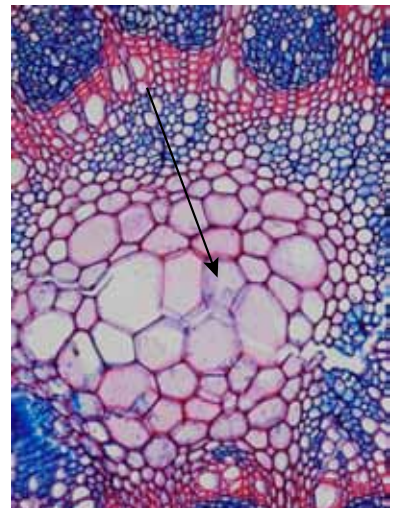


Fig. 37 *Rubus idaeus*, angular parenchyma cells.

Thickness of parenchyma cell walls

All transitions occur between types with very thin-walled (e.g. *Prunus padus*, Fig. 38), thin-walled and thick-walled cells (e.g. *Sorbus aria*, Fig. 39). Cell wall thickness is not related to lignification.

Lignification of parenchyma cells

Principally central cells are either lignified (e.g. *Fagus sylvatica*, Fig. 40) or not lignified (e.g. *Prunus padus*, Fig. 41). The difference can only be recognized on double stained slides. Lignification of pith cells is probably species-relevant.

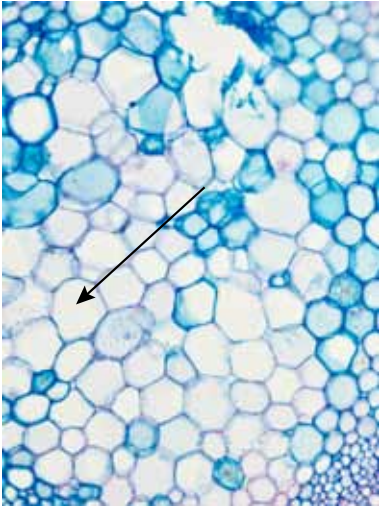


Fig. 38 *Prunus padus*, very thin-walled parenchyma cells (400x).

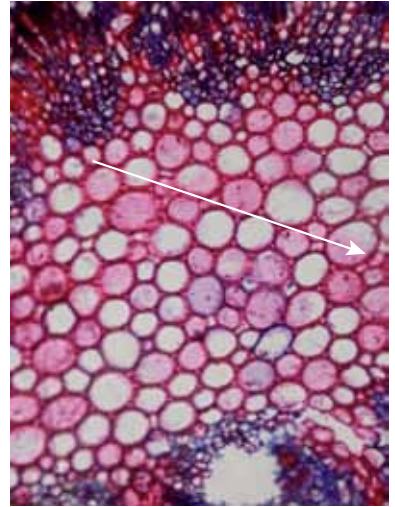


Fig. 39 *Sorbus aria*, thin- to thick-walled parenchyma cells (400x).

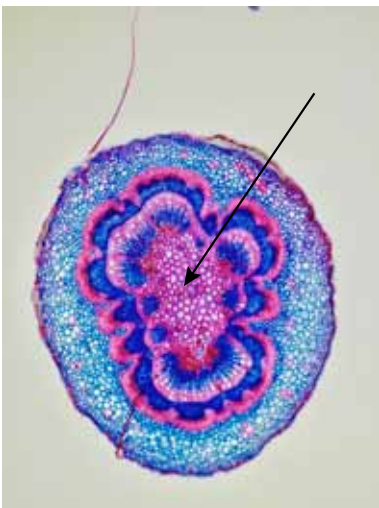


Fig. 40 *Fagus sylvatica*, pith lignified (100x).

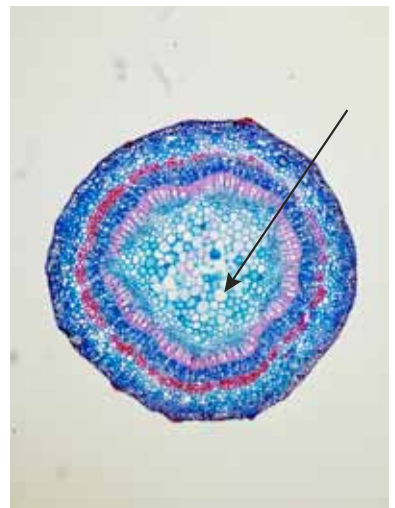


Fig. 41 *Prunus padus*, pith not lignified (100x).

Xylem first ring

Figs. 42-49 show different types of vascular bundles in fruit stalks. Our dataset contains collateral closed (e.g. *Lilium martagon*, Fig. 42), collateral open (e.g. *Platanus x acerifolia*, Fig. 43) and bi-collateral open vascular bundles (e.g. *Cucumis melo*, Fig. 44).

Collateral closed types are characteristic for monocots. Collateral open types are specific for most dicots. Bicollateral open types are characteristic for Cucurbitaceae (dicots).

Collateral open types have at least in a juvenile stage an active cambium which allows secondary radial growth. Its longevity is always limited to one vegetation period.

The lignification of the proto- and metaxylem of vascular bundles and initial stages of secondary growth varies. Most frequent are types with non-lignified proto- and metaxylem zone (e.g. *Robinia pseudoacacia*, Fig. 45). Such types can easily be recognized (see also Fig. 42). The proto- and metaxylem zone is rarely lignified (e.g. *Fragaria vesca*, Fig. 46). Initial zones of vascular bundles can be small (e.g. *Vitis vinifera*, Fig. 47), large (e.g. *Laburnum anagyroides*, Fig. 48), or they are diffuse and not to recognize (e.g. *Carpinus betulus*, Fig. 49).

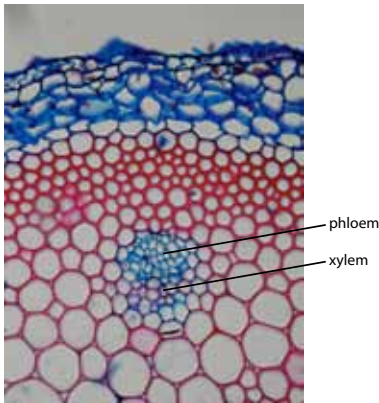


Fig. 42 *Lilium martagon*, collateral closed vascular bundles (400x).

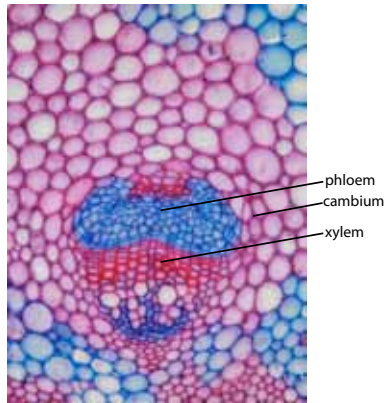


Fig. 43 *Platanus x acerifolia*, collateral open vascular bundles (400x).

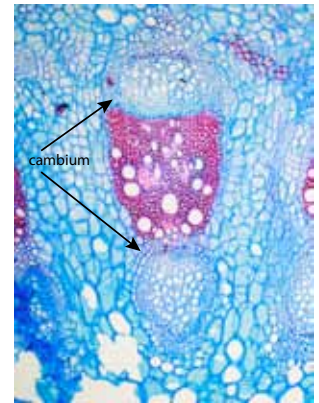


Fig. 44 *Cucumis melo*, bicollateral vascular bundles (400x).

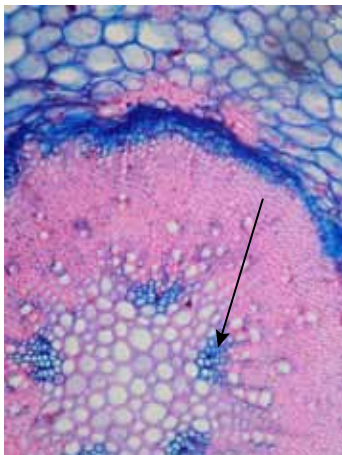


Fig. 45 *Robinia pseudoacacia*, not lignified protoxylem (400x).

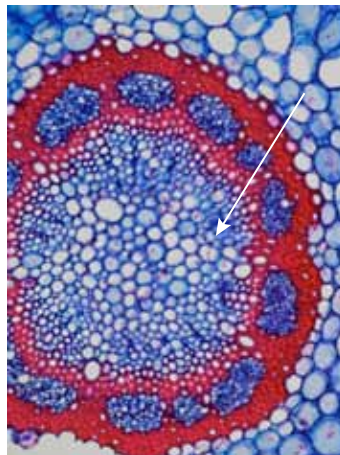


Fig. 46 *Fragaria vesca*, not lignified protoxylem (400x).

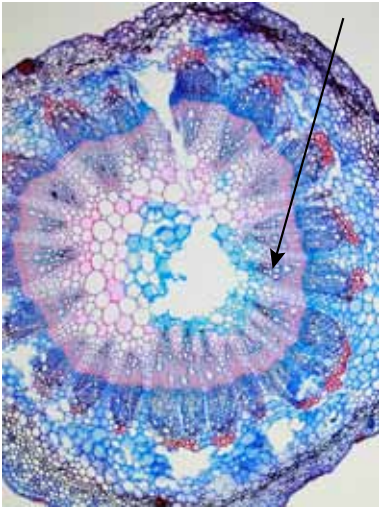


Fig. 47 *Vitis vinifera*, small vascular bundles (100x).

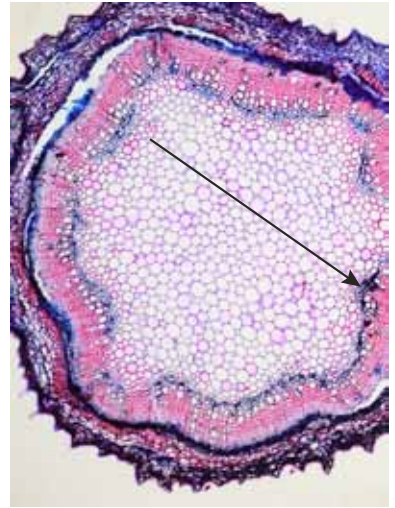


Fig. 48 *Laburnum anagyroides*, large vascular bundles (100x).

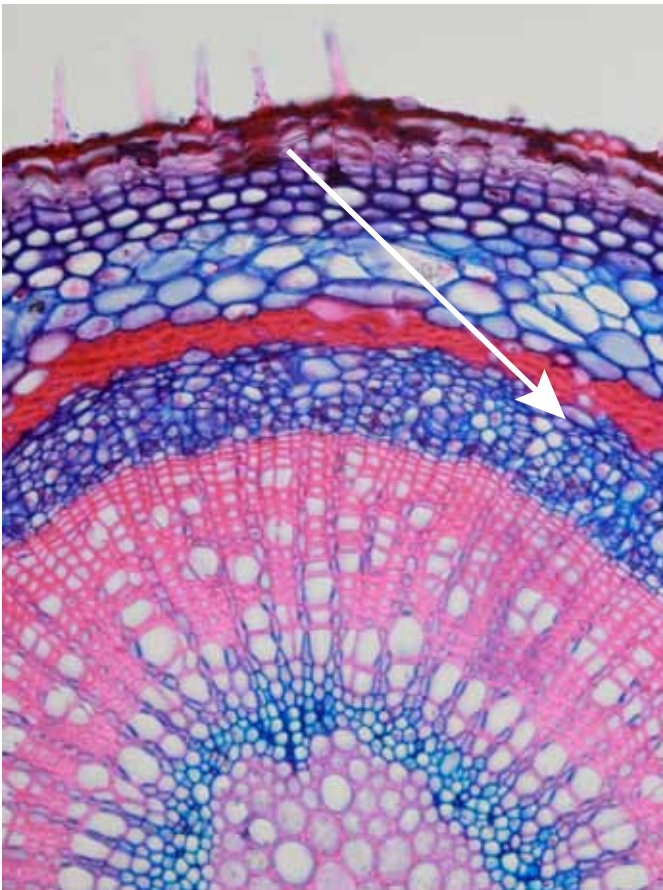


Fig. 49 *Carpinus betulus*, indistinct vascular bundles (400x).

Number of vascular bundles around the pith

The frequency of vascular bundles around the pith varies. Fairly rare are types with less than 6 bundles (e.g. *Malva moschata*, Fig. 50). Most frequent are types with more than 6 bundles (e.g. *Rubus idaeus*, Fig. 51).

Vessel arrangement

Vessel arrangement in the xylem of fruit stalks is similar to that in the xylem of stems. Most frequent are types with vessels in short or longer radial rows (e.g. *Staphyllea pinnata*, Fig. 52).

Relatively rare at types with an irregular vessel distribution (e.g. *Geum reptans*, Fig. 53) or solitary vessels (e.g. *Robinia pseudoacacia*, Fig. 54).

Characteristics of the initial zone around the pith (initial xylem)

We found two forms of initial xylem. (1) The xylem starts with vascular bundle forms. Bundles remain isolated (e.g. *Cucumis melo*, Fig. 55) or are later laterally connected (see Fig. 51). (2) The xylem starts with a continuous band. Vascular bundles are absent or difficult to recognize (e.g. *Citrus sinensis*, Fig. 56; see also Fig. 49).

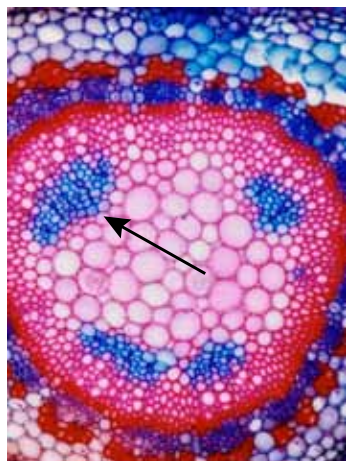


Fig. 50 *Malva moschata*, less than 6 vascular bundles (400x).

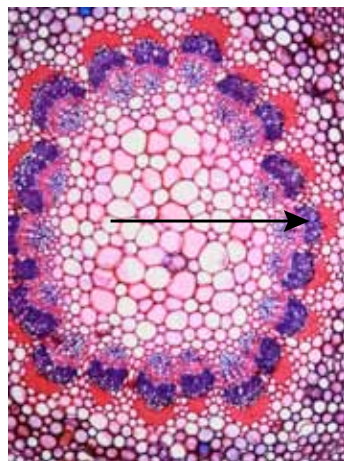


Fig. 51 *Rubus idaeus*, more than 6 vascular bundles (200x).

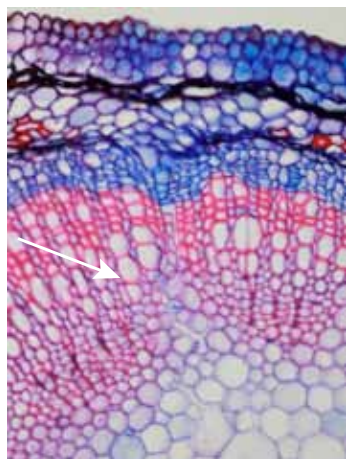


Fig. 52 *Staphyllea pinnata*, vessels radial (400x).

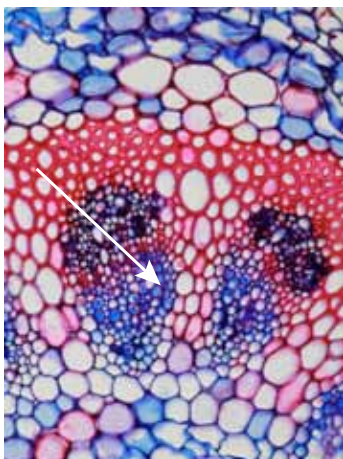


Fig. 53 *Geum reptans*, vessels irregular (400x).

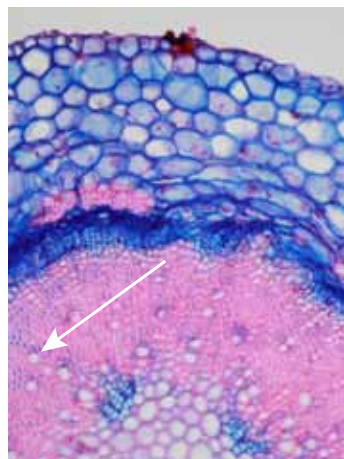


Fig. 54 *Robinia pseudoacacia*, vessels solitary (400x).

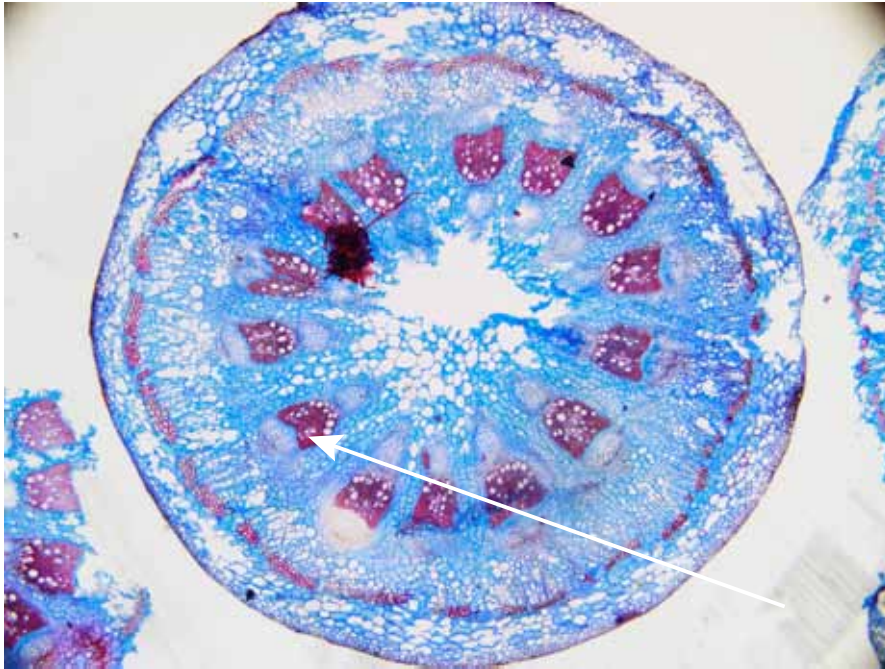


Fig. 55 *Cucumis melo*, isolated vascular bundles around the pith (100x).

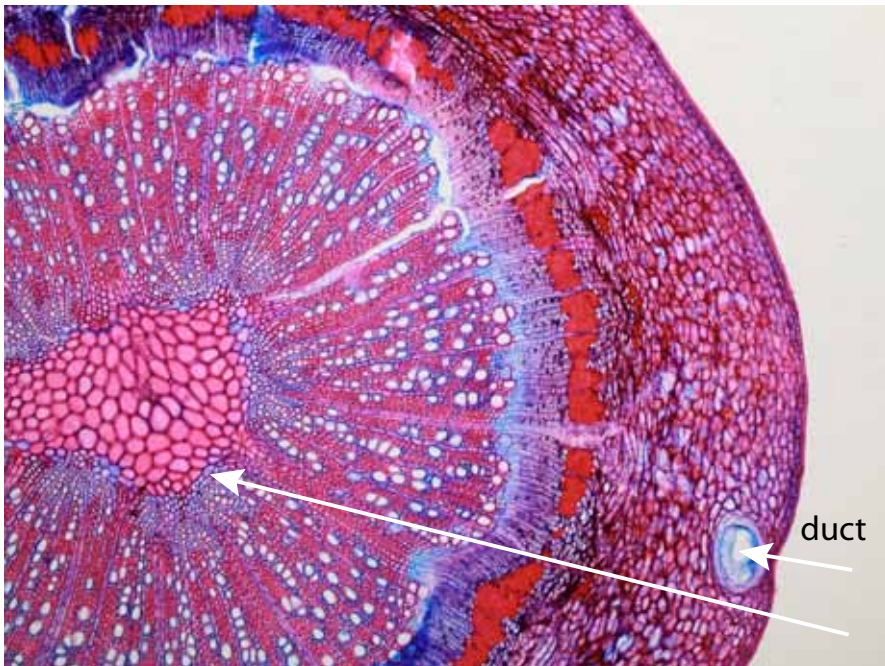


Fig. 56 *Citrus sinensis*, closed ring of vascular bundles around the pith (100x).

Acer campestre L.

Sapindaceae

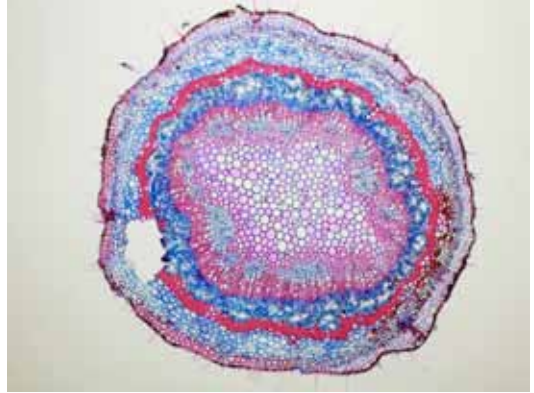
- Fruit stalk circular with a diameter of 1300 μm
- External width of the cortex at the longest side 150 μm
- External width of the phloem at the longest side 100 μm
- External width of the xylem at the longest side 110 μm
- Width of the pith at the longest side 800 μm

Xylem and phloem forming a continuous belt. Pith is surrounded by >10 single, large vascular bundles with an unligified initial zone. Vessels radially arranged. Largest vessels with tangential diameter of 15 μm . Xy-

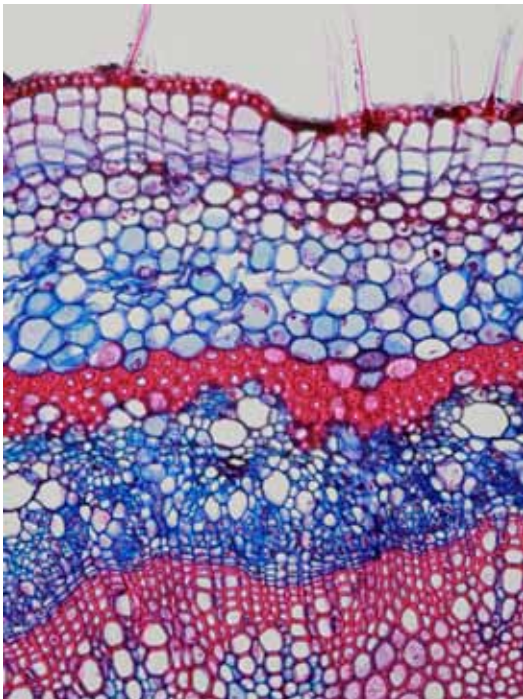
lem with a distinct latewood zone. Phloem in a rayless continuous belt with distinct, large cells. Cortex consists of an external, unligified parenchymatic zone and an internal belt of thick-walled, ligified fibers. Cortex and phloem with prismatic crystals and crystal druses. Periderm consists of 4-5 rectangular cells. Epidermis consists of small, thick-walled cells and long unicellular hairs. Pith polygonal, homocellular, with large and small round cells surrounded by a discontinuous medullary sheath.



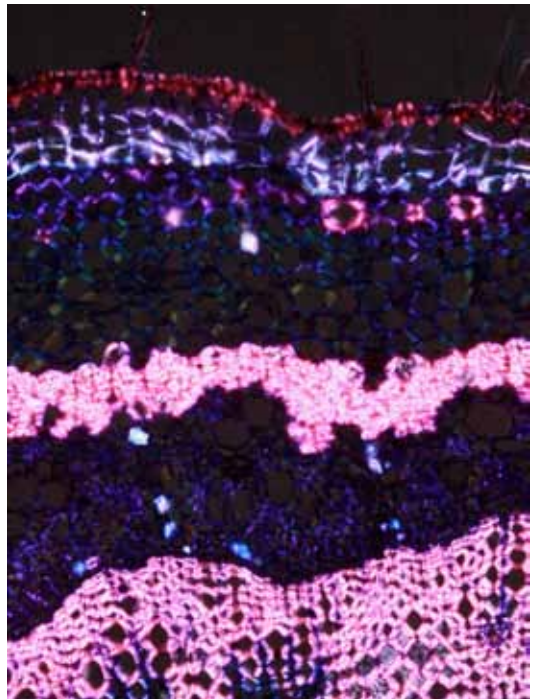
fruit



fruit stalk (100x)



fruit stalk (400x)



fruit stalk, polarized light (400x)

Acer pseudoplatanus L.

Sapindaceae

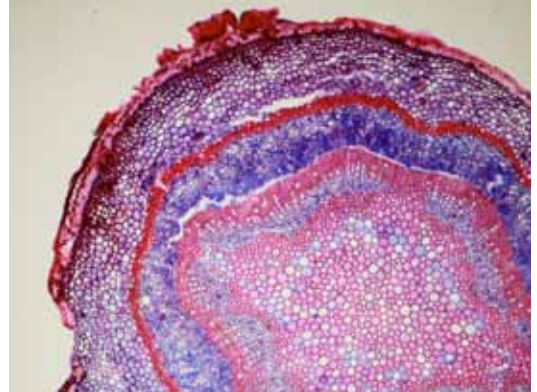
- Fruit stalk circular with a diameter of 2000 μm
- External width of the cortex at the longest side 200 μm
- External width of the phloem at the longest side 170 μm
- External width of the xylem at the longest side 130 μm
- Width of the pith at the longest side 800 μm

Xylem and phloem forming a continuous belt. Pith is surrounded by >10 single, large vascular bundles with an unligified initial zone. Vessels radially arranged. Largest vessels with tangential diameter of 15 μm . Xy-

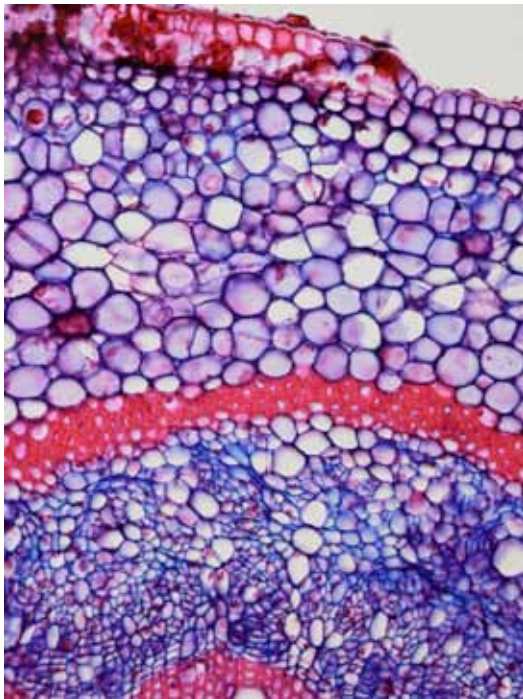
lem with a distinct latewood zone. Phloem in an almost rayless continuous belt with distinct, large cells. Cortex consists of an external, unligified parenchymatic zone and an internal belt of thick-walled, lignified fibers. Cortex and phloem without crystals. Discontinuous periderm consisting of 1-2 rectangular cells. Epidermis consists of thin- to thick-walled cells. Pith polygonal, homocellular, with large and small round cells surrounded by a medullary sheath.



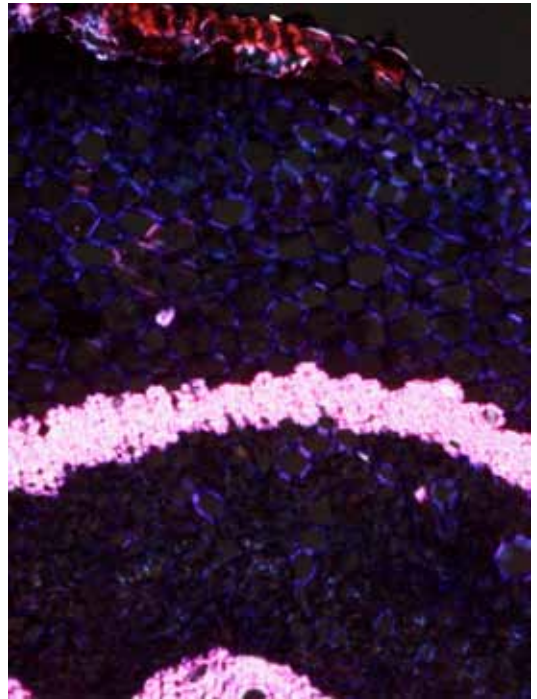
fruit



fruit stalk (100x)



fruit stalk (400x)



fruit stalk, polarized light (400x)