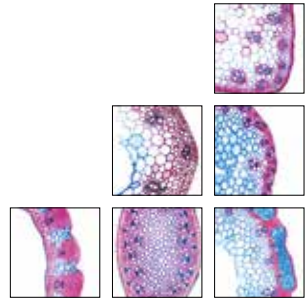


Anatomy of Grass Culms

Atlas of Central European Poaceae

Vol. 1



Fritz H. Schweingruber
Hugo Berger

Coverphoto
Avena sativa

Species on the cover

Top: *Botriochloa ischaemum*

Middle (left to right): *Bromus rigidus*, *Eragrostis minor*

Base (left to right): *Melica ciliata*, *Muhlenbergia schreberi*, *Poa nemoralis*

2. Auflage, 2018

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Content

1 Introduction	5
2 Basics	6
2.1 Material and herbarium vouchers	6
2.2 Anatomical preparation techniques	6
2.3 Ecological classification	7
3 Definition of anatomical features	8
3.1 Definition of the features	8
4 Monographic presentation	21
4.1 Structure of the monographic presentation	21
4.2 Characterisation of 301 species	22
5 Results	322
6 Frequency in relation to ecological factors	323
6.1 Relation to vegetation zones	323
6.2 Relation to humidity	325
6.3 Relation to culm length	327
7 Differences between genera	329
8 Conclusion	329
9 Acknowledgements	330
10 References	330
11 Index	331

1. Introduction

Flower stalks are the most obvious parts of grasses. They are part of the photosynthetic system and guarantee generative reproduction by exposing flowers to various permanent and extreme environment factors. Therefore they must be green, stiff and flexible. The response to these three characteristics is reflected in the anatomy of culms. Various culm sizes and forms however let assume that internal adaptations modify the general structure.

These basics of culm and leaf anatomical structures have been recognized and described more than 200 years ago (De Candolle 1813, Möbius 1937). Leaf structures were in focus since the beginning of detailed studies because they are taxonomically more significant than that of culms. (Metcalf 1960, Conert 1998). Metcalfe (1960) created an anatomical base for anatomical descriptions with his gigantic work. He characterized hundreds of species in detail. His ultimate goal was to underline and enlarge taxonomic classification with anatomical characteristics.

He was aware that the anatomy varies along culms and that ecological conditions can modify the structure. Based on his studies and own experiences with grasses from the Himalaya (Dolezal et al. 2017) we decided to enlarge his taxonomic approach with ecological questions and formulated the following concept:

- Presentation of anatomical structures of a large number of species within the family of Poaceae in the region of the Alps from sea level to the nival zone.
- Evaluation and presentation of major characteristic anatomical features.
- Relating all microscopic features to plant size, altitude and hydrological conditions and taxonomic origin.

The study is based on cross sections of culms. Each section of 300 Poaceae specimen from natural sites are located at internodes above leaf sheathes, approximately in the middle part of the total length of culms. Analyzed are all genera but only one specimen of each species, which occur in the alpine region (Aeschimann et al. 2004). The material includes species of all vegetation zones from 100 to 3000 m a.s.l. of all possible habitats from wet to arid, from calcifuge to acid and from nutrient rich to poor and salty sites. Respected are endemic and introduced species. Since anatomical variation is minimized by the constant internal location of the section within the culm, the whole set of analyzed material is comparable. Double staining gives additional information about the distribution of lignified and unligified parts.

With this sampling and preparation strategy we are able to describe general culm characteristics and modifications related to ecology and taxonomy.

Since Conert 1998 and Hubbard 1985 described morphological traits in details we present only a few general characteristics of each species. Temperature and precipitations indicator values, defined by (Aeschlimann et al. 2005) are the basis for anatomical comparisons. Plant names correspond with Aeschlimann et al. 2005.

We know, that the analysis of one specimen of each species gives an overlook but does not allow final conclusions.

The Poaceae atlas is part of a stem anatomical project of northern hemispheric seed plants (Schweingruber 1990, Schweingruber et al 2011 and 2013, Dolezal et al 2017).

2. Basics

2.1 Material for sections and herbarium vouchers

The present study is based exclusively on material from the United Herbaria Z+ZT of the University and ETH Zürich. The plants as well as the labels and the position of the section of each analyzed plant are documented in the herbarium specimen database of the United Herbaria Z+ZT. For finding the individual voucher please enter the corresponding barcode in the menu "Search database for Specimen" in the webportal <http://www.herbarien.uzh.ch/en/datenbanken/belegsuche.html>

2.2 Anatomical preparation techniques

Comparability of microstructures is a major goal of this atlas. Therefore all micro-photographs are based on recently prepared new microscopic slides. The detailed technique is described in by Gaertner and Schweingruber 2013. After moistening the material with water for a few hours, most cross sections have been made with razor blades under stereomicroscopic control. Very dense culms have been sectioned with a sliding microtome, type Reichert. All sections were stained with a one to one mixture of Safranin/Astrablue for a few minutes. Staining and dehydration with ethanol 96 %, absolute ethanol and xylene occurred directly on the glass. Permanent slides were embedded in Canada Balsam. Photographs have been made in transmitting, normal light with an Olympus BX51 microscope. Sections were documented by magnifications 100 and 400 times.

2.3 Ecological classification

Most important feature for grasses is the length of the culm. It is influenced by mechanical forces, altitude, vegetation zones and the humidity of the sites (Aeschimann et al 2005).

Vegetation zones are the dominating ecological factors. These factors have been classified as follows:

Length of the culm	0-15 cm 15-40 cm > 40 cm
Vegetation zones	alpine alpine/subalpine subalpine/mountain mountain/low altitude (colline) low altitude (colline)
Humidity of the site	very dry/dry dry/rather moist rather moist/moist moist wet

3. Definition of anatomical features

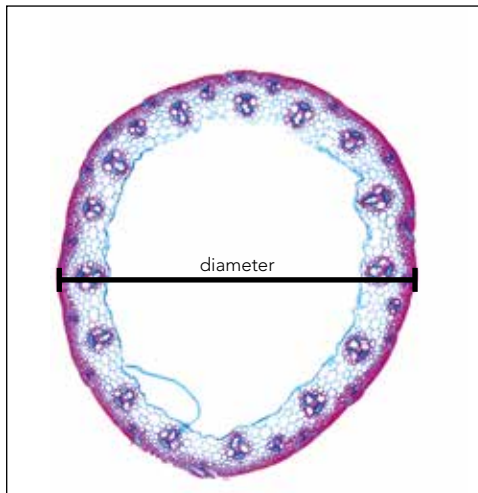
Anatomical key traits have primarily been defined by Metcalfe 1960. The present material however allowed a more specific classification and a standardization of features.

The anatomical key relies on the main structure of culms. The majority of culms are tubular. The periphery consists of an epidermis with stomata and a subepidermal part of unlignified chlorenchyma (parenchyma containing chloroplasts) a layer of lignified sclerenchyma and a thin-walled parenchyma. Collateral closed vascular bundles are embedded in the parenchymatic and fibrous part. The key contains 15 anatomical characteristics which are defined by 44 different anatomical features. That is the basis for statistical analyses. To describe these different anatomic features we used a standardized wording.

The feature numbers correspond with those of a key in preparation for all monocots of the temperate zones.

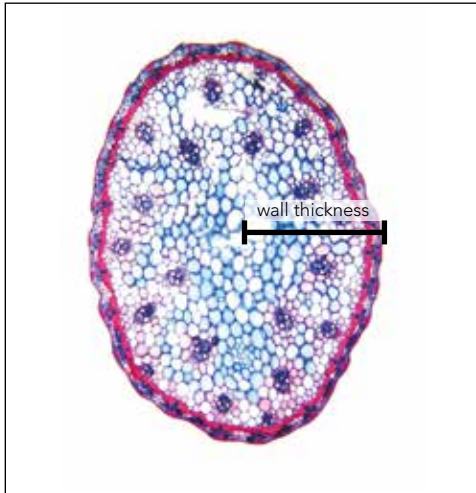
3.1 Definition of the features

Culm-diameter

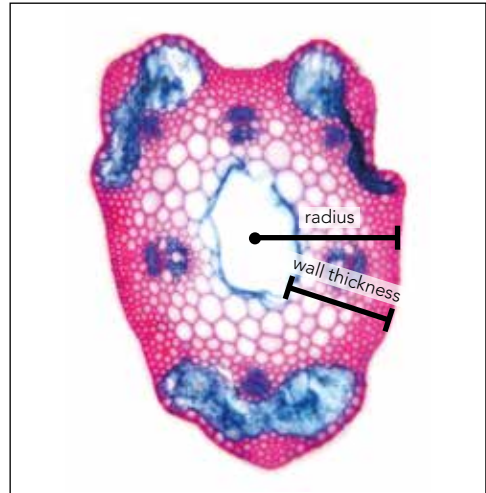


- 4a** Culm-diameter < 0.5 mm
- 4b** Culm-diameter 0.5-1 mm
- 5** Culm-diameter 1-2 mm
- 6** Culm-diameter 2-5 mm
- 7** Culm-diameter 5-10 mm

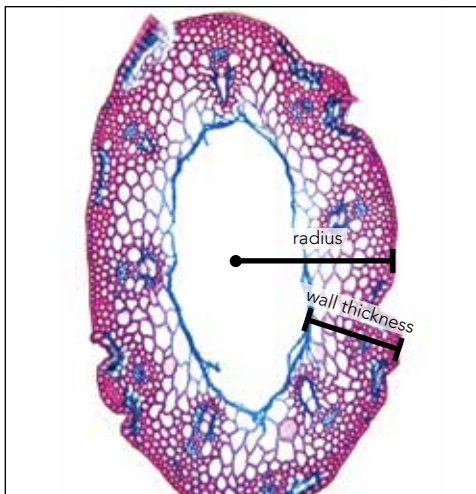
Culm-radius in relation to culm-wall



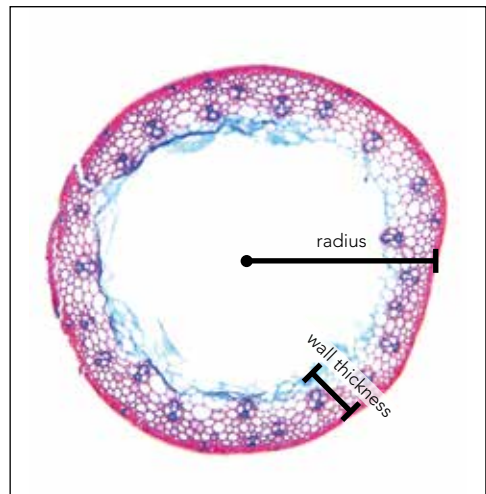
9a Center full, radius of culm in relation to wall thickness 1:1.



9b Wall very large, radius of culm in relation to wall thickness approximately 1:0.75.

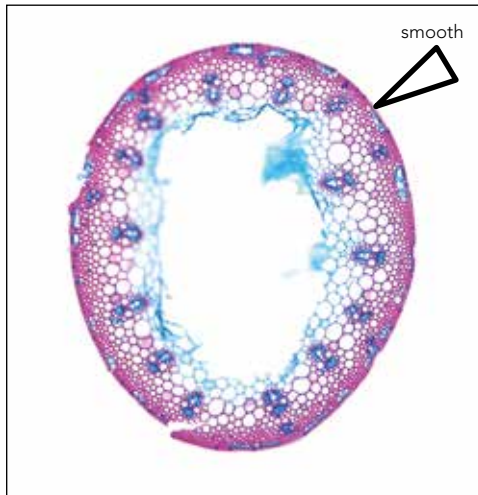


9c Wall large, radius of culm in relation to wall thickness approximately 1:0.5.

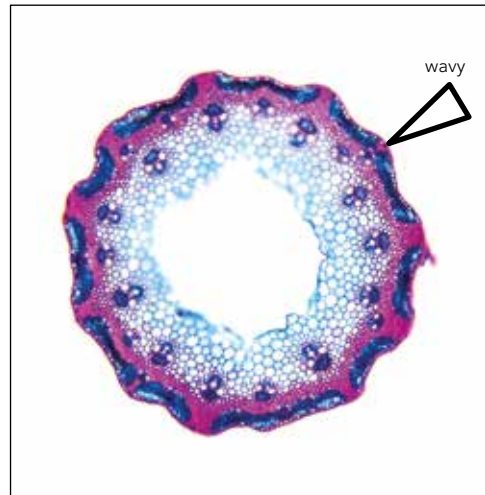


9d Wall thin, radius of culm in relation to wall thickness approximately 1:0.25 or < 0.25.

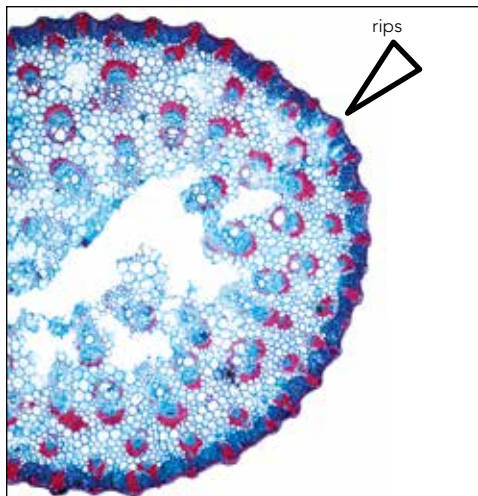
Form of outline



10 Outline circular with a smooth surface.

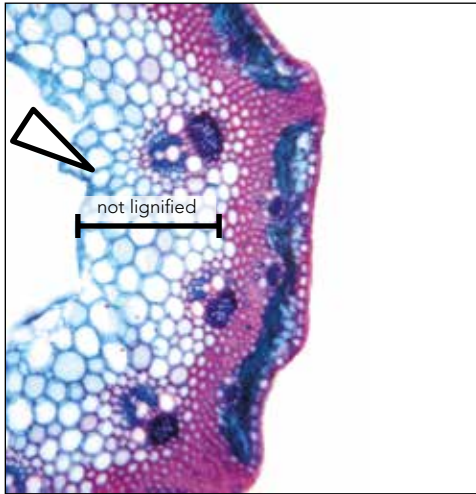


11 Outline circular wavy.

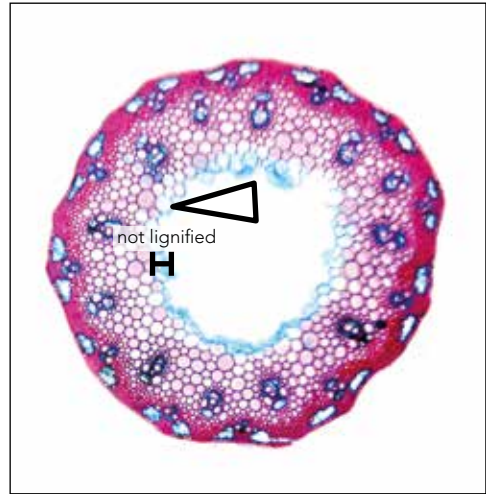


12 Outline circular, with rips.

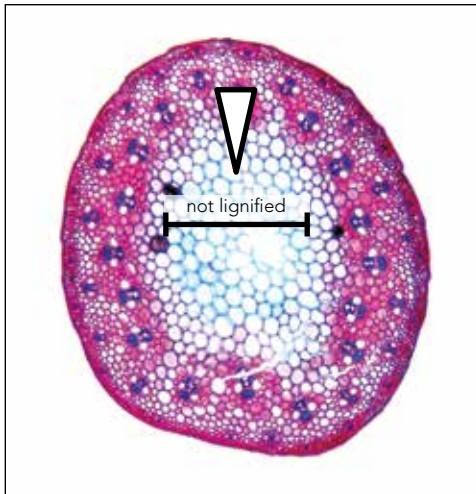
Construction of culm center



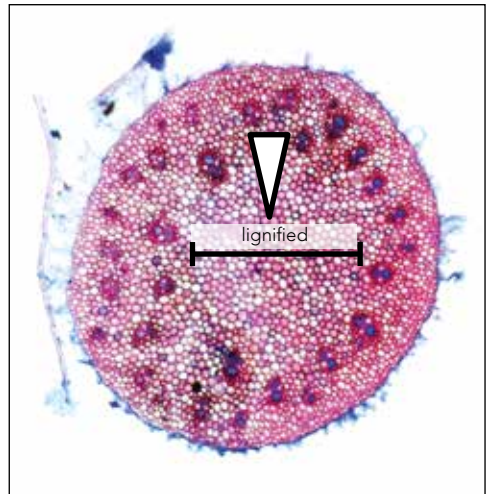
19a Culm-center hollow and surrounded by many large thin-walled, not lignified cells.



19b Culm-center hollow and surrounded by a few thin-walled, not lignified cells.

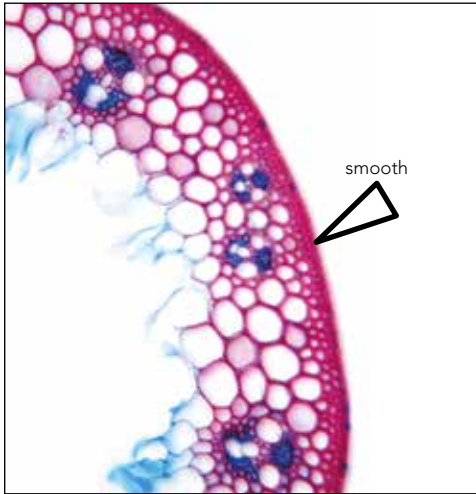


20a Culm-center full, containing unligified cells.

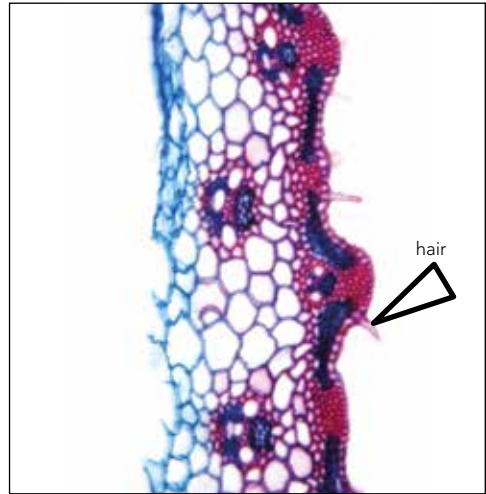


20b Culm-center full, containing lignified cells.

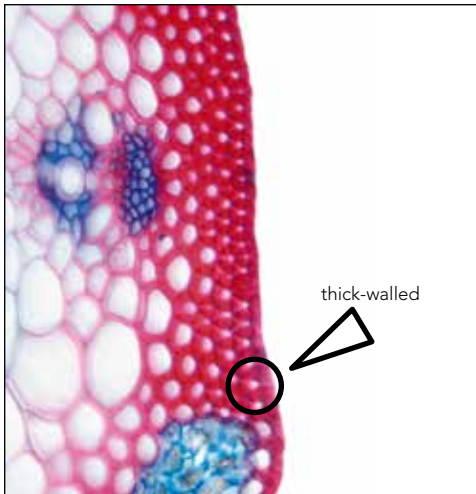
Epidermis



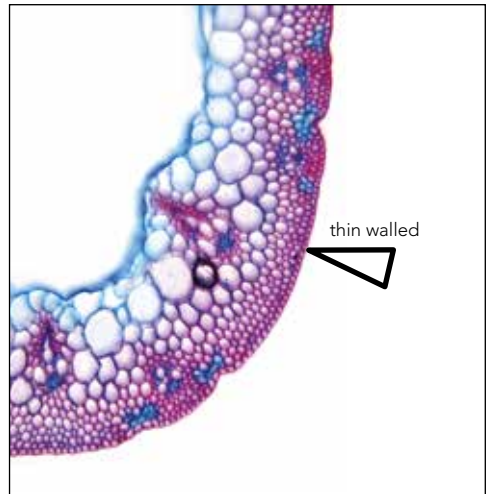
30 Epidermis smooth.



32 Epidermis with hairs.

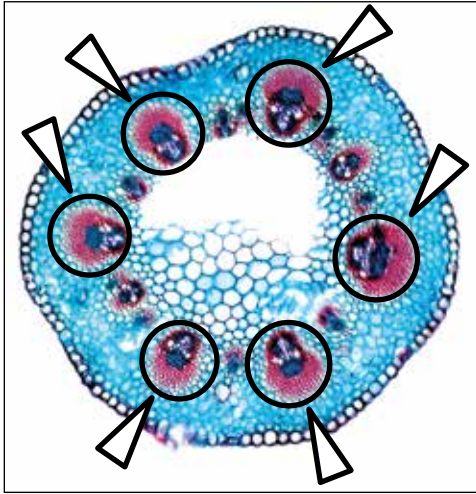


36b Epidermis-cells thick-walled all around.

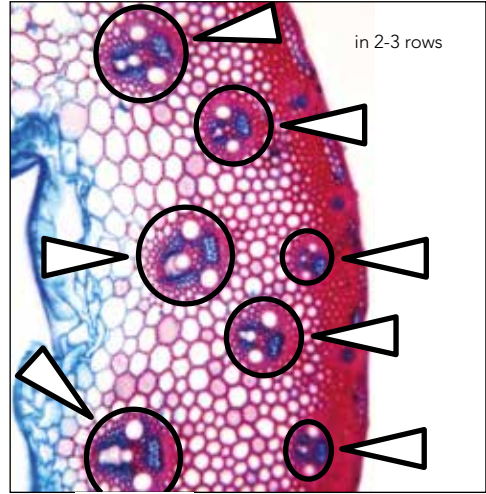


36c Epidermis-cells thin-walled all around. Corresponds with feature 34 in Vol. III + IV.

Arrangement of large vascular bundles in uniform stems

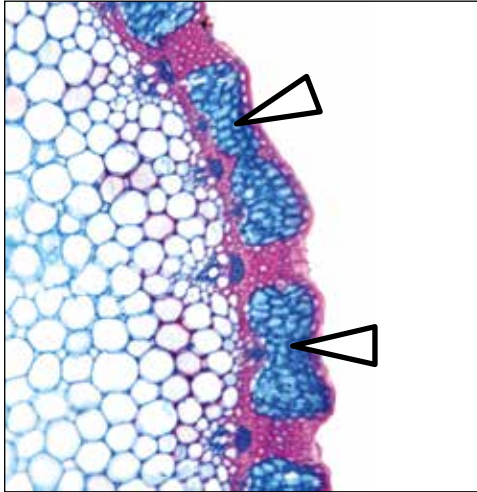


41 Large vascular bundles arranged in one peripheral row.

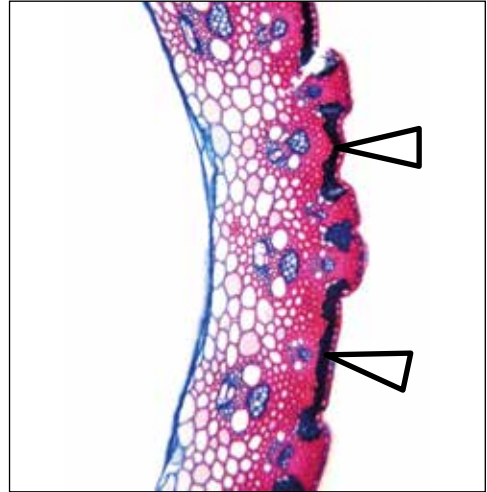


41a Large vascular bundles arranged in 2-3 peripheral rows.

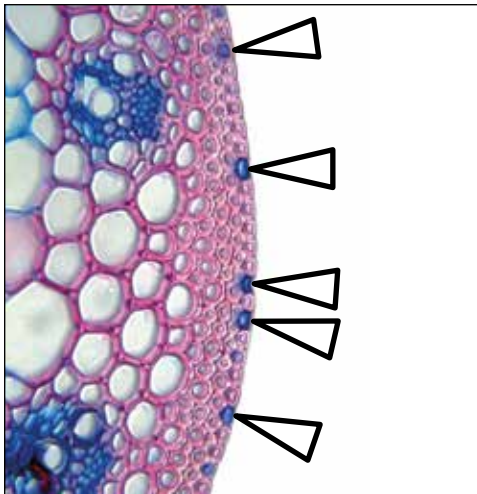
Chlorenchyma



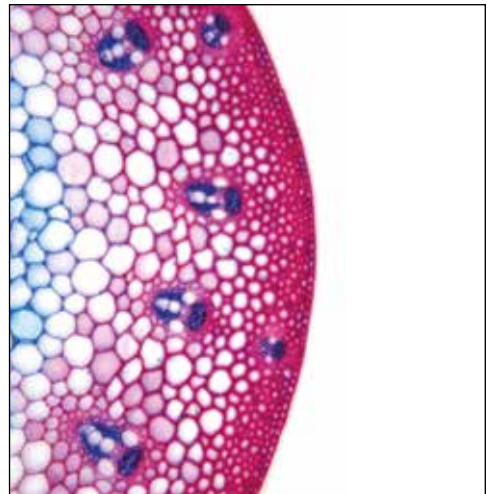
48a Chlorenchyma in round, oval, square or rectangular groups.



48b Chlorenchyma in tangentially enlarged groups.

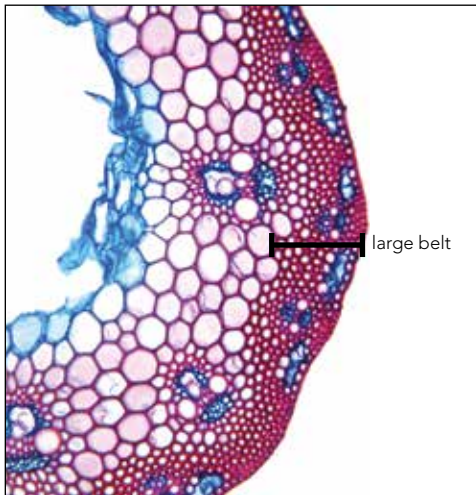


49a Chlorenchyma very small in 1-3 lined up cells.

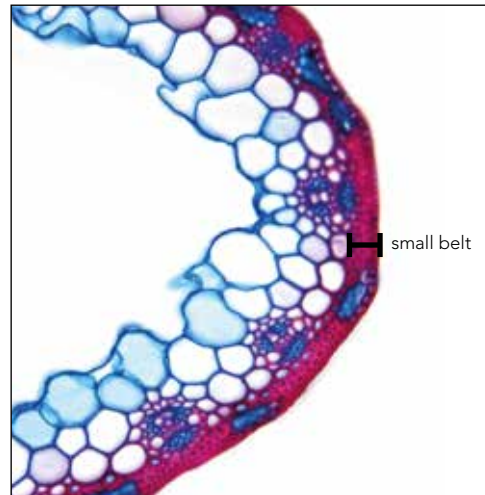


49b Chlorenchyma absent.

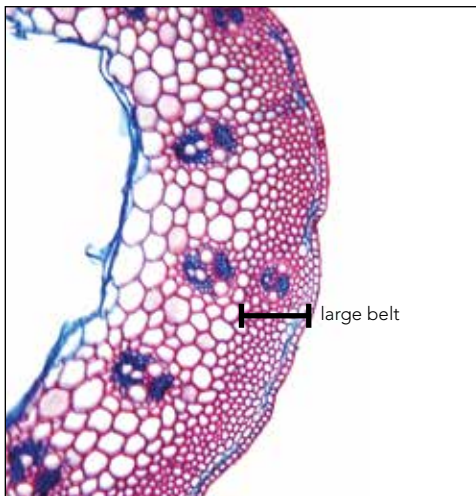
Peripheral sclerenchyma belt



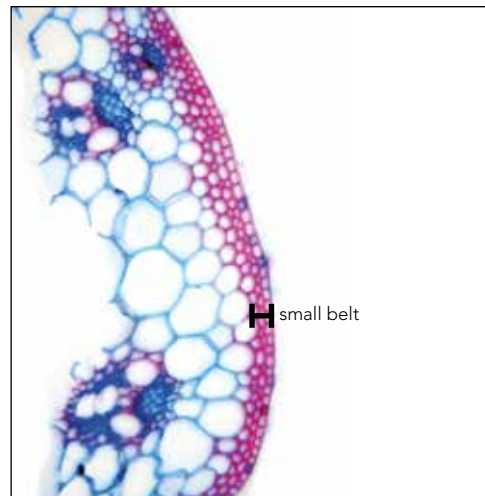
52a Sclerenchyma in a large, peripheral continuous belt (>3 cells), cells thick-walled.



52b Sclerenchyma in a small, peripheral continuous belt (< 4 cells), cells thick-walled.

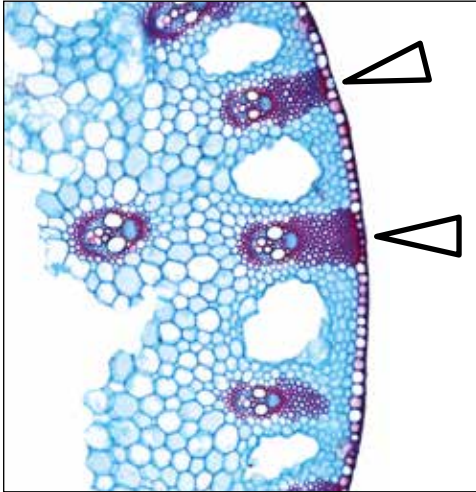


52c Sclerenchyma in a large, peripheral continuous belt (> 3 cells), cells medium thick-walled.

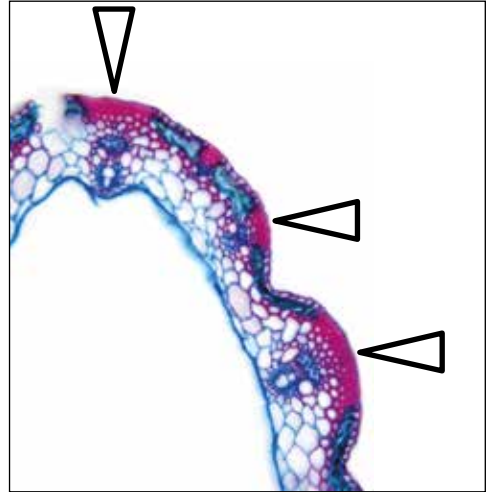


52d Sclerenchyma in a small, peripheral continuous belt (< 4 cells), cells medium thick-walled.

Scelenchyma girders

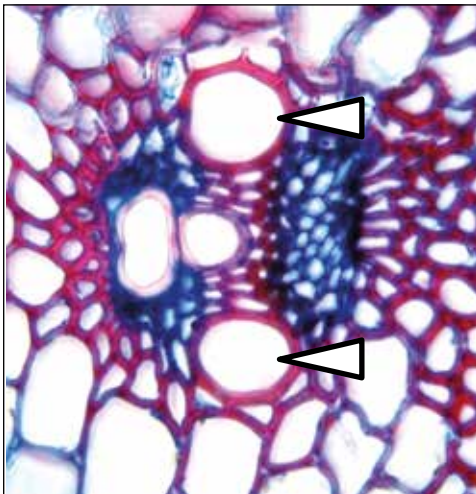


55a Girders square or rectangular.



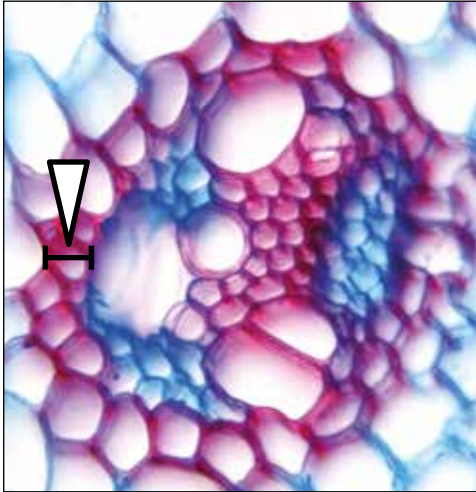
55d Girders tangentially enlarged.

Vessel arrangement

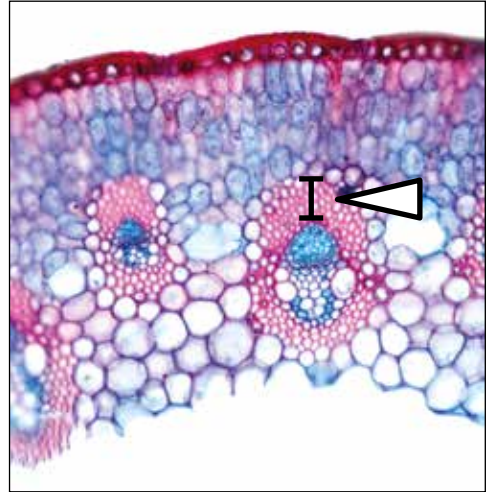


90a Largest vessels in vascular bundles in lateral position.

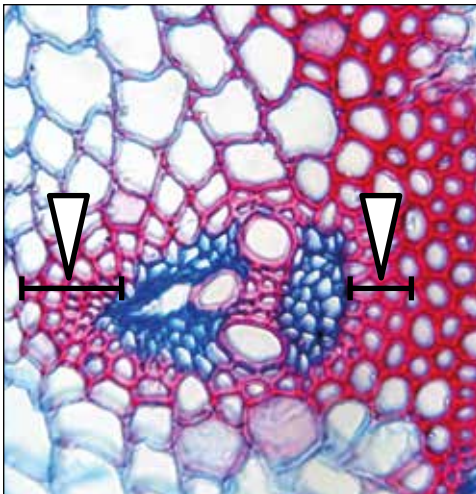
Sclerenchymatic sheath around vascular bundles



82 Small sclerenchymatic sheath with 1-2 cells around vascular bundles.

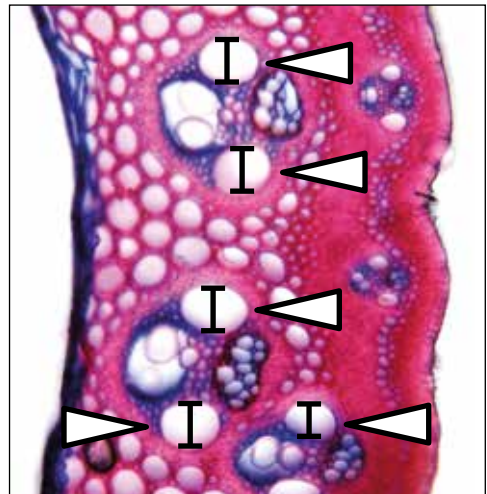
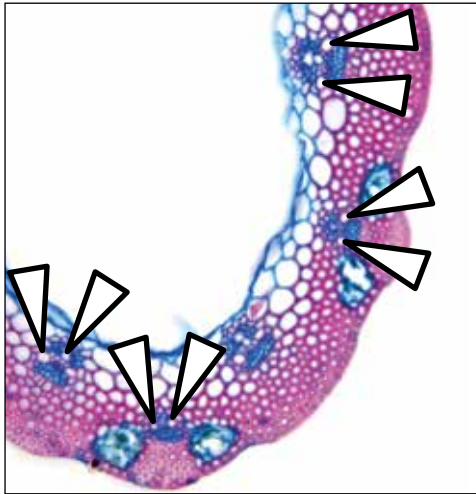


83 Sclerenchymatic sheath around vascular bundles large, 3 to x cells.



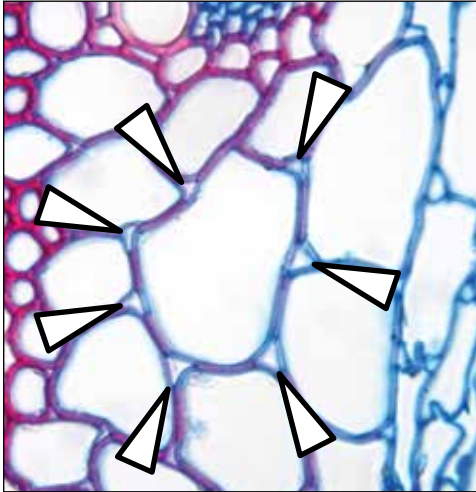
84 Sclerenchymatic sheath bilateral, large at both radial ends of vascular bundles.

Vessel size



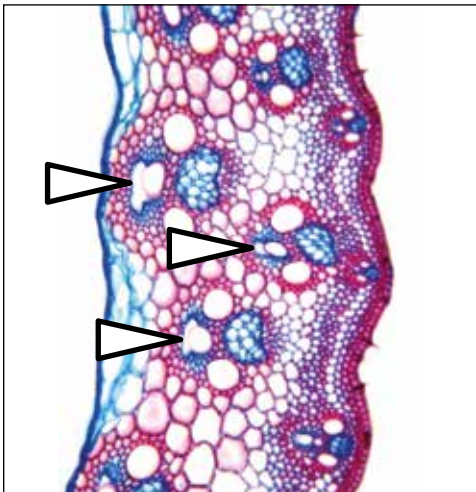
- 95** Largest vessel in the bundle small, $< 20 \mu\text{m}$
- 96** Largest vessel in the bundle $20\text{-}50 \mu\text{m}$
- 97** Largest vessel in the bundle $50\text{-}100 \mu\text{m}$
- 98** Largest vessel in the bundle $> 100 \mu\text{m}$

Cavities (intercellulars) between parenchyma cells in uniform culms



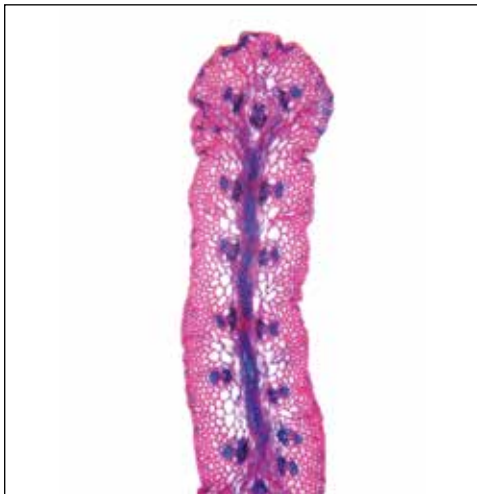
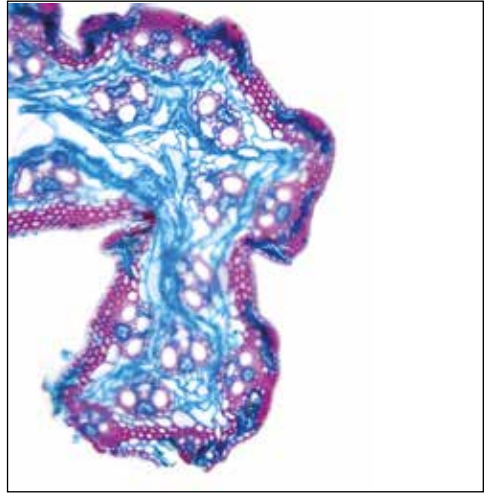
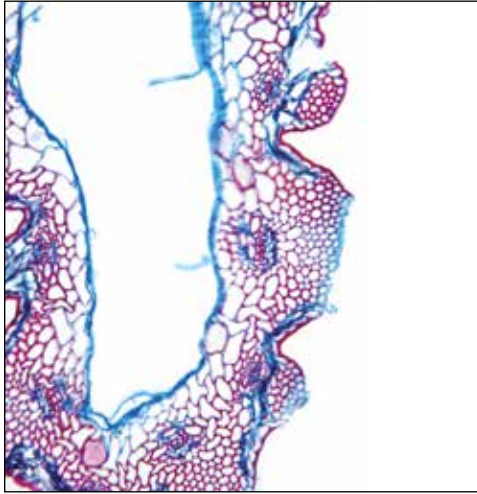
101a Cavities (intercellulars) between parenchyma-cells present, small, often triangular.

Cavities in vascular bundles



110a Distinct cavities (intercellulars) in the protoxylem area of vascular bundles.

Artefacts



- 130** Artefacts on material from herbaria, e.g. compressed and deformed culms or exaggerated distinct ribs.

4. Monographic presentation

4.1 Structure of the monographic presentation

Genera ↓ **Species** ↓ **Author** ↓ **Family** ↓

Brachypodium retusum (Pers.) P. Beauv. **Poaceae**
Syn. *Brachypodium ramosum* ← **Synonym**

Life form, plant size and ecology
↓
Perennial, 20-50 cm tall, erect culm, dry habitats in dry habitats at lower altitude.



Magnification 100 times



Magnification 400 times

Analyzed specimen: Between Porto and Partinella, Corsica. France. Length of culm 50 cm.

↑
Information about the analysed specimen, e.g. locality, ecology, etc.

Culm-diameter 0.5-1 mm, wall thin, radius of culm in relation to wall thickness approximately 1: 0.25 or < 0.25. Outline circular with a smooth surface. Culm-center hollow and surrounded by a few thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in 2-3 peripheral rows. Chlorenchyma in round, oval, square or rectangular groups. Sclerenchyma in a large, peripheral continuous belt (> 3 cells). Cells thick-walled. Girders square, rectangular or conic. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle small, < 20µm. Cavities (intercellulars) between parenchyma-cells present, small, often triangular. Distict cavities (intercellulars) in the protoxylem area of vascular bundles.

↑
Anatomical description of the species, composed of the definitions of the the Poaceae-Features

ZT-00078019

Barcode: Open the webportal <http://www.herbarien.uzh.ch/en/datenbanken/belegsuche.html> and with the corresponding barcode you will find the record of the herbarium voucher

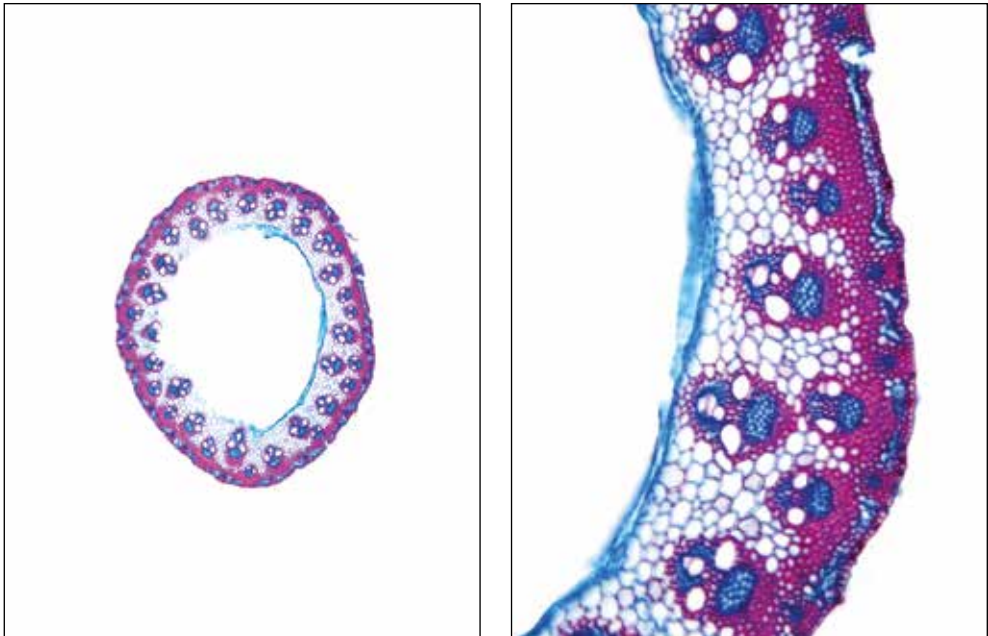
4.2 Characterisation of 300 species

Achnatherum calamagrostis Bertol.

Poaceae

Syn. *Stipa calamagrostis*

25-60 cm tall, erect, densely caespitose, dry habitat at lower altitude.



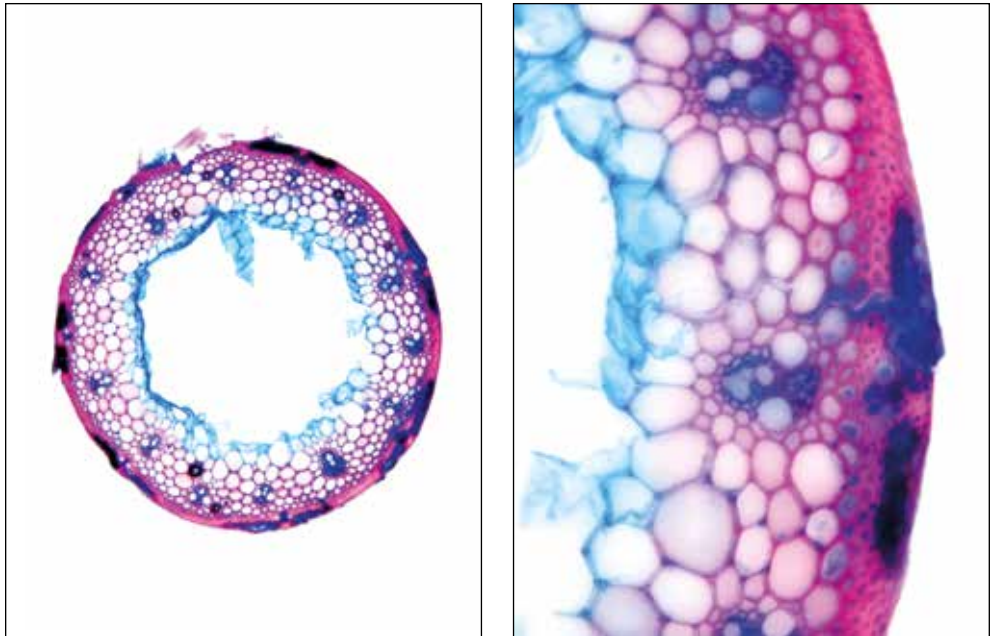
Analyzed specimen: Lauterbrunnen, Trümelbach, Canton of Bern, 900 m a.s.l. Switzerland.
Lime stone scree. Length of culm 80 cm.

Culm-diameter 1-2 mm, center full, radius of culm in relation to wall thickness 1:1. Outline circular with a smooth surface. Culm-center hollow and surrounded by many large thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in 2-3 peripheral rows. Chlorenchyma in tangentially enlarged groups. Sclerenchyma in a small, peripheral continuous belt (< 4 cells). Cells thick-walled. Sclerenchymatic sheath around vascular bundles large, 3 to x cells. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 2-50 μm . Distict cavities (intercellulars) in the protoxylem area of vascular bundles.

***Aegilops cylindrica* Host**

Poaceae

Annual, 20-45 cm tall, erect culms, caespitose, dry habitats at lower altitude.



Analyzed specimen: Botanical Garden Bern, 550 m a.s.l., Switzerland. Length of culm 40 cm.

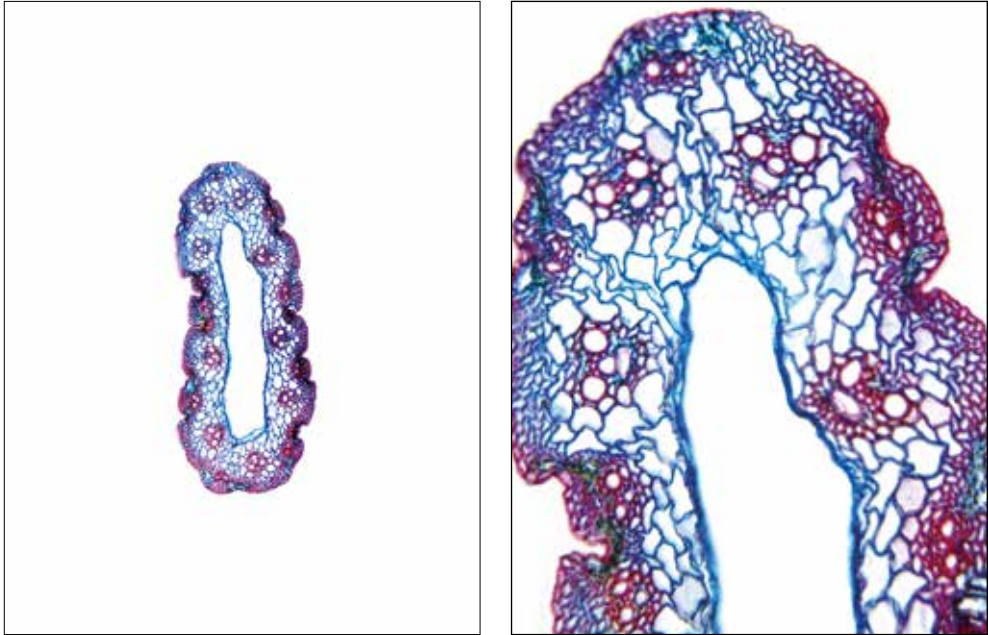
Culm-diameter 1-2 mm, wall large, radius of culm in relation to wall thickness 1:0.5. Outline circular with a smooth surface. Culm-center hollow and surrounded by a few thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in one peripheral row. Chlorenchyma in tangentially enlarged groups. Sclerenchyma in a small, peripheral continuous belt (< 4 cells). Cells thick-walled. Girders tangentially enlarged. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 20-50 μm .

***Aegilops neglecta* Bertol.**

Syn. *Aegilops triaristata*

Poaceae

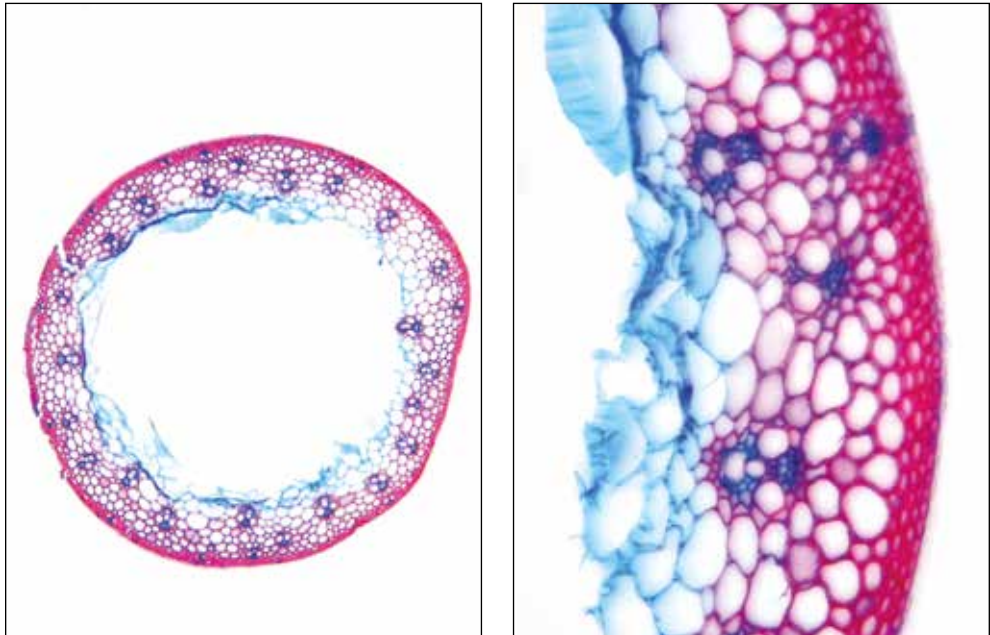
Annual, 20-45 cm tall, erect culms, caespitose, dry habitats at lower altitude.



Analyzed specimen: Central railway station of Basel. On gravel. Length of culm 35 cm.

Culm-diameter 1-2 mm, wall large, radius of culm in relation to wall thickness 1:0.5. Outline circular wavy. Culm-center hollow and surrounded by many large thin-walled, not lignified cells. Epidermis-cells thin-walled all around. Large vascular bundles arranged in one peripheral row. Chlorenchyma in round, oval, square or rectangular groups. Sclerenchyma in a small, peripheral continuous belt (< 4 cells). Cells medium thick-walled. Girders square, rectangular or conic. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 20-50 μm . Cavities (intercellulars) between parenchyma-cells present, small, often triangular.

Annual, 30-60 cm tall, erect culms, caespitose, dry habitats at lower altitude.



Analyzed specimen: Botanical Garden Bern, 550m a.s.l., Switzerland. Length of culm 60 cm.

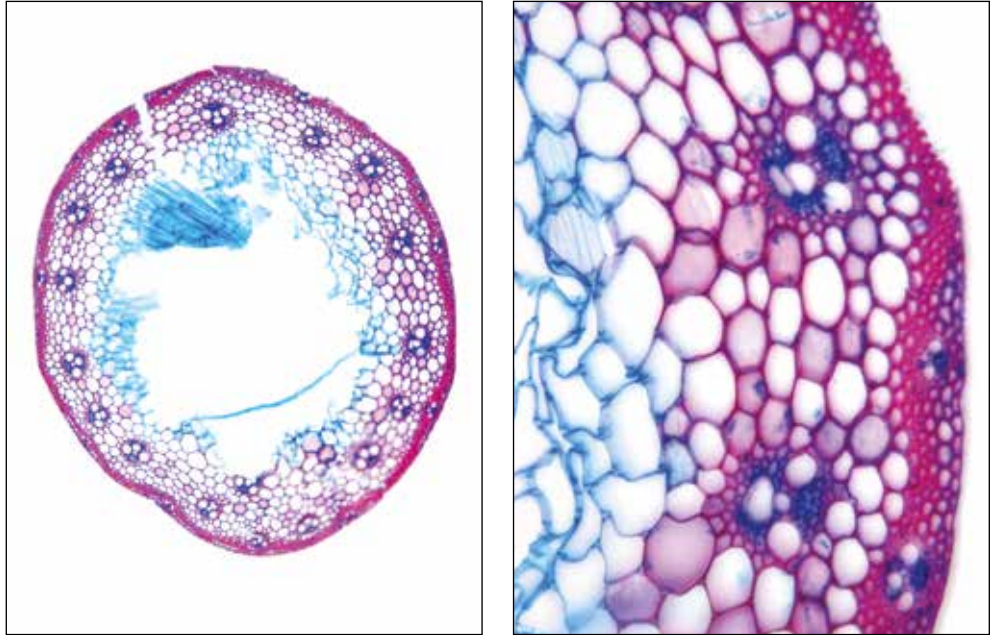
Culm-diameter 1-2 mm, wall thin, radius of culm in relation to wall thickness approximately 1:0.25 or < 0.25. Outline circular with a smooth surface. Culm-center hollow and surrounded by a few thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in 2-3 peripheral rows. Chlorenchyma very small in 1-3 lined-up cells. Sclerenchyma in a small, peripheral continuous belt (< 4 cells). Cells thick-walled. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 20-50 μm . Cavities (intercellulars) between parenchyma-cells present, small, often triangular.

Aegilops tauschii Coss.

Syn. *Aegilops squarrosa*

Poaceae

20-40 cm tall erect, solitary grass as weed in dry grain fields.



Analyzed specimen: Botanical Garden Bern, 550m a.s.l., Switzerland. Length of culm 60 cm.

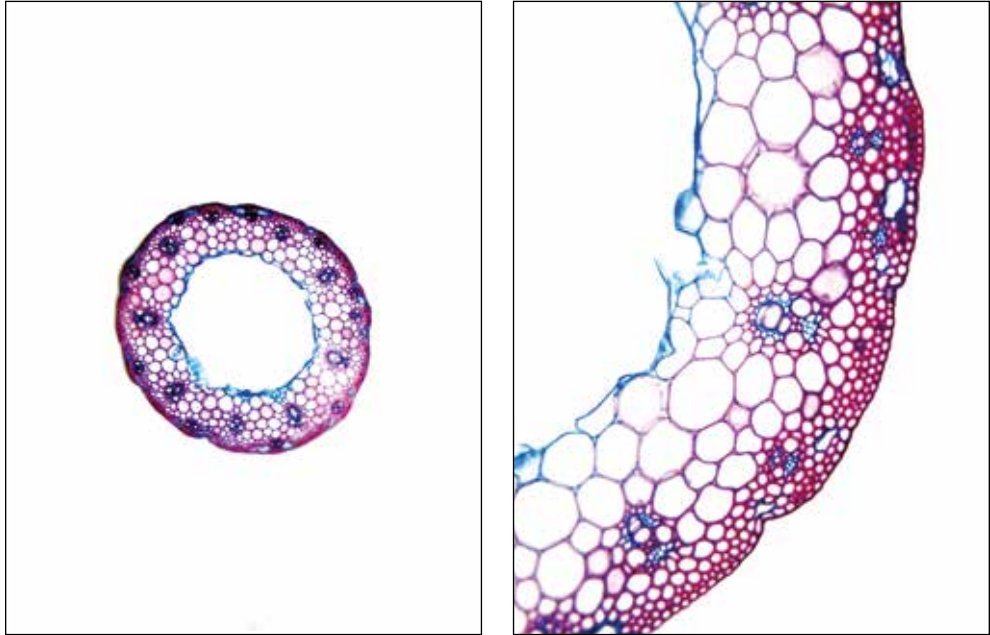
Culm-diameter 2-5 mm, wall large, radius of culm in relation to wall thickness approximately 1:0.5. Outline circular with a smooth surface. Epidermis-cells thin-walled all around. Large vascular bundles arranged in one peripheral row. Chlorenchyma very small in 1-3 lined-up cells. Sclerenchyma in a large, peripheral continuous belt (> 3 cells). Cells thick-walled. Sclerenchymatic sheath around vascular bundles large, 3 to x cells. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 20-50 μm . Cavities (intercellulars) between parenchyma-cells present, small, often triangular. Distinct cavities (intercellulars) in the protoxylem area of vascular bundles.

***Aegilops triuncialis* L.**

Syn. *Tritium triuncialis*

Poaceae

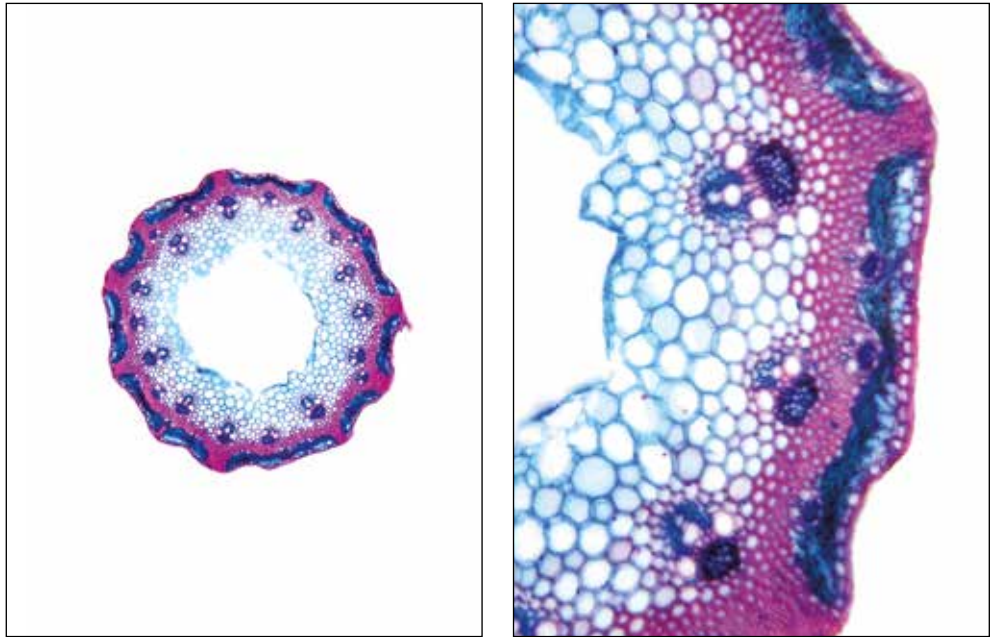
Annual, 20-45 cm tall, erect culms, caespitose, dry habitats at lower altitude.



Analyzed specimen: Warehouse near Zurich, Canton of Zurich. Switzerland.
Length of culm 30 cm.

Culm-diameter 0.5-1 mm, wall large, radius of culm in relation to wall thickness 1:0.5. Outline circular with a smooth surface. Culm-center hollow and surrounded by a few thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in 2-3 peripheral rows. Chlorenchyma in round, oval, square or rectangular groups. Sclerenchyma in a large, peripheral continuous belt (> 3 cells). Cells medium thick-walled. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 20-50 μm . Cavities (intercellulars) between parenchyma-cells present, small, often triangular. Distict cavities (intercellulars) in the protoxylem area of vascular bundles.

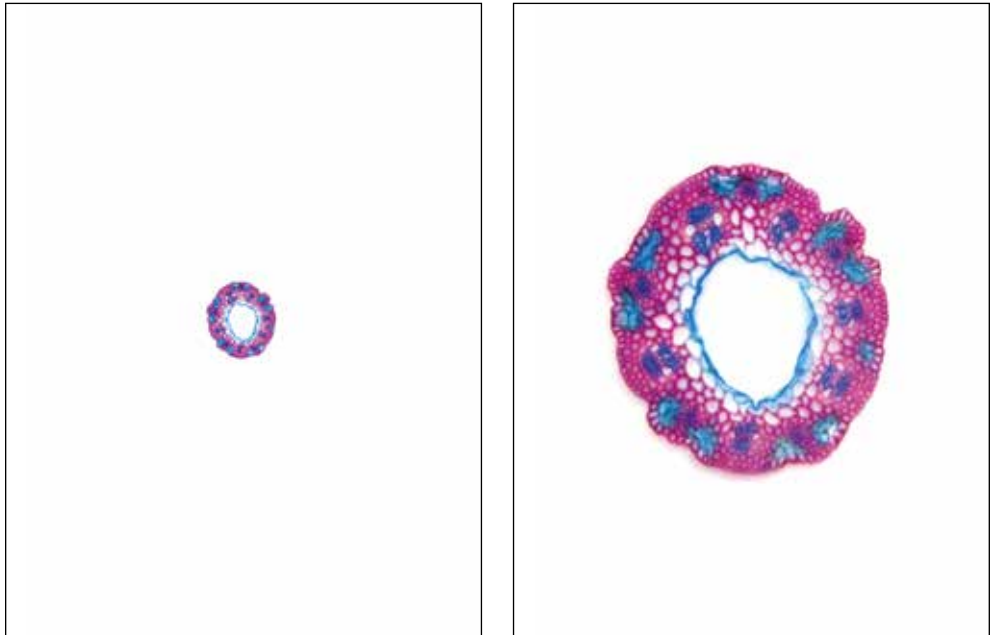
Perennial, 20-45 cm tall, erect culms, loosely caespitose, dry habitats at lower altitude.



Analyzed specimen: Leithagebirge Burgenland, 300 m a.s.l. Austria. Length of culm 40 cm.

Culm-diameter 1-2 mm, wall very large, radius of culm in relation to wall thickness approximately 1:0.75. Outline circular wavy. Culm-center hollow and surrounded by many large thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in 2-3 peripheral rows. Chlorenchyma in tangentially enlarged groups. Sclerenchyma in a large, peripheral continuous belt (> 3 cells). Cells medium thick-walled. Girders square, rectangular or conic. Sclerenchymatic sheath around vascular bundles large, 3 to x cells. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle 20-50 μm . Cavities (intercellulars) between parenchyma-cells present, small, often triangular. Distict cavities (intercellulars) in the protoxylem area of vascular bundles.

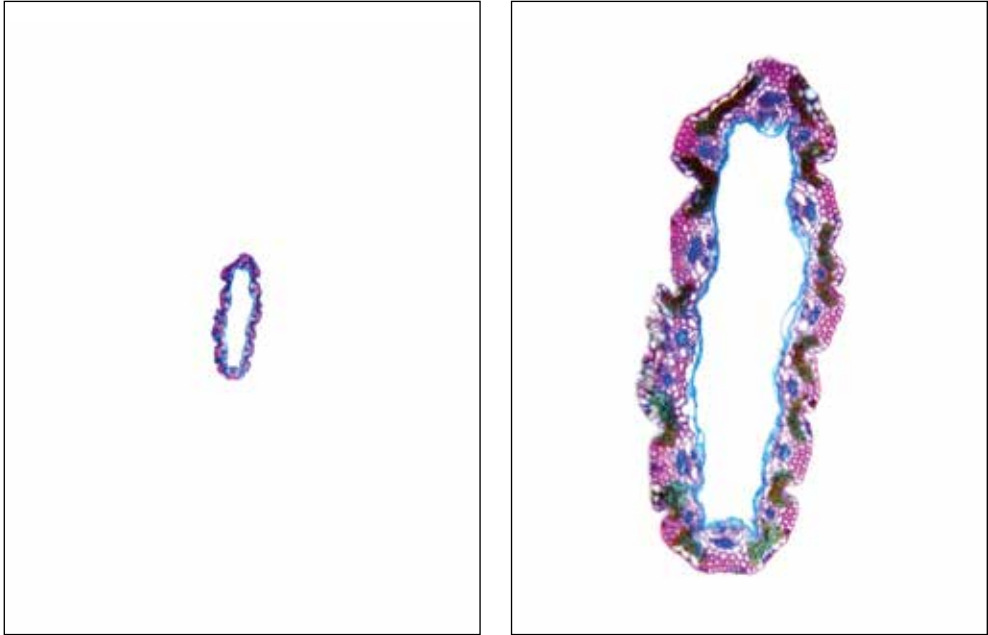
Perennial, 10-3 cm tall, caespitose, erect and geniculate culm, wet habitat at lower altitude.



Analyzed specimen: Constainas, Val Müstair, Canton of Grisons, 2450 m.s.l. Switzerland.
Wet meadow. Length of culm 15 cm.

Culm-diameter < 0.5 mm, wall very large, radius of culm in relation to wall thickness approximately 1:0.75. Outline circular with a smooth surface. Culm-center hollow and surrounded by a few thin-walled, not lignified cells. Epidermis-cells thick-walled all around. Large vascular bundles arranged in one peripheral row. Chlorenchyma in round, oval, square or rectangular groups. Sclerenchyma in a large, peripheral continuous belt (> 3 cells). Cells medium thick-walled. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle small, < 20µm. Distict cavities (intercellulars) in the protoxylem area of vascular bundles.

Perennial, 15-75 cm tall, densely caespitose with long rhizomes, erect, wet acid habitats at lower altitudes.



Analyzed specimen: Chlepfimoos, Burgäschisee, Canton of Bern, 460 m.a.s.l. Switzerland. Bog. Length of culm 40 cm.

Culm-diameter 0.5-1 mm, wall thin, radius of culm in relation to wall thickness approximately 1:0.25 or < 0.25. Outline circular wavy. Culm-center hollow and surrounded by a few thin-walled, not lignified cells. Epidermis-cells thin-walled all around. Large vascular bundles arranged in one peripheral row. Chlorenchyma in round, oval, square or rectangular groups. Sclerenchyma in a small, peripheral continuous belt (< 4 cells). Cells medium thick-walled. Girders square, rectangular or conic. Small sclerenchymatic sheath with 1-2 cells around vascular bundles. Largest vessels in vascular bundles in lateral position. Largest vessel in the bundle small, < 20 μ m.