

IAWA LIST OF MICROSCOPIC FEATURES FOR SOFTWOOD IDENTIFICATION

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PREFACE

A definitive list of anatomical features of softwoods has long been needed. The hardwood list (IAWA Committee 1989) has been adopted throughout the world, not least because it provides a succinct, unambiguous illustrated glossary of hardwood characters that can be used for a variety of purposes, not just identification. This publication is intended to do the same job for softwoods. Identifying softwoods relies on careful observation of a number of subtle characters, and great care has been taken to show high quality photomicrographs that remove most of the ambiguity that definitions alone would provide.

Unlike the Hardwood Committee, the Softwood Committee never met in its full composition. The softwood committee members attending the XVI International Botanical Congress in St. Louis in August 1999 met for a day to discuss an early draft. The editing of the list was coordinated by Jorgo (H.G.) Richter, who intensively communicated by e-mail with all committee members. At the IAWA meeting in Portland, Oregon in July 2003, several committee members discussed a late draft. All the photographs were taken by Dietger Grosser and Immo Heinz, whose MSc thesis work was the catalyst for the formation of the committee (Heinz 1997). Peter Gasson then did the final editing and cross-referencing of text and plates before sending the entire work to Leiden for publication.

We hope that all present and future colleagues engaged in wood identification and descriptive wood anatomy will find this list a valuable guide and reference.

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LIST OF FEATURES

Name (nomenclature)

GENERAL INFORMATION

Geographical distribution — *p. 12*

1. Europe and temperate Asia (Brazier and Franklin region 74)
 2. Europe, excl. Mediterranean
 3. Mediterranean incl. Northern Africa and Middle East
 4. Temperate Asia (China, Japan, Russia)
5. Central South Asia (Brazier and Franklin region 75)
 6. India, Pakistan, Sri Lanka
 7. Burma (Myanmar)
8. Southeast Asia and the Pacific (Brazier and Franklin region 76)
 9. Thailand, Laos, Vietnam, Cambodia (Indochina)
 10. Indomalesia (Indonesia, Philippines, Malaysia, Brunei, Singapore, Papua New Guinea, and Solomon Islands)
 11. Pacific Islands (incl. New Caledonia, Samoa, Hawaii, and Fiji)
12. Australia and New Zealand (Brazier and Franklin region 77)
 13. Australia
 14. New Zealand
15. Tropical mainland Africa and adjacent islands (Brazier and Franklin region 78)
 16. Tropical Africa
 17. Madagascar, Mauritius, Reunion and Comores
18. Southern Africa (south of the Tropic of Capricorn) (Brazier and Franklin region 79)
19. North America (north of Mexico) (Brazier and Franklin region 80)
20. Neotropics and temperate Brazil (Brazier and Franklin region 81)
 21. Mexico and Central America
 22. Caribbean
 23. Tropical South America
 24. Southern Brazil
25. Temperate South America including Argentina, Chile, Uruguay and southern Paraguay (Brazier and Franklin region 82)

PHYSICAL PROPERTIES

Heartwood colour — *p. 12*

26. Brown or shades of brown
27. Red or shades of red
28. Yellow or shades of yellow
29. Light coloured (whitish, creamy, grey)
30. Purple or shades of purple
31. Other than above (specify)

Difference between heartwood and sapwood colour — *p. 14*

- 32. Heartwood colour similar to sapwood colour
- 33. Heartwood colour distinct from sapwood colour

Presence of heartwood with colour streaks — *p. 14*

- 34. Heartwood with streaks

Presence of a distinct odour — *p. 14*

- 35. Odour distinct (specify)

Average air-dry density / basic specific gravity — *p. 15*

- 36. ... < g/cm³ >

Average air-dry density [g/cm³] (categories) — *p. 15*

- 37. Less than 0.48 g/cm³
- 38. 0.48–0.60 g/cm³
- 39. Above 0.60 g/cm³

GROWTH RINGS

Presence of growth ring boundaries — *p. 16*

- 40. Growth ring boundaries distinct
- 41. Growth ring boundaries indistinct or absent

Transition from earlywood to latewood — *p. 16*

- 42. Abrupt
- 43. Gradual

TRACHEIDS

Tracheid pitting in radial walls (in earlywood only) — *p. 19*

- 44. (predominantly) Uniseriate
- 45. (predominantly) Two or more seriate

Arrangement of (two or more seriate) tracheid pitting in radial walls (earlywood only) — *p. 19*

- 46. Opposite
- 47. Alternate

Organic deposits (in heartwood tracheids) — *p. 21*

- 48. Present

Average tracheid length — *p. 22*

- 49. ... < μm >

Average tracheid length (size classes) — *p. 22*

- 50. Short (less than 3000 μm)
- 51. Medium (3000 to 5000 μm)
- 52. Long (over 5000 μm)

Intercellular spaces throughout the wood (in transverse section) — *p. 23*

53. Present

Latewood tracheid wall thickness — *p. 24*

54. Thin-walled (double wall thickness less than radial lumen diameter)

55. Thick-walled (double wall thickness larger than radial lumen diameter)

Torus (pits in earlywood tracheids only) — *p. 25*

56. Present

57. Scalloped

Torus extensions — *p. 26*

58. Present

Pits with notched borders — *p. 28*

59. Present

Warty layer (visible under the light microscope) — *p. 28*

60. Present

HELICAL AND OTHER WALL THICKENINGS

Helical thickenings in tracheids — *p. 30*

Helical thickenings in longitudinal tracheids (presence) — *p. 32*

61. Present

Helical thickenings (in longitudinal tracheids - location) — *p. 32*

62. Present throughout the growth increment

63. Well developed only in earlywood

64. Well developed only in latewood

Helical thickenings (in longitudinal tracheids - whether single or grouped) — *p. 32*

65. Single

66. Grouped (double or triple)

Helical thickenings (in longitudinal tracheids - spacing, earlywood tracheids only) — *p. 32*

67. Narrowly spaced (number of coils more than 120 per mm)

68. Widely spaced (number of coils less than 120 per mm)

Helical thickenings in ray tracheids — *p. 33*

69. Commonly present

70. (present but) Rare

Callitroid thickenings — *p. 34*

71. Present

AXIAL PARENCHYMA

Axial parenchyma (excl. epithelial and subsidiary cells of intercellular canals) — *p. 35*

72. Present

Arrangement of axial parenchyma — *p. 37*

73. Diffuse (evenly scattered throughout the entire growth increment)

74. Tangentially zonate

75. Marginal

Transverse end walls — *p. 39*

76. Smooth

77. Irregularly thickened

78. Beaded or nodular

RAY COMPOSITION

Ray tracheids — *p. 40*

79. Commonly present

80. Absent or very rare

Cell walls of ray tracheids — *p. 43*

81. Smooth

82. Dentate

83. Reticulate

Ray tracheid pit borders angular or with dentate thickenings (radial section, *Larix* & *Picea* only) — *p. 45*

84. Present

End walls of ray parenchyma cells — *p. 47*

85. Smooth (unpitted)

86. Distinctly pitted

Horizontal walls of ray parenchyma cells — *p. 48*

87. Smooth (unpitted)

88. Distinctly pitted

Indentures — *p. 49*

89. Present

CROSS-FIELD PITTING

Cross-field pitting (according to Phillips 1948, amended by Vogel 1995) — *p. 51*

90. "Window-like" (fenestriform)

91. Pinoid

92. Piceoid

93. Cupressoid

94. Taxodioid

95. Araucarioid

Number of pits per cross-field (earlywood tracheids only) — *p. 54*

96. ... < number per crossfield >

Number of pits per cross-field (earlywood only – categories) — *p. 54*

97. (large window-like) 1–2

98. 1–3

99. 3–5

100. 6 or more

RAY SIZE

Average ray height — *p. 55*

101. ... < μm >

Average ray height (number of cells) — *p. 57*

102. Very low (up to 4 cells)

103. Medium (5 to 15 cells)

104. High (from 16 to 30 cells)

105. Very high (more than 30 cells)

Average fusiform ray height — *p. 57*

106. ... < μm >

Ray width (cells) — *p. 57*

107. Exclusively uniseriate

108. 2–3-seriate in part

INTERCELLULAR CANALS

Axial intercellular (resin) **canals** — *p. 58*

109. Present

Radial intercellular (resin) **canals** — *p. 60*

110. Present

Traumatic (resin) **canals** (axial, radial) — *p. 60*

111. Present

Average diameter of normal axial intercellular canals — *p. 60*

112. Tangential diameter, delimited by epithelial cells (Method A) < μm >

113. Tangential diameter of entire resin canal complex (Method B) < μm >

114. Radial diameter, delimited by epithelial cells (Method C) < μm >

Average diameter of normal radial intercellular canals — *p. 62*

115. ... < μm >

Epithelial cells (of intercellular canals) — *p. 62*

116. Thick-walled

117. Thin-walled

MINERAL INCLUSIONS**Crystals** — *p. 65*

118. Present

Type of crystals — *p. 65*

119. Prismatic

120. Druses

121. Other forms (specify)

Crystals located in — *p. 65*

122. Rays

123. Axial parenchyma

124. Cells associated with intercellular canals

SOFTWOODS

Definition:

In the context of this annotated list the softwoods include the following families of the Pinopsida (Coniferales) and Ginkgoopsida: Araucariaceae, Cephalotaxaceae, Cupressaceae (including Taxodiaceae), Ginkgoaceae, Phyllocladaceae, Pinaceae, Podocarpaceae, Sciadopityaceae, and Taxaceae (Farjon 2001).

NOMENCLATURE

Record the full taxonomic information on the specimens, i.e. family, genus, species, authority. For accepted scientific names and familial affinities, refer to recent checklists like “The World Checklist of Conifers” (Welch & Haddow 1993) and the “World Checklist and Bibliography of Conifers” (Farjon 2001), dictionaries such as “The Plant-Book” (Mabberley 1997), monographs such as “Flora of North America” or “The Families and Genera of Vascular Plants” (Kubitzki 1990). For authorities follow the commonly used abbreviations listed in Brummitt & Powell (1992). Current plant names and synonyms can be found in Farjon (2001), at the International Plant Names Index web site under the address: <http://www.ipni.org/>, or at other sites such as www.conifers.org and the GRIN database under <http://www.ars-grin.gov/npgs/tax/taxfam.html>. The web site of the Royal Botanic Gardens Kew (<http://www.kew.org/data/index.html>) offers links to many useful indices of plant names. When creating a database, record information on the number of species and/or specimens examined for creating a coded taxon description. Collection data (xylarium designation, collector and number, country of origin, etc.) on each specimen should also be recorded.

In this list the cited botanical names have been adopted from Farjon (2001), who includes Taxodiaceae in Cupressaceae.

Many conifer species are listed as threatened according to IUCN (International Union for the conservation of Nature) criteria (see also Farjon 2001).

Information on the protection status under CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) or under specific national regulations could be added as useful information. The CITES regulations in general and the list of protected taxa can be obtained from the following source:

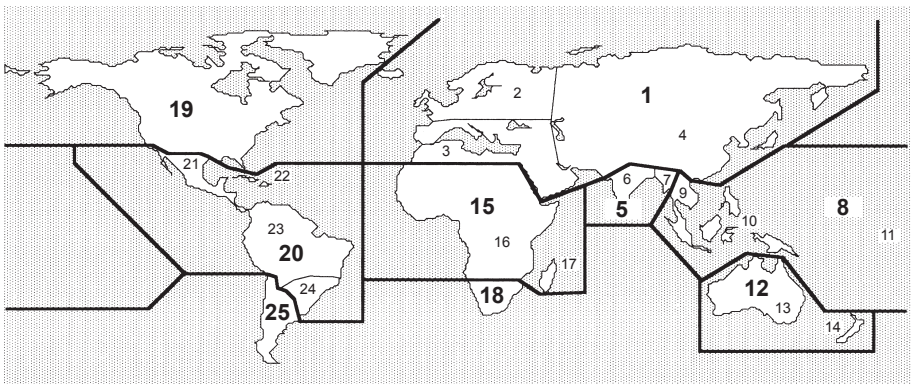
<http://www.tropicalforestfoundation.org/cites.html#appendix1>

Commercial potential should also be recorded, and refers to woods of both historical and current commercial importance. The term ‘of commercial importance’ is somewhat vague, and should not be used when identifying an unknown. When identifying some wooden artefacts, e.g., furniture, it can be helpful to segregate commercial species from non-commercial species.

GENERAL INFORMATION

GEOGRAPHICAL DISTRIBUTION

- 1. Europe and temperate Asia** (Brazier and Franklin region 74)
 2. Europe, excl. Mediterranean
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 4. Temperate Asia (China, Japan, Russia)
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- 12. Australia and New Zealand** (Brazier and Franklin region 77)
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- 20. Neotropics and temperate Brazil** (Brazier and Franklin region 81)
 21. Mexico and Central America
 22. Caribbean
 23. Tropical South America
 24. Southern Brazil
- 25. Temperate South America** including Argentina, Chile, Uruguay and southern Paraguay (Brazier and Franklin region 82)



Geographical distribution (features 1–25)

Comment:

There is no single ideal way of dividing the world. The above is a mixture of political and biogeographical criteria. It retains the major geographical regions of Brazier and Franklin (1961), but some regions are subdivided. The divisions here are the same as those in the hardwood list (IAWA Committee 1989). The floristic region "Southern Brazil" is roughly defined as between 30° and 20° latitude south and between 44° and 57° longitude (west of Greenwich); it includes parts of northern Argentina and eastern Paraguay.

PHYSICAL PROPERTIES

HEARTWOOD COLOUR

- 26. Brown or shades of brown**
- 27. Red or shades of red**
- 28. Yellow or shades of yellow**
- 29. Light coloured (whitish, creamy, grey)**
- 30. Purple or shades of purple**
- 31. Other than above (specify)**

Comments:

The variety of colours, shades, and combinations of heartwood colour makes it impossible to categorise them all. In general, the colour of heartwood in conifers is either brown, red, yellow, white, or some shade or a combination of these colours. Basically white or grey and brown heartwood are very common; red and yellow are less frequent; shades of orange (*Pseudotsuga*) or very dark brown (*Cryptomeria japonica*) are rather rare. The heartwood of many taxa is not restricted to one colour, but is a combination of colours. When appropriate, these should be recorded and may be used when identifying an unknown.

The heartwood colour of fresh wood is different from that of dry wood; wood colour may change during drying due to the polymerisation of low molecular weight components during dehydration and also subsequently due to the influence of light (UV radiation) and oxygen. Therefore wood colour should be determined on a longitudinal surface of a dry, freshly planed specimen.

Examples of characteristic colours or colour combinations include: chocolate-brown in *Taxus* spp. (Taxaceae), reddish-brown in *Sequoia sempervirens* and *Fitzroya cupressoides* (Cupressaceae); purplish-brown in *Juniperus virginiana* and *Calocedrus decurrens* (Cupressaceae); yellow in *Xanthocyparis (Chamaecyparis) nootkatensis*, *Thujaopsis dolabrata* (Cupressaceae), *Torreya* spp. (Taxaceae); yellowish-brown in *Pinus* spp., *Larix* spp. and *Pseudotsuga* spp. (Pinaceae), the latter two often with an orange to reddish hue.

Very light coloured woods would be recorded as combinations of white (to grey) and brown and/or yellow, e.g. *Picea* spp., *Abies* spp., and *Tsuga* spp. (all Pinaceae).

Caution:

It is usually impractical to use heartwood colour to help with identifying archaeological material, or other specimens whose colour has been altered by burial, time, treatment, or decay. Wood remains from shipwrecks are often discoloured by contact

with metals, e. g., barrel staves, floor and ceiling planks, and other elements may acquire shades of pink to purple simply by contact with metals.

Be particularly careful when using the feature ‘heartwood basically white to grey’, because a whitish specimen may represent sapwood and not heartwood. Timber from fast growing trees raised in plantations, particularly pines (*Pinus* spp.), may be all sapwood as trees are felled at an age when heartwood has not yet formed or reached any significant proportion.

Wetwood, often observed in true fir (*Abies* spp.), hemlock (*Tsuga* spp.), and Hoop pine (*Araucaria cunninghamii*) may darken the heartwood and should not be interpreted as coloured heartwood. For further information on wetwood refer to Ward & Pong (1980).

Compression wood can be recognised by its usually eccentric stem (transverse section) with typically wide growth rings and a reddish-brown colour. Be careful not to record compression wood as coloured heartwood. If you are uncertain if the sample is compression wood, use microscopic observation; compression wood is characterised by the circular outline of individual tracheids, frequent intercellular spaces, and spiral grooves in the secondary wall. For a detailed account of compression wood refer to Timell (1986).

DIFFERENCE BETWEEN HEARTWOOD AND SAPWOOD COLOUR

32. Heartwood colour similar to sapwood colour

33. Heartwood colour distinct from sapwood colour

Comment:

In many coniferous taxa the heartwood is markedly different in colour from the light coloured sapwood, e. g., dark reddish brown in *Sequoia sempervirens* and *Fitzroya cupressoides* (Cupressaceae); purplish brown in *Juniperus* spp. (Cupressaceae); yellowish brown in *Pinus* spp. (Pinaceae), yellow to orange brown in *Pseudotsuga menziesii* (Pinaceae), or chocolate brown in *Taxus* spp. (Taxaceae). In a few taxa, e. g., *Picea sitchensis*, the heartwood is only slightly darker than the sapwood, but can still be distinguished from it (= heartwood colour distinct from sapwood colour). In still other taxa, e. g., *Abies* spp., *Picea* spp., *Tsuga* spp. (Pinaceae), *Xanthocyparis* (*Chamaecyparis*) *nootkatensis* (Cupressaceae), heartwood and sapwood cannot be distinguished by colour (= heartwood colour similar to sapwood colour).

PRESENCE OF HEARTWOOD WITH COLOUR STREAKS

34. Heartwood with streaks

The feature ‘heartwood with streaks’ is used in conjunction with the general heartwood colour. Colour streaks are not very common among coniferous woods; reddish-brown to orange-brown streaks are characteristic for, e. g., *Podocarpus totara*, *Dacrydium nausoriense* (Podocarpaceae), and *Araucaria angustifolia* (Araucariaceae).

Caution:

Juniperus virginiana (Cupressaceae) and possibly other species of *Juniperus* regularly contain so called “included sapwood” (McGuinness et al. 1969; Vogel 1994), i. e. restricted areas within the heartwood in which no coloured accessory compounds have been deposited. Do not interpret this phenomenon as ‘heartwood with streaks’.

PRESENCE OF A DISTINCT ODOUR

35. Odour distinct (specify)

A characteristic odour can be a very useful aid in wood identification. For example, Douglas-fir (*Pseudotsuga menziesii*, Pinaceae) can be distinguished from the macroscopically similar larch (*Larix* spp., Pinaceae) by its characteristic (rather unpleasant) odour. The odour of *Xanthocyparis* (*Chamaecyparis*) *nootkatensis* is distinctly different from that of the otherwise very similar *Thujopsis dolabrata*. Other coniferous woods with a characteristic odour include *Thuja* spp., *Juniperus* spp., many species of *Cupressus* and *Chamaecyparis*, *Thujopsis dolabrata*, *Cryptomeria japonica* and *Cunninghamia konishii* (Cupressaceae), *Torreya nucifera* (Taxaceae) and *Cedrus* spp. (Pinaceae). For further examples of fragrant coniferous woods consult Phillips (1948) and Panshin & DeZeeuw (1980).

Procedure:

In dry wood specimens the chemicals responsible for the odour may have volatilised from the surface, so sand the surface, add moisture by breathing on the wood, or wet the wood with water and warm it.

Caution:

Odour is variable, and individual perceptions of odour often differ. Therefore, use this feature with caution and only in the positive sense. Odour should not be used with archaeological specimens, particularly from moist environments such as shipwrecks and swamps as they tend to 'develop' particular odours derived from the deposits of entombment and/or fungal decay. The absence of odour is not diagnostic.

AVERAGE AIR-DRY DENSITY / BASIC SPECIFIC GRAVITY

36. ... < g/cm³ >

Definitions:

Air-dry density = wood weight and volume at a moisture content at equilibrium with atmospheric conditions, usually around 12% MC in temperate and 15% MC in tropical regions [g/cm³].

Basic specific gravity = ratio of the oven-dry weight to the weight of water displaced by the wood when it is completely swollen (i.e. green volume) [without units].

Comments:

When creating a database for softwood identification either of the indicated alternatives may be used to describe this material property of wood. The introduction to the database should contain an explicit statement which of the two values is used for species description. Air-dry density at 12–15% MC (and at other levels of moisture content) corresponding to the respective basic specific gravity values can be estimated from conversion tables in Miller (1981). For converting air-dry density to basic specific gravity values (and vice versa) the following equations can also be used:

air-dry density = $-0.028 + 1.260 \times \text{basic specific gravity}$, or

basic specific gravity = $(\text{air-dry density} + 0.028) / 1.260$

Caution:

Wood density can vary considerably between mature trunk wood, juvenile wood, branch wood, and root wood. If not specified otherwise, published data on wood density usually refer to the mature trunk wood.

AVERAGE AIR-DRY DENSITY [g/cm³] (categories)

37. Less than 0.48 g/cm³

38. 0.48–0.60 g/cm³

39. Above 0.60 g/cm³

Examples for average air-dry density below 0.48 g/cm³: *Metasequoia glyptostroboides*, *Sequoia sempervirens*, *Sequoiadendron giganteum*, *Thuja plicata* (Cupressaceae).

Examples for average air-dry density above 0.60 g/cm³: *Amentotaxus*, *Taxus* spp., *Torreya* spp. (Taxaceae), *Cephalotaxus* (Cephalotaxaceae), species of *Dacrydium* and *Podocarpus* sensu lato (Podocarpaceae), species of *Pinus*, sect. *Taeda* (Pinaceae).

Most softwoods are in the medium specific gravity range.

GROWTH RINGS

PRESENCE OF GROWTH RING BOUNDARIES

40. Growth ring boundaries distinct

41. Growth ring boundaries indistinct or absent

Definitions:

Growth ring boundaries distinct = growth rings with an abrupt structural change at the boundaries between them, usually including a change in tracheid wall thickness and/or tracheid radial diameter (fig. 1, 3, 4). Macroscopically, such structural changes are accompanied by distinct differences in colour between earlywood (light) and latewood (dark).

Growth ring boundaries indistinct or absent = growth ring boundaries vague and with marked gradual structural changes, or not visible (fig. 2).

Comments:

Coniferous trees from temperate and boreal regions usually have distinct growth ring boundaries. Taxa growing under tropical conditions often have indistinct or no growth ring boundaries, those from subtropical or higher altitude tropical regions may have more or less distinct growth ring boundaries (Schweingruber 1990), e.g., species of *Dacrydium* and *Podocarpus* (Podocarpaceae). Furthermore, growth ring boundaries are usually difficult to detect macroscopically as well as microscopically in young trees of plantation-grown tropical pines, e.g., *Pinus caribaea*, *P. merkusii* (Pinaceae).

Caution:

Nonperiodical, sporadic occurrence of more or less distinct ring boundaries (due to unusual climatic extremes or traumatic events) represent so called “false” growth rings. These often discontinuous tangential zones should not be interpreted as “distinct” growth rings.

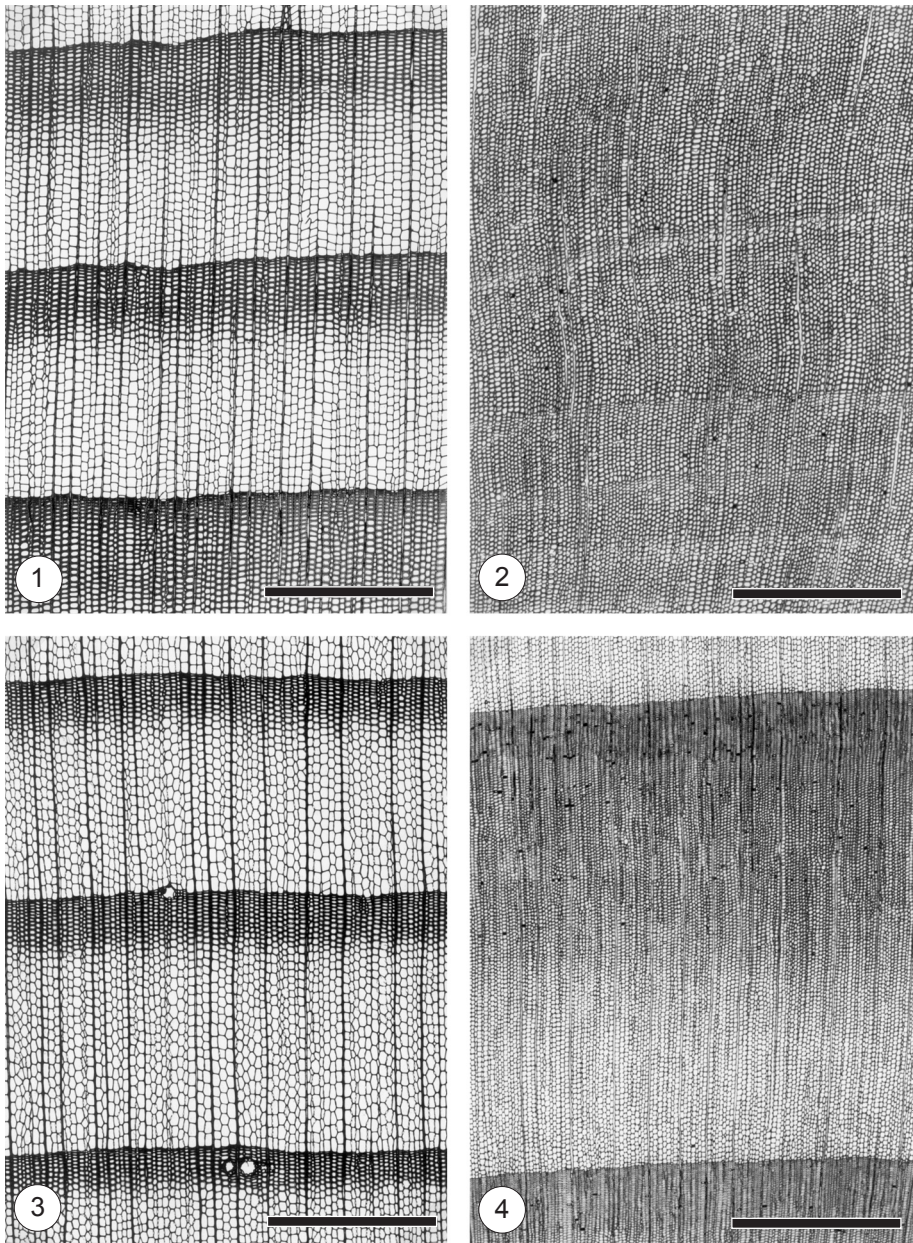


Fig. 1–4. Growth rings (features 40–43), cross sections. — 1: Growth ring boundaries distinct (feature 40). *Abies alba*. — 2: Growth ring boundaries indistinct or absent (feature 41). *Austrotaxus spicata*. — 1 & 3: Transition from earlywood to latewood abrupt (feature 42). *Larix decidua*. — 4: Transition from earlywood to latewood gradual (feature 43). *Cryptomeria japonica*. — Scale bars for 1–4 = 1 mm.

TRANSITION FROM EARLYWOOD TO LATEWOOD

42. Abrupt

43. Gradual

Definition:

The transition between earlywood and latewood of the same growth ring is marked by structural changes, usually a change in tracheid wall thickness and radial diameter. Earlywood tracheids are thin-walled and have a wide lumen whereas latewood tracheids are thicker-walled with a smaller radial diameter. The transition can be gradual or abrupt.

Comment:

An abrupt transition (***within the same growth ring***) is characteristic for *Larix* spp. (fig. 3), species of the “hard pines” group (*Pinus* spp., sect. *Taeda*), *Pseudotsuga* spp. (Core et al. 1979), and *Keteleeria davidiana* (all Pinaceae). A gradual transition is characteristic of most other softwoods with distinct growth ring boundaries (fig. 4).

Caution:

This character has limited diagnostic value as both gradual and abrupt transition may be observed in a given specimen. For example, species of *Picea* are commonly characterised by a gradual transition, but at times abrupt changes can occur due to atypical growth conditions (weather, periodic thinnings, etc.) (Krause & Eckstein 1992). On the other hand, species of *Larix* and *Pseudotsuga*, with a normally abrupt transition, may also develop gradual changes, particularly in the wide rings of fast grown trees. The transition may also be affected by compression wood, false growth rings, and flood-induced wood structure. When coding taxa for this character only mature wood free from compression wood should be considered and the predominant state entered, based on observation of several growth rings.

The very narrow growth rings resulting from slow radial growth usually do not permit a reliable differentiation of gradual vs. abrupt transition between early- and latewood. This difficulty is particularly evident in *Sequoia sempervirens* and *Thuja plicata* (Cupressaceae), *Tsuga heterophylla* (Pinaceae) and *Pseudotsuga menziesii* (Pinaceae) from old growth stands.

TRACHEIDS

TRACHEID PITTING IN RADIAL WALLS (IN EARLYWOOD ONLY)

44. (predominantly) Uniseriate**45. (predominantly) Two or more seriate***Comments:*

When coding taxa for the number of pit rows in radial walls, particularly the “uniseriate” condition, it is important to consider the entire length of the tracheid. When coding or identifying wood specimens, do not interpret the occasional presence of locally biseriate pits as the “two or more seriate” condition.

Uniseriate pitting in radial tracheid walls is the most common condition in coniferous woods (fig. 5); in *Larix* spp. (Pinaceae) pitting in earlywood tracheids is often biseriate; typically tri- or more seriate pitting (fig. 6–8) occurs in *Sequoia sempervirens*, *Taiwania cryptomerioides*, and *Taxodium* spp. (Cupressaceae) (Core et al. 1979), and in Araucariaceae.

ARRANGEMENT OF (TWO OR MORE SERIATE) TRACHEID PITTING IN RADIAL WALLS
(EARLYWOOD ONLY)**46. Opposite****47. Alternate***Comments:*

Alternate pitting occurs regularly only in members of Araucariaceae, e.g., *Agathis*, *Araucaria* (Phillips 1948) (fig. 7 & 8), and *Wollemia* (Heady et al. 2002).

Among Pinaceae a tendency toward “alternate” arrangement can occasionally be observed in *Cedrus* spp. and *Keteleeria* spp. when the pits are crowded. These can be distinguished from the Araucariaceae by the circular pit outline and by their larger size (Phillips 1948).

Pitting is usually opposite in all other taxa with multiseriate tracheid pits, e.g., in *Larix* spp. (Pinaceae) and several taxa of Cupressaceae, e.g., *Sequoia sempervirens*, *Taiwania cryptomerioides*, and *Taxodium* (fig. 6).

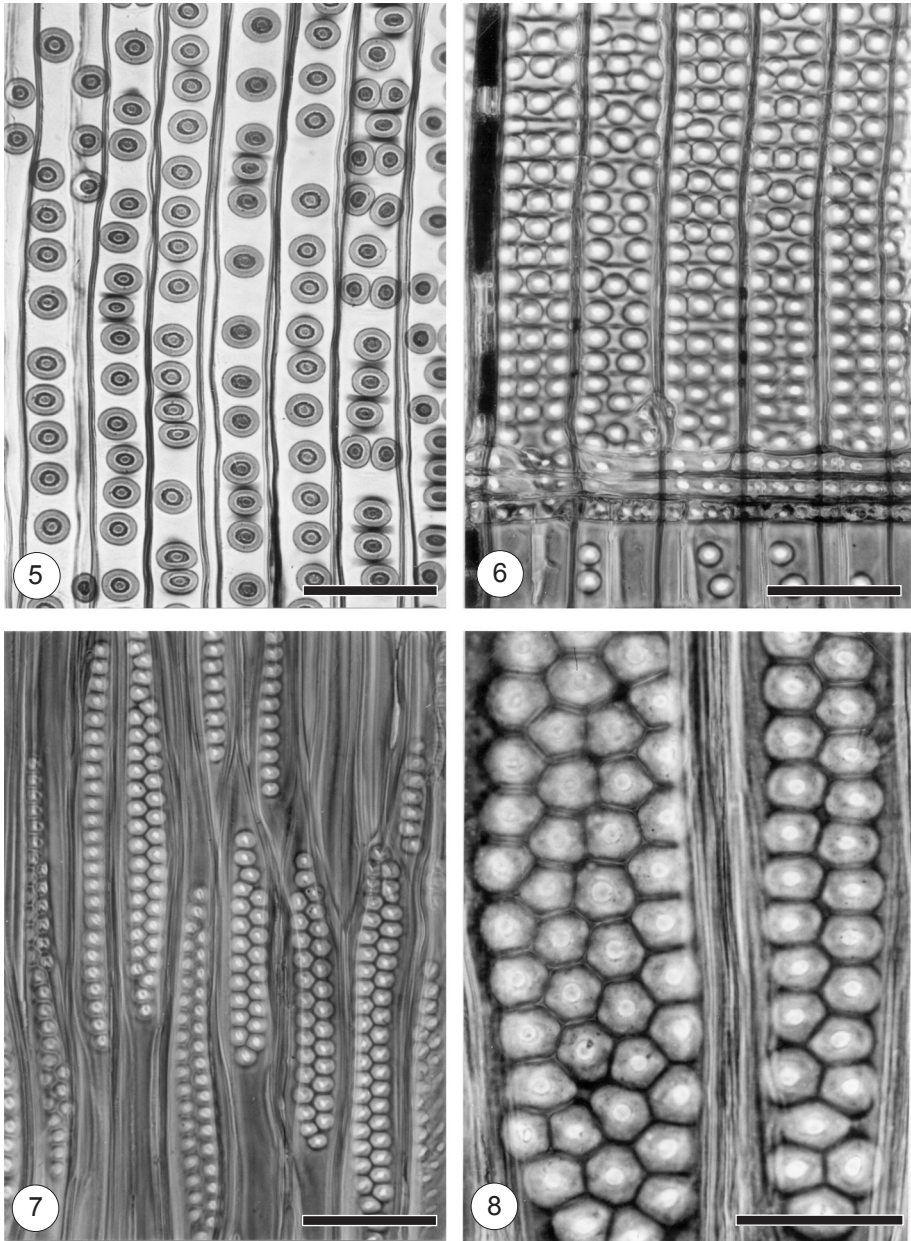


Fig. 5–8. Tracheid pitting in radial walls (features 44–47), radial sections. — 5: Tracheid pitting mostly uniseriate (feature 44). *Pinus sylvestris*. — 6: Tracheid pitting two or three seriate (feature 45) and arrangement opposite (feature 46). *Taxodium distichum*. — 7 & 8: Tracheid pitting two and more seriate (feature 45) and arrangement alternate (feature 47). *Araucaria angustifolia*. — Scale bars for 5–7 = 100 μm ; for 8 = 50 μm .

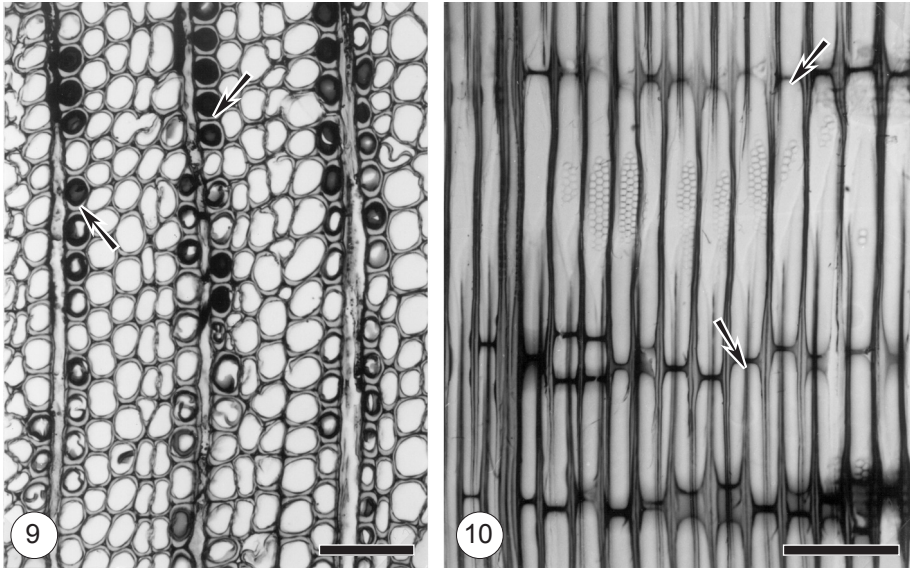


Fig. 9 & 10. Organic deposits (resin plugs) in heartwood tracheids (feature 48). – 9: *Agathis labillardieri*, cross section, see arrows. – 10. *Agathis labillardieri*, radial section, see arrows. – Scale bars for 9 & 10 = 200 μm .

ORGANIC DEPOSITS (IN HEARTWOOD TRACHEIDS)

48. Present

Comments:

Organic deposits in heartwood tracheids, variously referred to as “resin plugs”, “resin spools”, “resin plates”, are best observed in longitudinal sections.

“Resin plugs” in tracheids occur regularly in few taxa and are therefore of some diagnostic value (fig. 9 & 10). They have been reported for *Agathis* and *Araucaria* (Araucariaceae) and are generally more abundant in *Agathis* than in *Araucaria* and often occur near rays. Organic deposits in parenchyma have been recorded in *Callitris glauca*, *Calocedrus* spp., *Cupressus* spp., *Fitzroya cupressoides*, *Juniperus procera*, *J. virginiana*, *Thuja plicata*, *T. standishii*, *Widdringtonia* spp. (Cupressaceae); *Dacrydium elatum*, *Podocarpus totara*, *Prumnopitys ferruginea* (*Podocarpus ferrugineus*), *Saxegothaea conspicua* (Podocarpaceae) (Barefoot & Hankins 1982). For details about organic deposits in *Torreya grandis* var. *yunnanensis* and *Picea sitchensis* refer to Kondo et al. (1996) and Kukachka (1960), respectively.

Caution:

Very thin resin plates in tracheids tend to look like the septa in hardwood fibres. However, the absence of birefringence under polarised light will confirm the resinous nature of the plates.

In archaeological woods, the cell structure is often impregnated with residues and compounds (paint, resins, tar, dye, peat, starch, oil, iron oxides) that are completely extraneous to the wood itself and should be disregarded.

Some organic deposits such as the “floccosoids” in species of *Tsuga* (Pinaceae) may dissolve during section preparation with the use of organic solvents (dehydration), others during bleaching of microscopic sections (Krahmer et al. 1970).

The absence of organic deposits is not diagnostic.

AVERAGE TRACHEID LENGTH

49. ... < μm >

Procedure:

Use macerations of mature trunk wood, and measure the length of at least 25 tracheids to determine the range, mean, and standard deviation. Because of the importance of tracheid length in wood quality studies, a variety of methods have been developed to ensure random selection for cell measurements (e.g. Dodd 1986; Hart & Swindel 1967). Tracheid length can also be measured from microscopic sections (Ladell 1959; Wilkins & Bamber 1983) but less accurately than from macerations. It is recommended to enter a mean and range for tracheid length, e.g., 1800–**3100**–4500 μm , the standard deviation, and the number of measurements ‘n’ (IAWA Committee 1989).

Comment:

Tracheid length differs with cambial age (juvenile vs. mature wood) and between stemwood, branchwood, and rootwood. Hence, data on tracheid length should be accompanied by information on the type of wood and the sampling method used. For general trends in fibre and tracheid length variation refer to, e.g., Fujita et al. (1987) for measuring techniques, and Dinwoodie (1961) and Sudo (1968) for trends in spruce (*Picea*).

AVERAGE TRACHEID LENGTH (SIZE CLASSES)

50. Short (less than 3000 μm)

51. Medium (3000 to 5000 μm)

52. Long (over 5000 μm)

To be able to make use of length categories recorded in earlier descriptions and multiple entry keys, e.g., “short”, “medium”, “long”, an additional character for tracheid length classes has been implemented. The following categories for tracheid length are suggested (Wagenführ 1989):

- 1) short (less than 3000 μm); example: *Taxus baccata* (Taxaceae), 1550–**1950**–2250 μm
- 2) medium (from 3000 to 5000 μm); example: *Larix decidua* (Pinaceae), 2300–**3400**–4300 μm
- 3) long (more than 5000 μm); example: *Araucaria angustifolia* (Araucariaceae), 5600–**7200**–9000 μm

Tracheid length of many softwoods, however, will fall into at least two of the above categories (overlap). Examples: *Picea abies* (Pinaceae), 1300–**2800**–4300 μm ; *Pseudotsuga menziesii* (Pinaceae), 2500–**4500**–5600 μm .

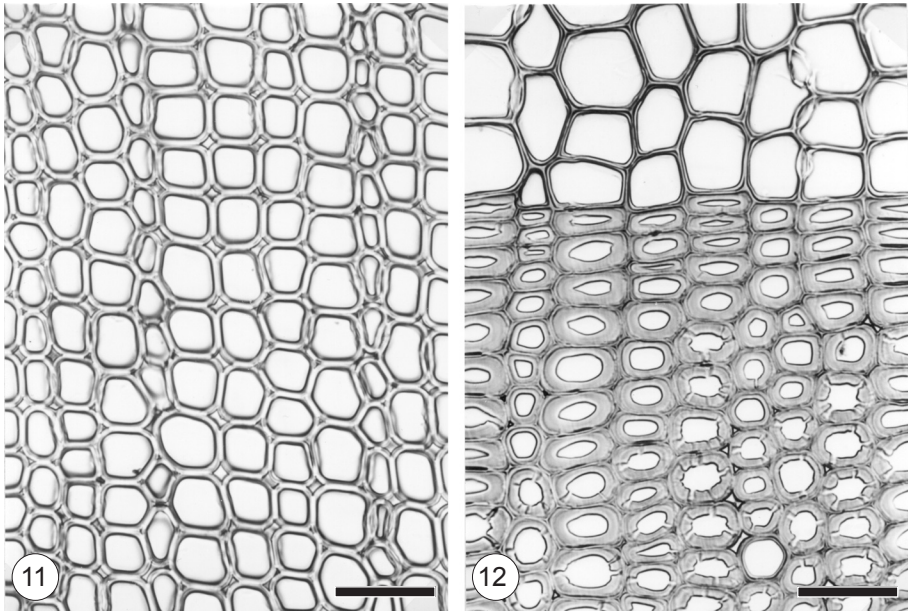


Fig. 11. Intercellular spaces between tracheids (feature 53). *Juniperus virginiana*, cross section. — Fig. 12: Compression wood. Latewood tracheids with rounded outlines and associated intercellular spaces. *Pseudotsuga menziesii*, cross section. — Scale bars for 11 & 12 = 50 μm .

INTERCELLULAR SPACES THROUGHOUT THE WOOD (in transverse section)

53. Present

Comments:

In most coniferous woods occasional small spaces between tracheids can be observed. The regular occurrence of intercellular spaces throughout the wood in conjunction with a more or less circular outline of tracheids is, however, characteristic for few taxa, e.g., *Juniperus communis*, *J. virginiana*, *Calocedrus formosana* (Cupressaceae), *Ginkgo biloba* (Ginkgoaceae – Torelli 1999). Such intercellular spaces can be recognised by their characteristic diamond shape with four slightly concave sides (fig. 11).

Cautions:

Do not record the intercellular spaces often associated with compression wood in this context (fig. 12). Compression wood can best be recognised in longitudinal sections by the spiral grooves in the secondary tracheid wall.

The absence of regular intercellular spaces is not diagnostic.

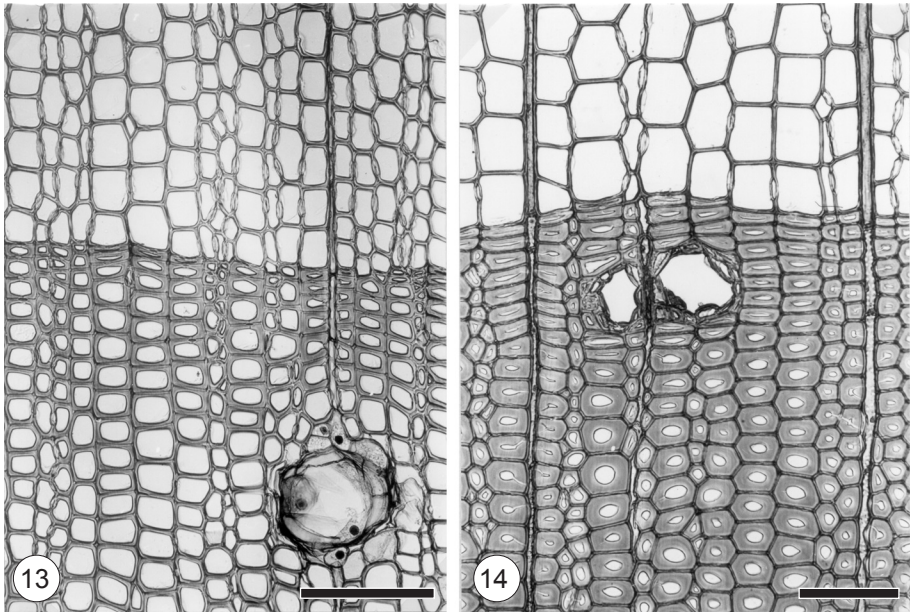


Fig. 13. Latewood tracheids thin-walled (feature 54). *Pinus strobus*, cross section. — Fig. 14. Latewood tracheids thick-walled (feature 55). *Larix decidua*, cross section. — Scale bars for 13 = 200 μm ; for 14 = 100 μm .

LATEWOOD TRACHEID WALL THICKNESS

54. Thin-walled (double wall thickness less than radial lumen diameter)

55. Thick-walled (double wall thickness larger than radial lumen diameter)

Definition:

The cell wall thickness of latewood tracheids, as used for diagnostic purposes, is based on the ratio of the double wall thickness and the lumen diameter. Since latewood tracheids are usually radially flattened the lumen outline becomes rectangular to oval and the ratio will be different in radial and tangential direction. As a common standard double wall thickness and lumen diameter should always be measured in the radial direction.

Comments:

The very time consuming effort of measuring cell wall thickness in statistically sufficient numbers is hardly justified in view of the relatively low diagnostic value of this character. Therefore, the character provides only for two categories (thin-walled and thick-walled).

Examples: thin-walled latewood tracheids (fig. 13) are characteristic for most species of the soft pines group; thick-walled latewood tracheids (fig. 14) are characteristic for most species of the southern yellow pines (*Pinus* spp.), *Larix* spp. (larch), and *Pseudotsuga menziesii* (Douglas-fir).

Caution:

Relative wall thickness should always be measured; do not rely on visual judgement for coding and/or identification.

Relative wall thickness should not be recorded for compression wood tracheids. Compression wood can best be recognised in longitudinal sections by the spiral grooves in the secondary wall.

TORUS (pits in earlywood tracheids only)**56. Present***Definitions:*

A torus is the thickened central region of the pit membrane (Wilson & White 1986). Two groups of coniferous taxa can be distinguished microscopically:

One with a well defined torus, i.e., a dense central area of the pit membrane with microfibrils deposited in circular or radial orientation (Harada et al. 1968) often incrustated with amorphous substances. The torus may be either disc-shaped (fig. 15) as in earlywood of *Abies*, *Cedrus*, *Keteleeria*, *Larix*, *Picea*, *Pinus*, *Pseudolarix*, *Tsuga* (Pinaceae); *Cryptomeria*, *Sequoia*, *Sequoiadendron* and all other Cupressaceae except *Thuja* and *Thujopsis*; in Podocarpaceae except *Saxegothaea*; in *Cephalotaxus harringtonii* (Cephalotaxaceae); or convex lens-shaped as in latewood of *Pinus* spp., *Sequoia*

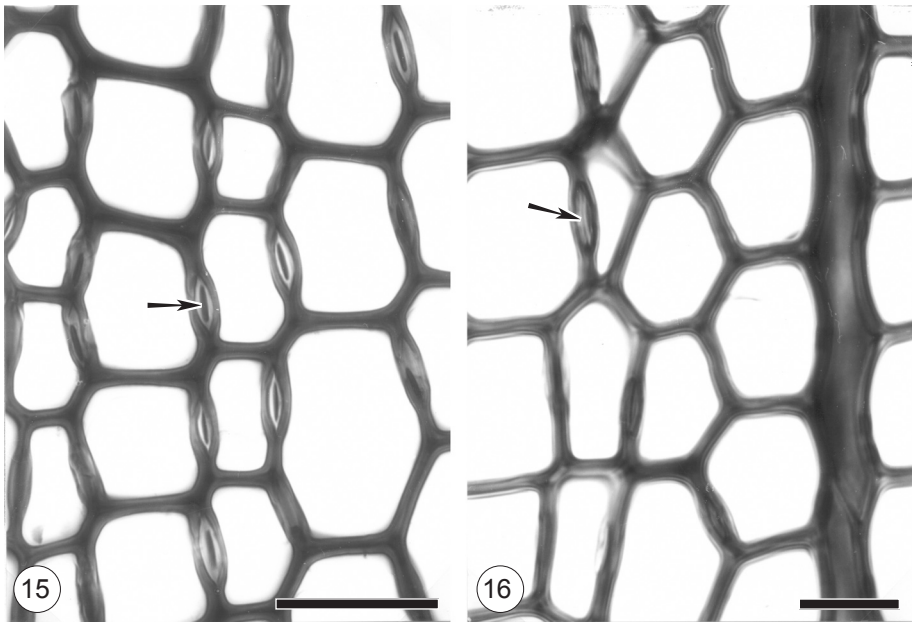


Fig. 15. Bordered pits in radial walls, with well defined disc-shaped torus, see arrow (feature 56). *Pinus sylvestris*, cross section. — Fig. 16. Bordered pits without a defined torus, see arrow (feature 56 absent). *Thuja plicata*, cross section. — Scale bars for 15 = 50 μ m; for 16 = 20 μ m.

and *Sequoiadendron*; or with a flat transition from torus to margo as in all species of *Agathis* and *Araucaria*, *Athrotaxis selaginoides*, *Cunninghamia lanceolata*, *Ginkgo biloba*, *Sciadopytis*, *Taiwania*, *Thujopsis*, all species of Taxaceae, and most species of *Thuja* (Bauch et al. 1972).

The other group is without a defined torus (fig. 16), i.e., the pit membrane is of nearly equal thickness throughout its entire extension, e.g., in Podocarpaceae, some species of *Thuja* and in *Thujopsis* (except *Thujopsis dolabrata* var. *hondae*). Within each group further subtypes are distinguished according to the orientation and density of the microfibrils and presence vs. absence of incrustations, based on scanning and transmission microscopy.

Procedure:

The torus can be best observed from unspirated pits in fresh material (transverse and tangential longitudinal sections). For light microscopic observation it is recommended to impregnate small wood blocks with polyethylene glycol (MW 1500) and cut thin sections with a razor blade. To enhance contrast, sections can be double stained with 1% aqueous solutions of astrablue and safranin (Bauch et al. 1972).

TORUS (when present)

The most common pit structure is defined by a regular and smooth outline of the pit and its torus. All deviations are attributed to one of the following special structures.

57. Scalloped

Definition:

Scalloped pits (synonym: ornamented pits) are bordered pits with an indented (“scalloped”) torus margin (IAWA Committee 1964).

Comment:

Well developed scalloped pits (fig. 17) are a characteristic feature only of the genus *Cedrus* (Pinaceae). Transitional forms can be observed occasionally in other Pinaceae, particularly *Pseudolarix* (Willebrand 1995), and in Cupressaceae.

Caution:

The absence of scalloped pits is not diagnostic; sporadic occurrence should not be coded but documented in a comment. For instance, decayed wood sometimes seems to have scalloped tori.

TORUS EXTENSIONS

58. Present

Definition:

Thickening bars (“margo straps”) in the pit membrane radiating from the torus to the margo periphery (fig. 19 & 20).

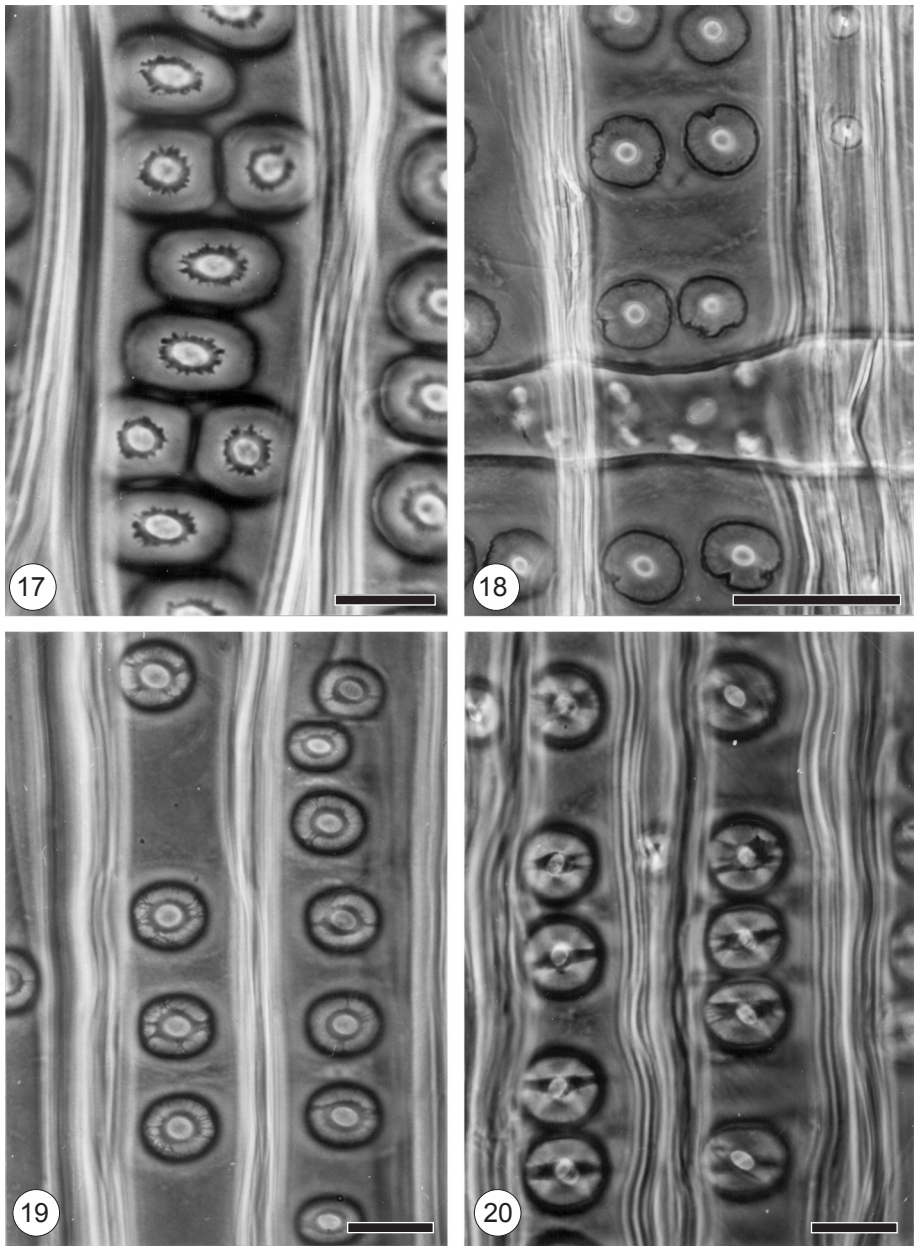


Fig. 17. Tracheid pits with scalloped torus margins (feature 57). *Cedrus atlantica*, radial section (phase contrast). — Fig. 18. Tracheid pits with notched borders on outer wall (feature 59). *Taiwania cryptomerioides*, radial section (phase contrast). — Fig. 19 & 20. Tracheid pits with characteristic torus extensions (feature 58). — 19: *Tsuga heterophylla*, radial section (phase contrast). — 20: *Lagarostrobos (Dacrydium) franklinii*, radial section (phase contrast). — Scale bars for 17, 19 & 20 = 20 μ m; for 18 = 50 μ m.

Comment:

Most textbooks refer to torus extensions as agglomerations of cellulose microfibrils forming dense straps extending radially from the torus to the margo periphery. Torus extensions can be observed most clearly under phase contrast and occur regularly in *Tsuga* (Pinaceae), *Widdringtonia* (Cupressaceae), and in *Lagarostrobos franklinii* (*Dacrydium franklinii*) (Podocarpaceae). Examples for a more sporadic presence are: *Abies sachalinensis* (Sano et al. 1999), *Actinostrobus* spp., *Fitzroya*, *Juniperus* spp., *Pilgerodendron*, *Thujopsis* (Cupressaceae), and *Abies* spp. (Pinaceae) (Willebrand 1995).

Caution:

Use this feature only when clearly visible (viz. *Lagarostrobos franklinii*); sporadic occurrence should not be coded but documented in a respective comment.

PITS WITH NOTCHED BORDERS**59. Present***Description:*

“Pits with notched borders” refer to local notches in the outer border of the pit (fig. 18). There may be one or a few notches at a distance from each other, or a series of consecutive notches rendering the periphery of the pit chamber irregular.

Comment:

A more or less common occurrence of notches in the pit border has been observed only in few species in particular genera (Willebrand 1995), i.e., *Athrotaxis cupressoides*, *A. selaginoides*, *Chamaecyparis pisifera*, *Cryptomeria*, *Cupressus dupreziana*, *Juniperus thurifera*, *Papuacedrus papuana*, *Sequoia*, *Taiwania*, and *Thuja occidentalis* (Cupressaceae), and in species of *Torreya* (*T. californica*, *T. nucifera* and *T. taxifolia*), Taxaceae. Due to its restricted occurrence this character appears to be of considerable diagnostic value in identification (Willebrand 1995), for example to separate the otherwise nearly identical woods of *Sequoia* and *Sequoiadendron*.

Caution:

Do not mistake bacterial or fungal degradation (“eroded pits” according to Phillips 1948) of the pit border for notches in the pit border. Enzymatic decomposition affects the entire pit, i.e., borders, membranes and tori, while notches are restricted to the pit borders.

WARTY LAYER (visible under the light microscope)**60. Present***Definition:*

Warts are small, unbranched protuberances on the inner layer of the secondary wall (S₃ or tertiary wall) of tracheids in gymnosperms (for detailed information on the warty layer see Wardrop & Davis 1962, Cronshaw 1965, Liese 1965, Takiya et al. 1976, Ohtani et al. 1984, Fujii 2000), and of vessel elements and fibres in dicotyledons. Warts

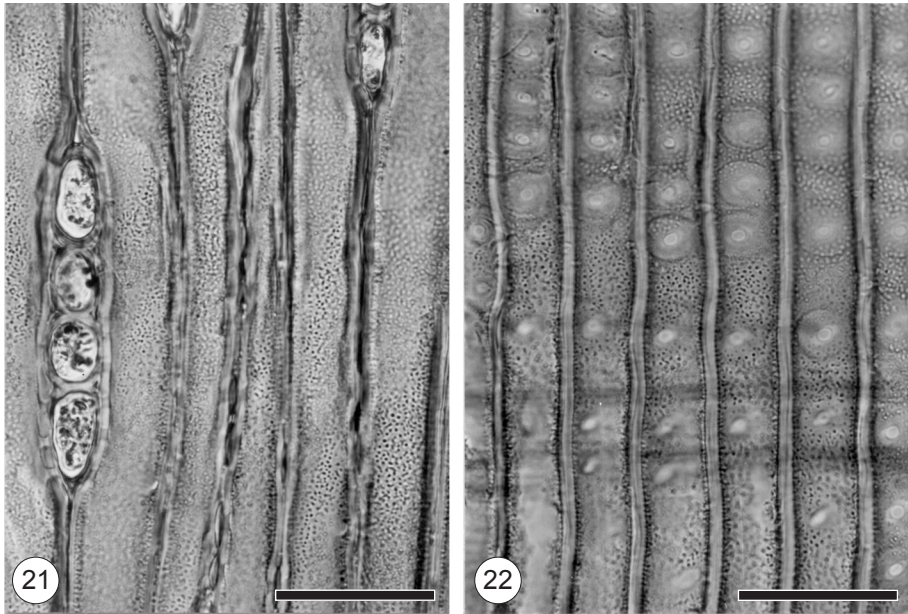


Fig. 21 & 22. Warty layer (feature 60), *Actinostrobus pyramidalis*. – 21: Tangential section. – 22. Radial section. — Scale bars for 21 & 22 = 50 μm .

are mainly composed of lignin and hemicelluloses and develop outside the plasma membrane forming an innermost layer of the cell wall distinct from the S_3 layer. Consequently, a true wart structure can be described as a thin layer lining the S_3 with small protrusions or warts. The warts are clearly revealed by electron microscopy, and in some instances coarse enough in texture to be detected by light microscopy (e.g., *Actinostrobus pyramidalis* in fig. 21 & 22, and species of *Callitris* in fig. 27). The average diameter of the individual warts is usually between 100 and 500 nm, rarely up to 1 μm , the average height between 500 nm and 1 μm (Liese 1957; Ohtani & Fujikawa 1971; Ohtani 1979). Distribution, size and frequency of warts show considerable variation between taxa (Liese 1965). The ontogeny and possible function of the warty layer have been the subject of numerous investigations (see Jansen et al. 1998).

Comments:

A warty layer is present in most coniferous taxa (Jansen et al. 1998). It has been reported as absent in some species of *Pinus* (Frey-Wyssling et al. 1955), *Taxus cuspidata*, *Taxus floridana*, *Torreya nucifera* (Taxaceae), *Cephalotaxus harringtonii* (Cephalotaxaceae), *Podocarpus macrophyllus* and *Nageia nagi* (Podocarpaceae) (Harada et al. 1968). Its presence can constitute a valuable aid in wood identification. Particularly large and densely packed warts, e.g., in *Callitris columellaris* (Ilic 1994), can be easily observed under the light microscope. Smaller and less numerous warts, e.g., in *Cedrus*, usually require electron microscopy for reliable observation.

Warts have been reported in Cupressaceae (*Athrotaxis*, *Callitris*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*, *Fitzroya*, *Juniperus*, *Sequoia*, *Sequoiadendron*, *Tetraclinis*, *Thuja*, *Thujopsis*, *Widdringtonia*), Pinaceae (*Abies*, *Cedrus*, *Pinus bungeana*, *P. massoniana*), and some Podocarpaceae (*Podocarpus*). For additional information consult the above cited literature.

HELICAL AND OTHER WALL THICKENINGS

HELICAL THICKENINGS IN TRACHEIDS

Definition:

Helical thickenings are ridges on the inner face of the tracheids. They may occur in both longitudinal as well as ray tracheids and usually extend over the entire body of the respective cell (fig. 23–26).

Comments:

Helical thickenings in longitudinal tracheids differ between taxa in terms of grouping (single or in pairs), spacing, inclination angle, thickness, branching, and connection to the inner cell wall (fig 23–25). Some of these parameters can be quantified and thus covered by individual character states, others are extremely variable and/or difficult to quantify. Such information should therefore be covered in a comment.

For grouping (single or in pairs) and spacing (number per axial mm) separate characters have been introduced (see below).

Inclination angle and thickness are somewhat correlated with spacing, i.e., spirals in taxa with narrow spacing such as *Pseudotsuga* and some species of *Picea* are thinner and tend to be rather flat forming a large angle with the cell axis (about 80° to nearly horizontal = 90° in fig. 24) while spirals with wider spacing, e.g., *Amentotaxus*, *Cephalotaxus*, *Taxus*, *Torreya*, are generally thicker and steeper (fig. 23). However, these are trends difficult to quantify as in any given specimen inclination angle and thickness may vary within the entire possible range.

Yoshizawa et al. (1985) report that helical thickenings in *Taxus*, *Torreya* and *Cephalotaxus* have a narrow base loosely connected to the inner layer of the secondary wall (S₃). On the other hand, the helical thickenings in *Pseudotsuga* have a broader base which is securely fastened to the S₃ layer by means of connecting microfibrils.

Caution:

Do not confuse helical thickenings with the “spiral grooves” typical of compression wood tracheids. Such grooves are openings ‘in’ the secondary wall usually running at fairly steep angles (around 45 degrees - Onaka 1949) to the cell axis.

Helical thickenings may also be confused with the often helical structure of soft rot cavities in cell walls caused by the enzymatic action of wood destroying fungi (Phillips 1948), or spiral etchings caused by chemical degradation in the surface layers of weathered timber (Feist 1990). Both types can often be seen in archaeological material.

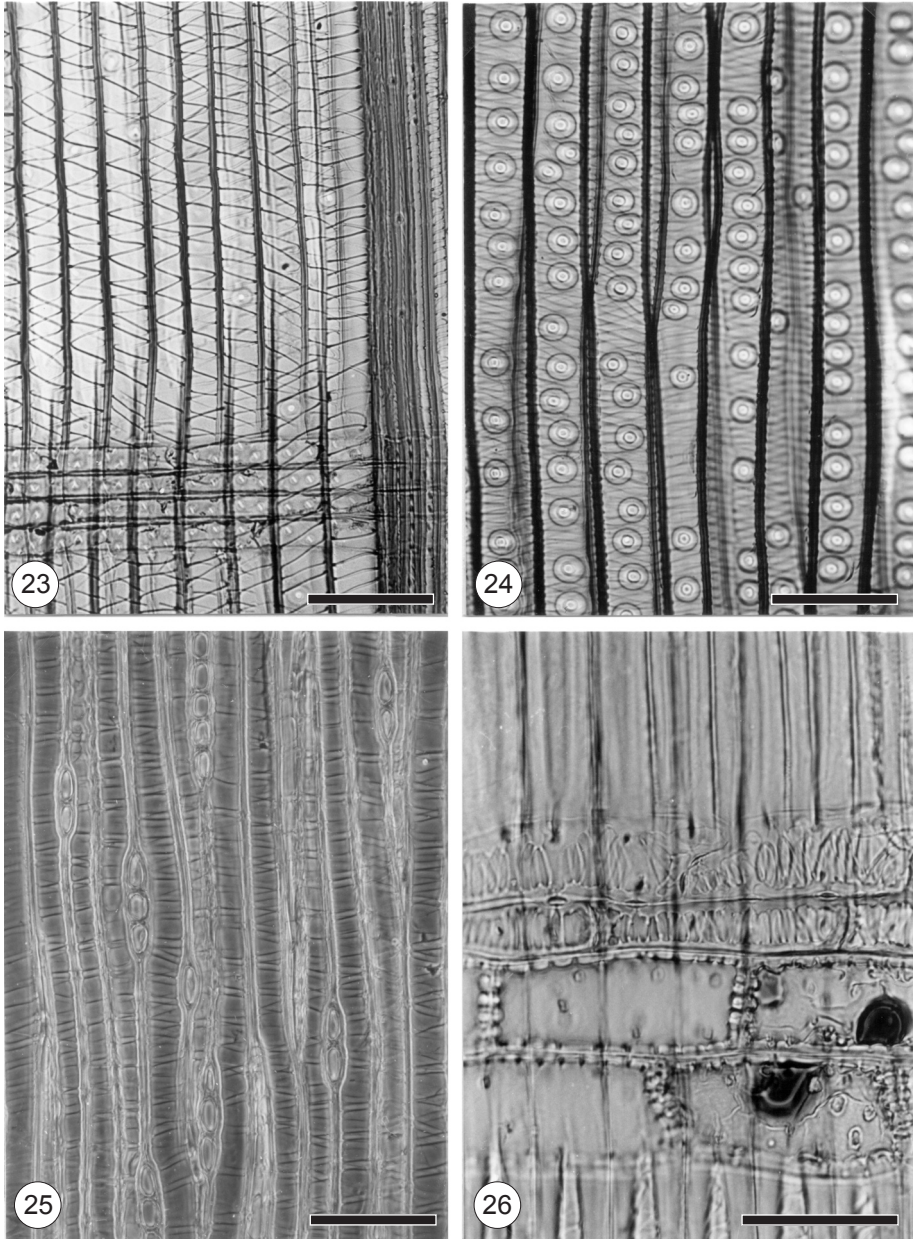


Fig. 23–25. Helical thickenings in longitudinal tracheids (feature 61). – 23: Helical thickenings single and widely spaced (features 65 & 68). *Taxus baccata*, radial section. – 24: Helical thickenings single and narrowly spaced (features 65 & 67). *Pseudotsuga menziesii*. – 25: Helical thickenings grouped in pairs and widely spaced (features 66 & 68). *Torreya californica*, tangential section (phase contrast). – Fig. 26. Helical thickenings in ray tracheids (feature 69). *Pseudotsuga japonica*, radial section. – Scale bars for 23–25 = 100 μm ; for 26 = 50 μm .

HELICAL THICKENINGS IN LONGITUDINAL TRACHEIDS (presence)**61. Present****HELICAL THICKENINGS (in longitudinal tracheids - location)****62. Present throughout the growth increment****63. Well developed only in earlywood****64. Well developed only in latewood**

Helical thickenings in longitudinal tracheids well developed throughout the growth increment, e.g., in *Amentotaxus*, *Taxus*, *Torreya* (Taxaceae) and *Cephalotaxus* (Cephalotaxaceae).

Helical thickenings in longitudinal tracheids well developed in earlywood but often poorly developed or missing in latewood tracheids, e.g., in *Pseudotsuga* (Pinaceae).

Helical thickenings in longitudinal tracheids well developed in latewood but often poorly developed or missing in earlywood tracheids, e.g., in *Larix potaninii* var. *himalaica* and some species of *Picea* (Pinaceae).

Comment:

In some species of *Picea* as well as in *Torreya* and *Cephalotaxus* helical thickenings may be present in branches and absent in stemwood (Yatsenko-Khmelevsky 1954). They have also been observed in the latewood of young stems and branches of *Larix* spp. (Yatsenko-Khmelevsky 1954; Chavchavadze 1979).

HELICAL THICKENINGS (in longitudinal tracheids - whether single or grouped)**65. Single****66. Grouped (double or triple)**

Helical thickenings usually single, e.g., in *Taxus* (Taxaceae) (fig. 23) and *Pseudotsuga* (Pinaceae) (fig. 24).

Helical thickenings typically grouped in pairs, e.g., in *Torreya* (Taxaceae) (fig. 25) and *Amentotaxus* (Taxaceae), in *Torreya* occasionally also as triplets.

In *Cephalotaxus* (Cephalotaxaceae) they may or may not be grouped.

HELICAL THICKENINGS (in longitudinal tracheids - spacing, earlywood tracheids only)**67. Narrowly spaced (number of coils more than 120 per mm)****68. Widely spaced (number of coils less than 120 per mm)**

The spacing of helical thickenings is considered narrow when there are commonly more than 120 per axial mm as in *Pseudotsuga* (120–180) (fig. 24) and *Picea smithiana* (150–200). The spacing is considered wide when the number is commonly less than 120 per axial mm as in *Torreya* with 80–100 (= 40 to 50 pairs), and *Taxus* (40–80) (fig. 23). *Cephalotaxus* (Cephalotaxaceae) with 80–140 may fall in either category depending on species and/or specimen.

Procedure:

The number of coils of helical thickenings per axial mm can be counted most easily in radial sections, in “optical section” of the tangential tracheid walls, rather than in surface view where helical thickenings of adjoining tracheids can be confused with each other.

HELICAL THICKENINGS IN RAY TRACHEIDS**69. Commonly present****70. (present but) Rare**

Helical thickenings in ray tracheids of mature stem wood commonly present, e.g., in *Pseudotsuga japonica* (fig. 26), some species of *Larix* (*L. potaninii* var. *himalaica* - Suzuki & Noshiro 1988), and *Picea* (*P. polita* = *P. torano* - Sudo 1968 and *P. abies* - fig. 40).

Helical thickenings in ray tracheids of mature stem wood are of rare occurrence in *Pseudotsuga menziesii* and *Larix kaempferi*.

Comment:

Helical thickenings in ray tracheids have also been observed occasionally in the latewood of young stems and branches of *Larix* spp. (Yatsenko-Khmelevsky 1954; Chavchavadze 1979).

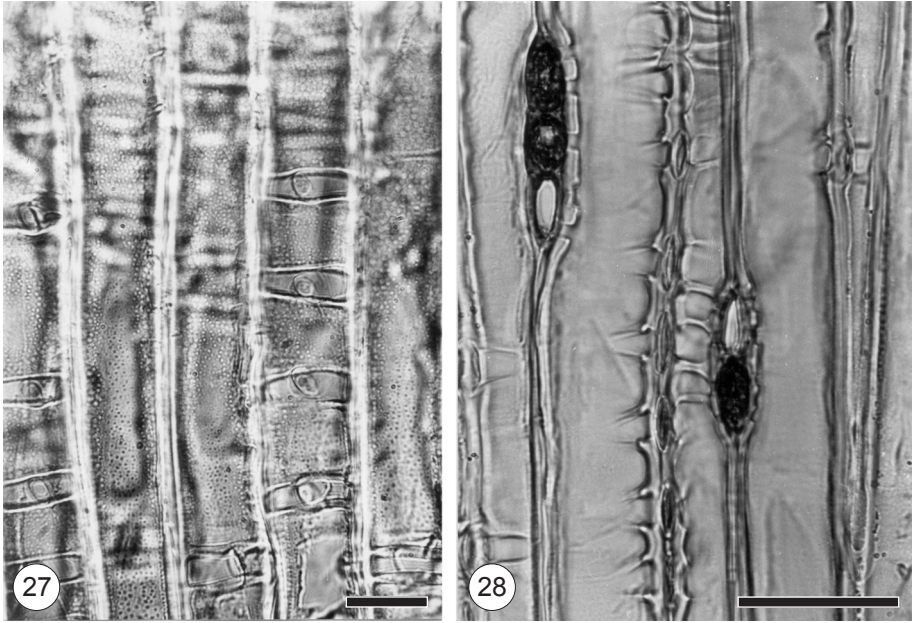


Fig. 27 & 28. Callitroid thickenings (feature 71). – 27: Tracheids also with a warty layer (feature 60). *Callitris preissii*, radial section. – 28: *Callitris columellaris*, tangential section. — Scale bars for 27 = 20 μm ; for 28 = 50 μm .

CALLITROID THICKENINGS

71. Present

Definition:

Callitroid thickenings are pairs of horizontal ridges enclosing (above and below) individual bordered pit pairs between tracheids (radial section) (fig. 27). Tangentially, they resemble awnings (roof-like overarched structures) (fig. 28). Synonyms: “callitrisoid” thickenings, “pits with awnings”.

Comments:

Callitroid thickenings occur mainly in species of the genus *Callitris* (Cupressaceae) except in *Callitris macleayana*. Phillips (1948) reports the occurrence of a few callitroid thickenings also in *Actinostrobus acuminatus* (Cupressaceae) and *Pseudolarix* spp. (Pinaceae).

SEM studies on *Callitris* by Heady & Evans (2000) have shown that callitroid thickenings may also occur in cross-field pits.

AXIAL PARENCHYMA

AXIAL PARENCHYMA (excluding epithelial and subsidiary cells of intercellular canals)

72. Present*Definitions:*

Parenchyma cells are responsible for storage of metabolites, and consist of cells with (almost always) simple pits that have not undergone intrusive tip-growth during differentiation from the xylem mother cells.

Ray parenchyma is present in all extant coniferous woods whereas axial parenchyma may be present or absent and thus constitutes a valuable character for identification.

Comments:

Axial parenchyma in coniferous woods is not as common as in hardwoods. When present but sparse, it is often located in the latewood. Axial parenchyma is absent in Araucariaceae, Phyllocladaceae, Sciadopityaceae, and Taxaceae.

Axial parenchyma is a regular feature of Cephalotaxaceae, Cupressaceae, and most Podocarpaceae.

Determine the presence of axial parenchyma and its predominant pattern(s) from the cross section using a broad field of view as even in taxa with a regular occurrence axial parenchyma may be sparse or absent in individual growth increments.

In longitudinal sections axial parenchyma can be recognised by the short length of the cells (subdivision of the fusiform initial yields a strand of axial parenchyma cells) with either smooth or irregularly thickened transverse walls.

Fusiform parenchyma (derived from fusiform initials without subsequent transverse division) has been observed only in the wood of young stems and branches of several genera of Pinaceae, and may be diagnostically useful when differentiating *Larix* and *Picea* branchwood (Noshiro & Fujii 1994).

Caution:

Although axial parenchyma in coniferous woods can usually be recognised by the frequent presence of dark contents, such contents may be removed during sample preparation. Equally, in decayed or archaeological wood (certainly in fossil wood) parenchyma cells may lack dark contents and are then more easily searched for in longitudinal sections.

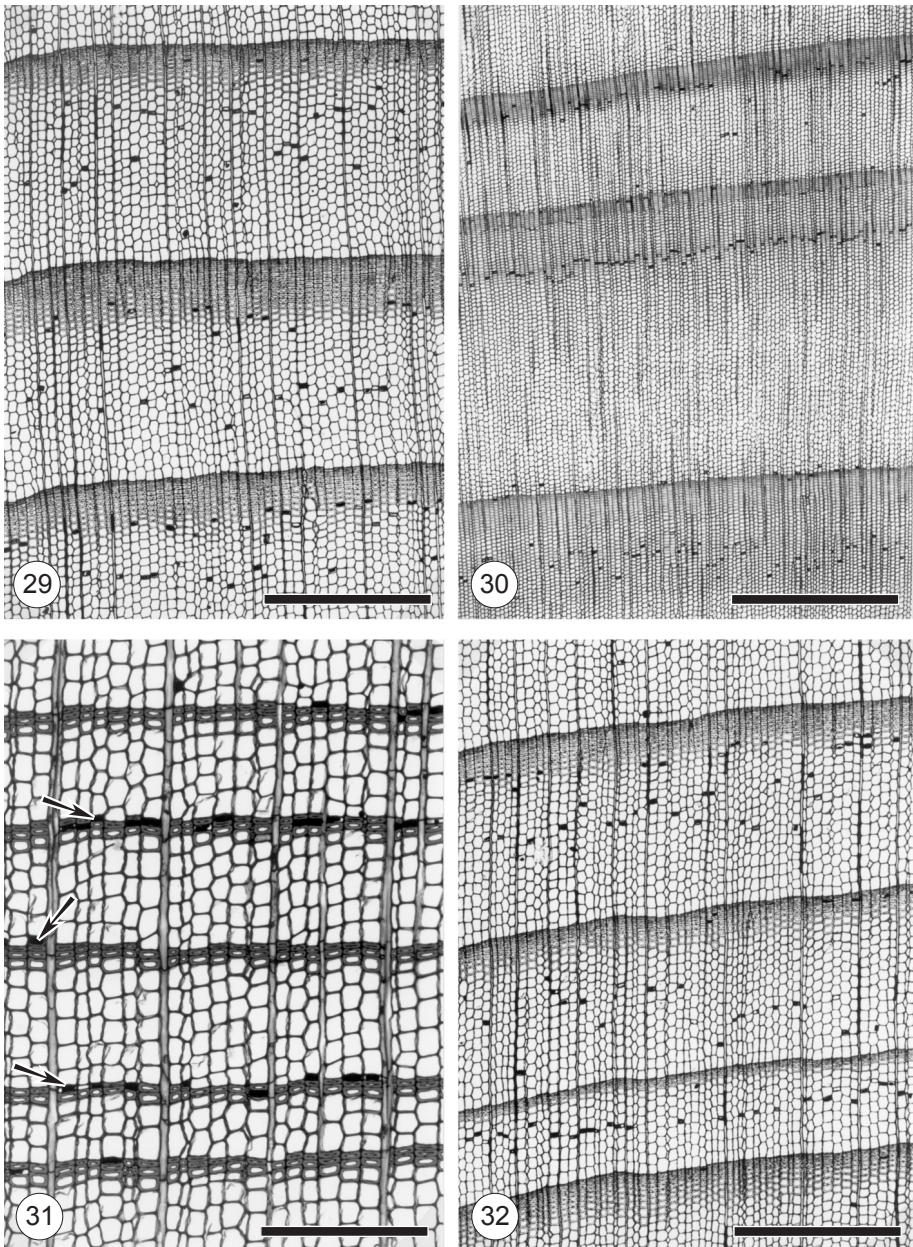


Fig. 29–32. Axial parenchyma present (feature 72), cross sections. – 29: Arrangement diffuse (feature 73). *Taxodium distichum*. – 30: Arrangement tangentially zonate (feature 74). *Cryptomeria japonica*. – 31: Arrangement tangentially zonate in latewood at the growth ring boundary, see arrows (features 74 & 75). *Sequoia sempervirens*. – 32: Arrangement diffuse and tangentially zonate (features 73 & 74). *Taxodium distichum*. — Scale bars for 29–32 = 1 mm.

ARRANGEMENT OF AXIAL PARENCHYMA**73. Diffuse (evenly scattered throughout the entire growth increment)****74. Tangentially zonate****75. Marginal***Definitions:*

Axial parenchyma diffuse = single parenchyma strands or pairs distributed evenly among the tracheids throughout the entire growth increment, e.g., *Taxodium distichum* (fig. 29), Cephalotaxaceae, Podocarpaceae.

Axial parenchyma tangentially zonate = parenchyma strands grouped into short or longer tangential (or oblique) lines more or less parallel to the growth ring boundaries, most frequent in the transition zone from earlywood to latewood or in latewood, e.g., Cupressaceae s.l. (sensu Farjon 2001) (fig. 30 & 31).

Marginal = single cells along the growth ring boundaries in the first row of earlywood or the last row of latewood, e.g., both juvenile and mature wood in certain species of *Abies*, *Cedrus*, *Keteleeria*, *Larix*, *Pseudotsuga*, and *Tsuga* (Pinaceae), and *Sequoia* (Cupressaceae) (fig. 31). It is more frequent in juvenile than in mature wood (Noshiro & Fujii 1994).

Comment:

In a given taxon axial parenchyma can be either diffuse or tangentially zonate or both (fig. 32). The more easily visible tangentially zonate axial parenchyma is characteristic for the genera *Callitris*, *Calocedrus*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*, *Juniperus*, *Taiwania*, *Taxodium* and *Thuja* (Cupressaceae), but may be missing or very sparse in individual specimens. It is most readily observed in transverse sections as cells with dark contents. However, its presence must always be confirmed from longitudinal sections by looking for the characteristic transverse end walls (see following character).

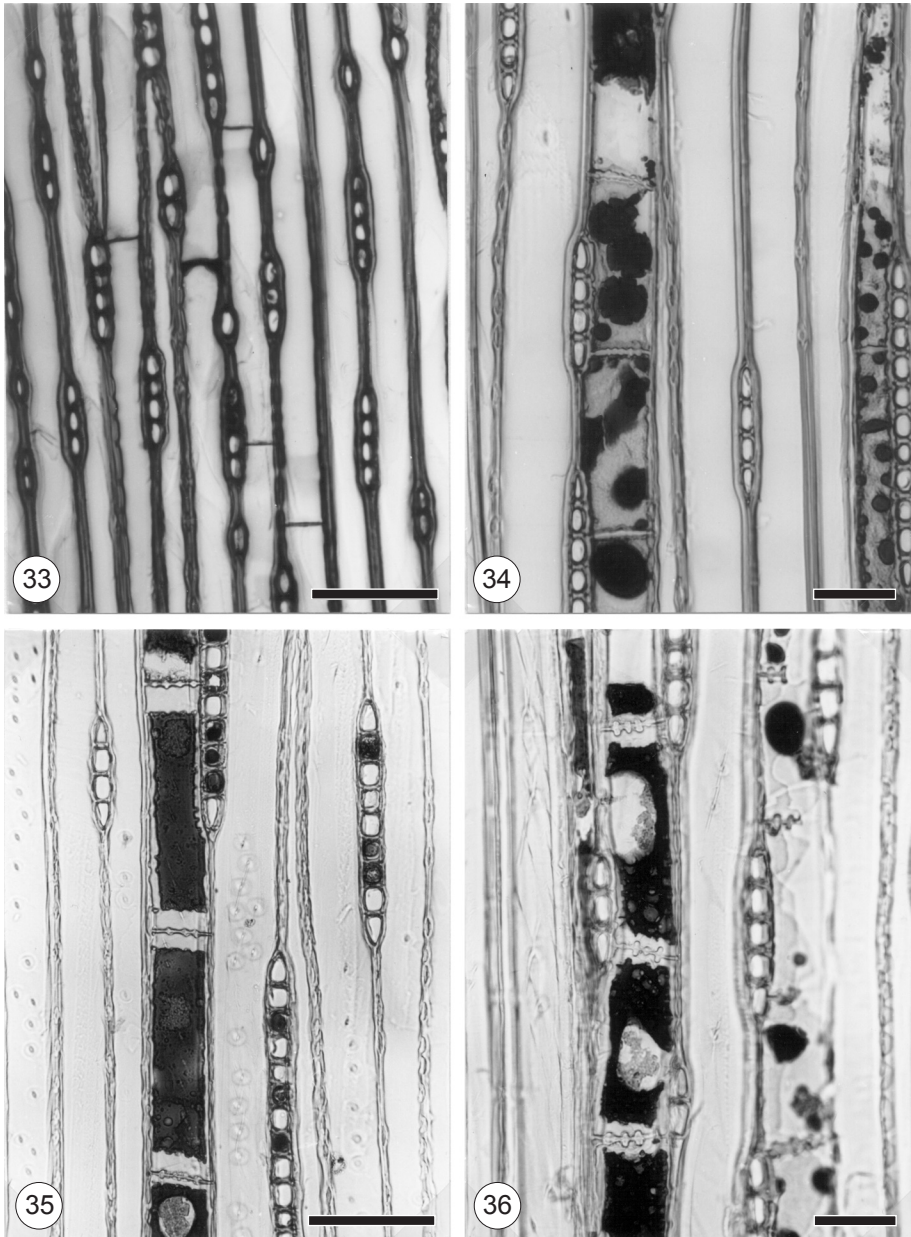


Fig. 33–36. Transverse end walls of axial parenchyma cells, tangential sections. – 33: End walls smooth (feature 76). *Podocarpus elongatus*. – 34: End walls irregularly thickened (feature 77). *Cryptomeria japonica*. – 35 & 36: End walls beaded or nodular (feature 78). *Taxodium distichum*. — Scale bars for 33 & 35 = 100 μ m; for 34 & 36 = 50 μ m.

TRANSVERSE END WALLS**76. Smooth****77. Irregularly thickened****78. Beaded or nodular**

Transverse end walls of axial parenchyma cells, observed in both tangential and radial sections, can be either smooth, irregularly thickened, or beaded/nodular.

Smooth end walls are present in *Callitris*, *Xanthocyparis* (*Chamaecyparis*) *nootkatensis*, *Tetraclinis articulata*, *Thuja occidentalis*, *Widdringtonia* spp. (Cupressaceae) and *Dacrydium cupressinum*, *Podocarpus* spp. (Podocarpaceae) (fig. 33).

Irregularly thickened end walls are a characteristic feature of *Chamaecyparis thuyoides* and *Cryptomeria japonica* (fig. 34). In most species with smooth end walls, some irregularly and inconspicuously thickened end walls also occur.

Markedly beaded or nodular end walls are commonly observed in, e.g., *Taxodium distichum* (fig. 35 & 36), *Calocedrus decurrens* and *C. formosana*, *Chamaecyparis obtusa* and *C. pisifera*, many species of *Juniperus*, *Thuja standishii*, and *Thujopsis dolabrata* (Cupressaceae), and *Abies*, *Cedrus*, *Keteleeria*, *Pseudolarix*, *Pseudotsuga*, and *Tsuga* (Pinaceae).

In Cupressaceae the nodular appearance is due to localised thickening of the primary wall, and is not due to pitting in the strict sense, whereas in *Abies*, *Cathaya*, *Keteleeria*, *Larix*, *Picea*, *Pseudotsuga*, *Tsuga*, a similar appearance is produced by true simple pitting of the secondary wall (Phillips 1948).

Nodular end walls are generally more conspicuous in tangential sections where they commonly appear either singly (e.g., *Cupressus macrocarpa*), or in series of two or more nodules per end wall. The localised thickenings and pits or pit fields (in *Abies*, *Cathaya*, *Larix*, *Keteleeria*, *Picea*, *Pseudotsuga*, *Tsuga*) are so arranged on these walls that in radial sections only a single nodule is visible (Phillips 1948; Yatsenko-Khmelevsky 1954).

Caution:

Nodular or beaded walls are often obscured by resin.

In *Taxodium distichum* and possibly other taxa, only on occasion and then in limited areas (e.g., juvenile wood) are the end walls smooth or nearly smooth.

RAY COMPOSITION

RAY TRACHEIDS

79. Commonly present**80. Absent or very rare***Definition:*

A ray tracheid is a tracheid (imperforate wood cell with bordered pits to congeneric elements (IAWA Committee 1964)) forming part of a ray. In coniferous woods only two kinds of rays are distinguished: rays composed solely of parenchyma cells (fig. 38), and rays composed of parenchyma cells and ray tracheids (fig. 37).

Comments:

To verify the presence of ray tracheids search very carefully for bordered pits, especially in common endwalls of two adjoining marginal and/or sub-marginal ray cells.

Ray tracheids are a regular feature of all Pinaceae that possess normal intercellular resin canals (see corresponding character), excluding *Tsuga*, and in *Xanthocyparis* (*Chamaecyparis*) *nootkatensis* (Cupressaceae) in which some rays may consist entirely of tracheids, others only of parenchyma cells.

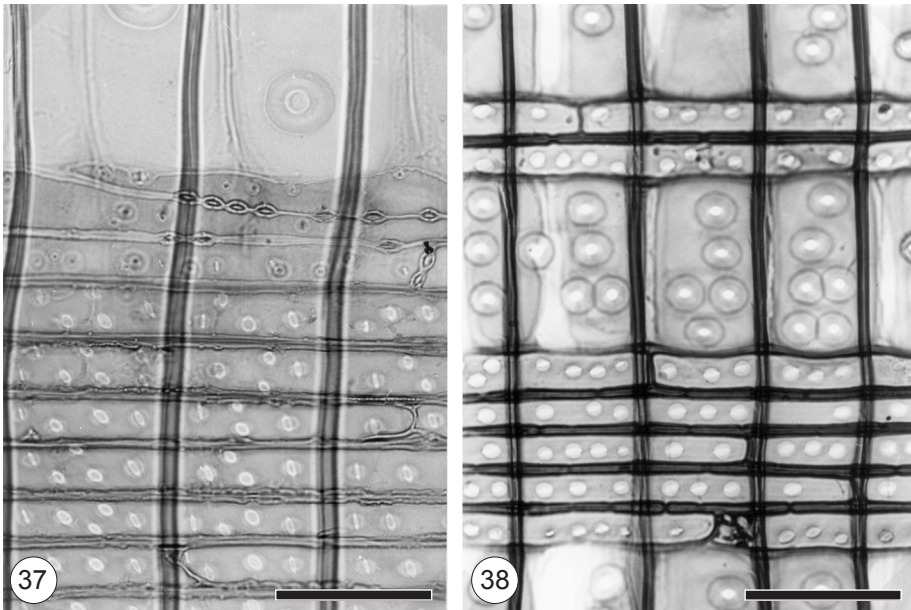


Fig. 37 & 38. Ray composition, radial sections. – 37: Ray with three rows of ray tracheids along upper part of ray (feature 79). *Picea abies*. – 38: Ray tracheids absent (feature 80). *Taxodium distichum*. — Scale bars for 37 & 38 = 50 μ m.

In genera of Pinaceae without normal resin canals ray tracheids are relatively frequent in *Cedrus* and *Tsuga*, but very rare in *Abies* and *Pseudolarix*. They are equally rare in some Cupressaceae, e.g., *Cupressus arizonica*, *Sequoia*, *Thujopsis dolabrata* (Phillips 1948). In these taxa only a few rays may feature ray tracheids in the marginal cell rows, at times mixed with normal ray parenchyma cells.

Ray tracheids may form usually only one (e.g., *Pseudotsuga*, *Tsuga*), one to occasionally 2 or 3 (e.g., *Larix*, *Picea*), or commonly several marginal cell rows (e.g., *Pinus* spp.). Some rays may be composed solely of tracheids as, for instance, in species of *Pinus* (belonging to the southern yellow pines) with more abundant ray tracheids and, very rarely, in species of *Picea* and *Larix* (Yatsenko-Khmelevsky 1954; Chavchavadze 1979). In species of *Pinus* rows of ray tracheids may be located not only at the upper and lower margins but also in the interior of the ray (Core et al. 1979).

Caution:

Archaeological material should be examined very carefully as the pit borders can be distorted or obscured by physical degradation and decay of cell walls.

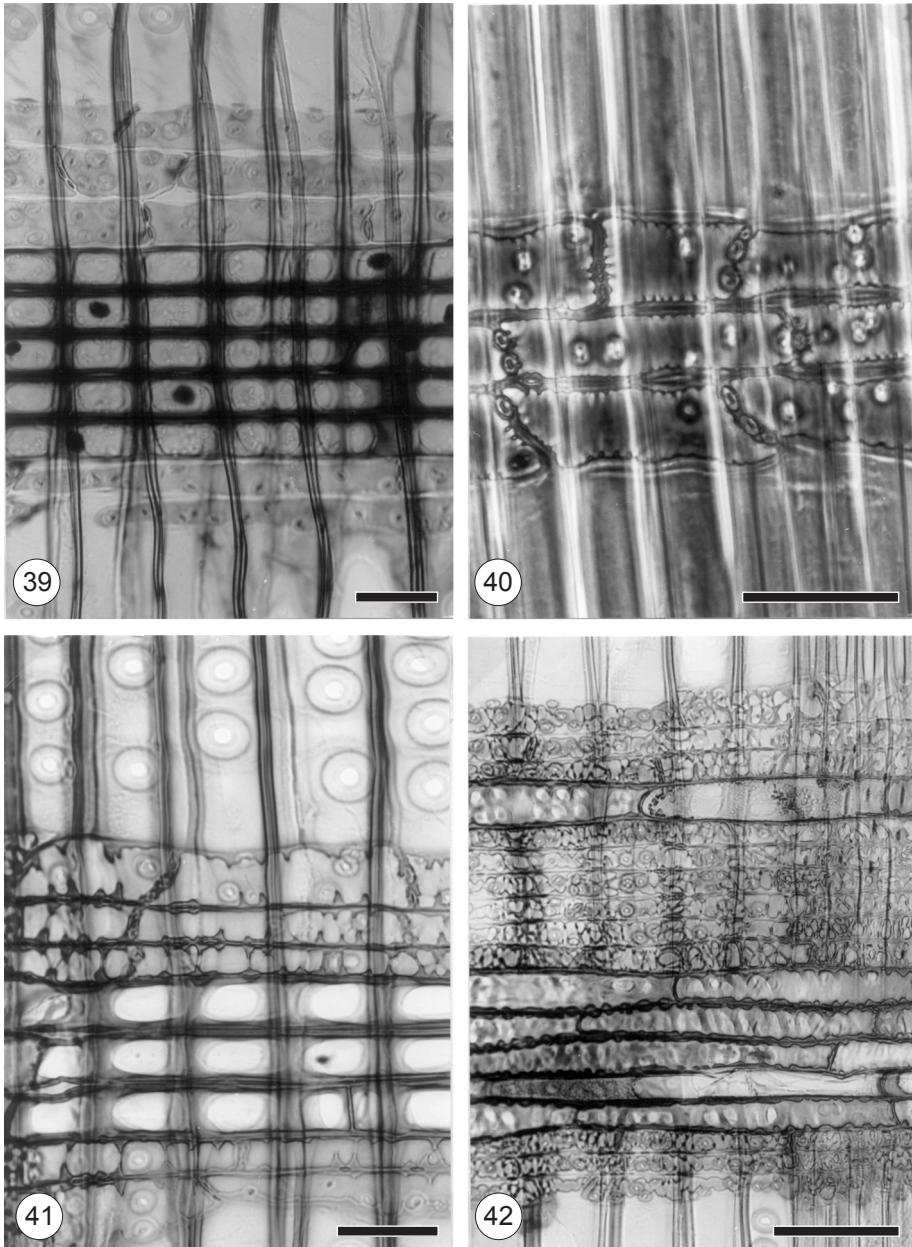


Fig. 39–42. Cell walls of ray tracheids, radial sections. – 39: Cell walls smooth (feature 81). *Pinus strobus*. – 40: Cell walls with helical thickenings resembling fine dentations (feature 69). *Pinus strobus*. – 41: Cell walls dentate, dentations prominent (feature 82). *Pinus sylvestris*. – 42: Cell walls reticulate (feature 83). *Pinus ponderosa*. — Scale bars for 39–41 = 50 μm ; for 42 = 100 μm .

CELL WALLS OF RAY TRACHEIDS**81. Smooth****82. Dentate****83. Reticulate**

Definitions (adopted from Rol 1932):

Ray tracheids smooth: walls with no ornamentation at all, and generally thin, e.g., in the “soft pines” group (*Pinus*, sect. *Strobus*, e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. strobus*) (fig. 39).

Ray tracheids dentate: walls of variable thickness bearing pronounced internal tooth-like protrusions from the upper and lower cell wall, generally more numerous in late-wood (fig. 41). These dentations are very prominent in *Pinus*, sections *Sylvestris* (e.g., *P. densiflora*, *P. nigra*, *P. resinosa*, *P. sylvestris*) and *Ponderosa* (e.g., *P. contorta*, *P. patula*, *P. pinaster*, *P. ponderosa*, *P. radiata*), and less prominent and with outer tracheid walls typically sinuous, e.g., in *Pinus*, sections *Sula* (*P. canariensis*, *P. halepensis*, *P. leucodermis*, *P. longifolia*) and *Khasya* (*P. khasya*); very small denticulations also occur in a few species of *Picea* (Phillips 1948).

Ray tracheids reticulate: walls generally thin, bearing very numerous, narrow, pointed, internal tooth-like protrusions from the upper and lower cell wall, united by transverse ridges, which give a characteristic reticulate appearance, e.g., in *Pinus*, sect. *Taeda* (including, i.a., *P. banksiana*, *P. palustris*, *P. taeda*) (fig. 42).

Caution:

Do not confuse dentations with spiral thickenings which may occur in species of *Larix*, *Picea* (fig. 40) and *Pseudotsuga*.

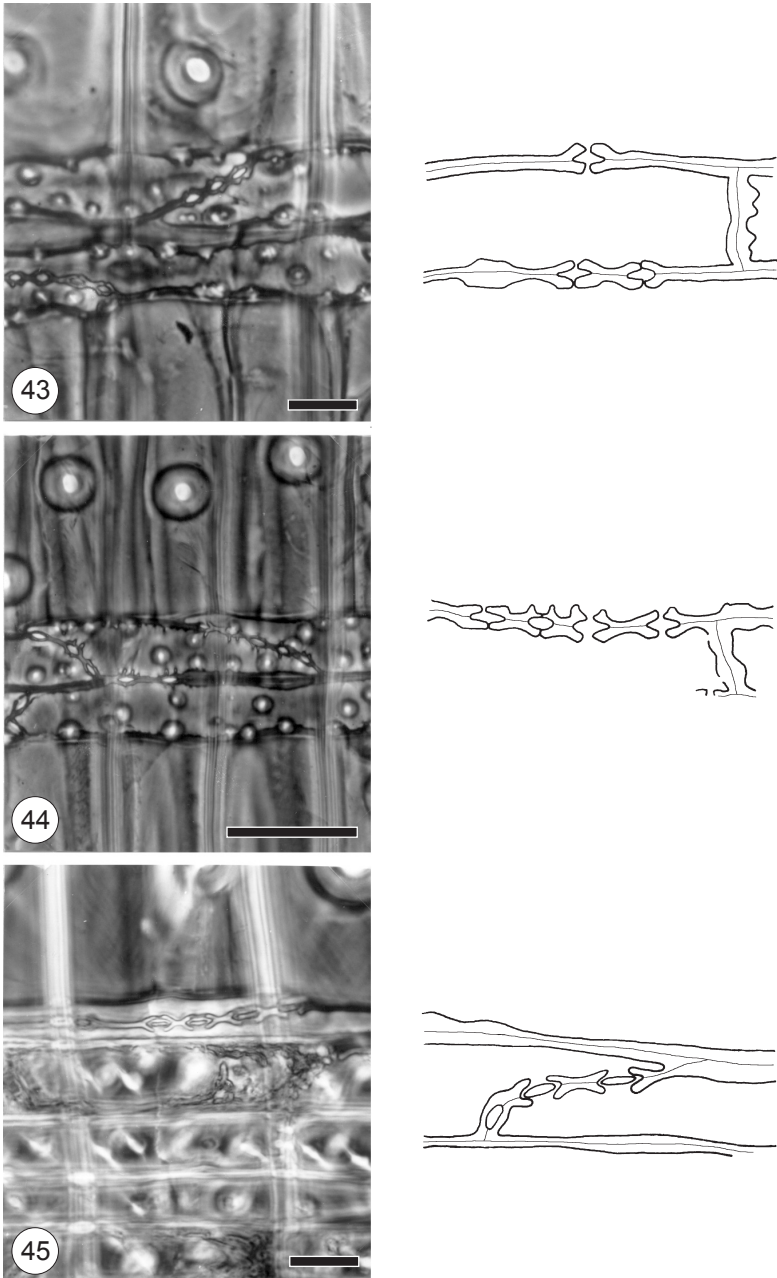


Fig. 43–45. Pit borders of ray tracheids in *Picea* and *Larix*, radial sections (phase contrast). — 43: Pitting with narrow apertures, pit borders angular (feature 84). *Picea abies*. — 44: Pit borders angular with dentate thickenings (feature 84). *Picea abies*. — 45: Pitting with wide apertures, pit borders rounded. *Larix kaempferi*. — Scale bars for 43 & 45 = 20 μm , for 44 = 50 μm . — Drawings after Bartholin (1979).

RAY TRACHEID PIT BORDERS ANGULAR OR WITH DENTATE THICKENINGS
(radial section)***84. Present***Definition:*

Ray tracheid pit borders may be thickened and lined with small, irregular lumps which make the pit opening appear like a narrow canal (*Picea*-1 type, fig. 43), or may feature additional dentate thickenings (“horns”) on the pit borders (*Picea*-2 type, fig. 44) (Bartholin 1979).

Comment:

The differentiation of *Picea* spp. and *Larix* spp. often poses considerable problems if features typical for *Larix* (biseriate pits in longitudinal tracheids, abrupt transition from earlywood to latewood within a growth increment, colour difference between sapwood and heartwood) are not pronounced or accessible. This character refers to the specific morphology of bordered pits in ray tracheids of *Picea* as opposed to *Larix* with rather large and wide pit openings according to Bartholin (1979) and Anagnost et al. (1994) (fig. 45).

*) This character refers to the difference between *Larix* and *Picea* type bordered pits in ray tracheid cell walls.

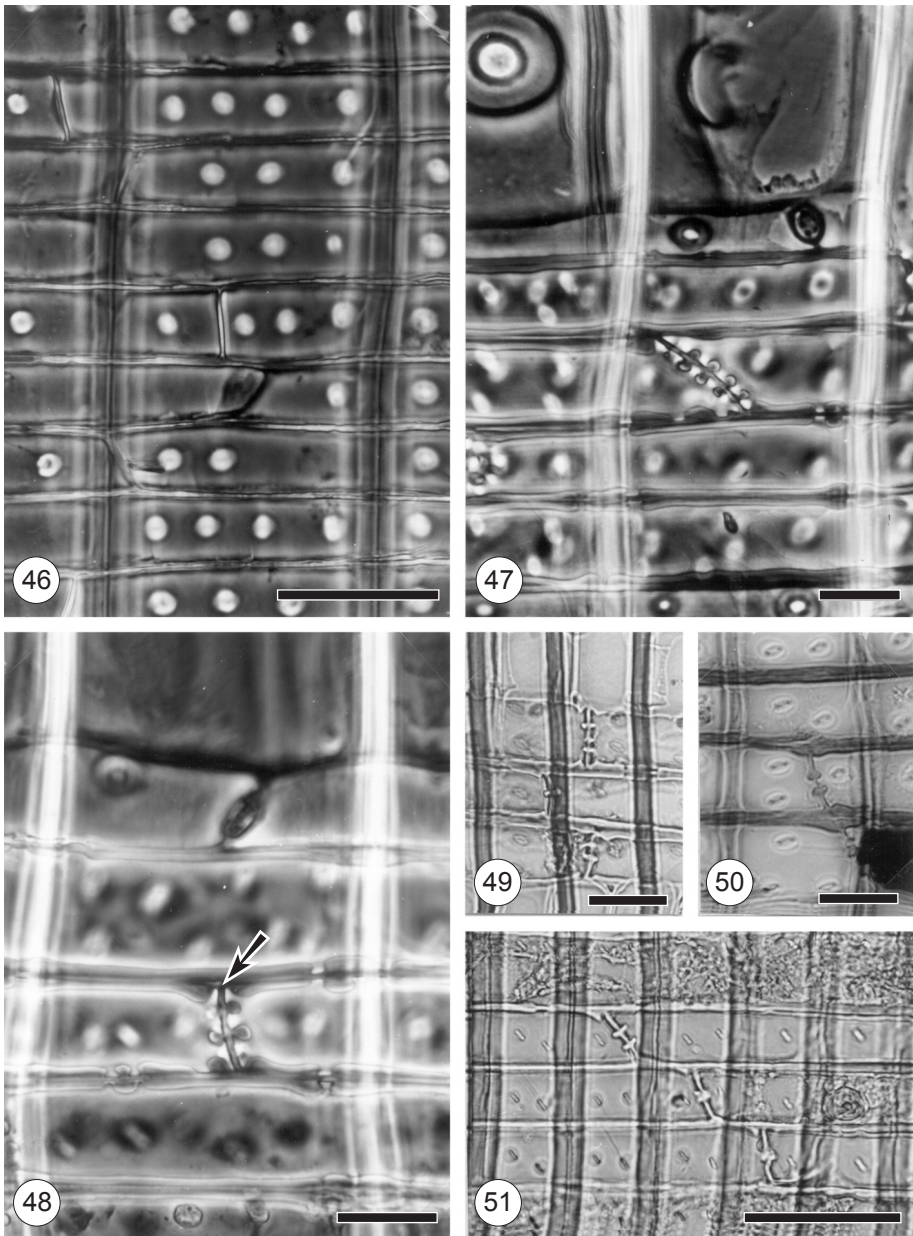


Fig. 46–51. End walls of ray parenchyma cells, radial sections. – 46: End walls smooth (feature 85). *Taiwania cryptomerioides*. – 47: End walls well pitted (= nodular) (feature 86). *Larix decidua*. – 48: Nodular end walls (feature 86) and indentures (arrowed) (feature 89). *Larix kaempferi*. – 49–51: Variation in appearance of nodular end walls in *Juniperus sabina* (49), *Cupressus goveniana* (50) and *Juniperus thurifera* (51). — Scale bars for 46 & 51 = 50 μm ; for 49 & 50 = 25 μm ; for 47 & 48 = 20 μm .

END WALLS OF RAY PARENCHYMA CELLS**85. Smooth (unpitted)****86. Distinctly pitted (nodular)***Comments:*

Smooth end walls (relatively thin with few or no pits) are characteristic for most coniferous taxa (fig. 46).

Distinctly pitted (also referred to as “nodular”) end walls are characteristic of the genera *Abies*, *Larix* (fig. 47 & 48), *Picea*, *Tsuga*, and *Pinus* sect. *Strobus* (e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. strobus*) of Pinaceae; they are also a distinctive feature, though of a slightly different appearance (see respective illustrations), of some species of *Juniperus*, e.g., *J. sabina* (fig. 49) and *J. thurifera* (fig. 51), *Calocedrus decurrens* and *C. formosana*, and *Cupressus goveniana* (fig. 50) (all Cupressaceae).

Caution:

The character state “distinctly pitted” should only be coded and used for identification when well developed, e.g., in *Abies* spp.

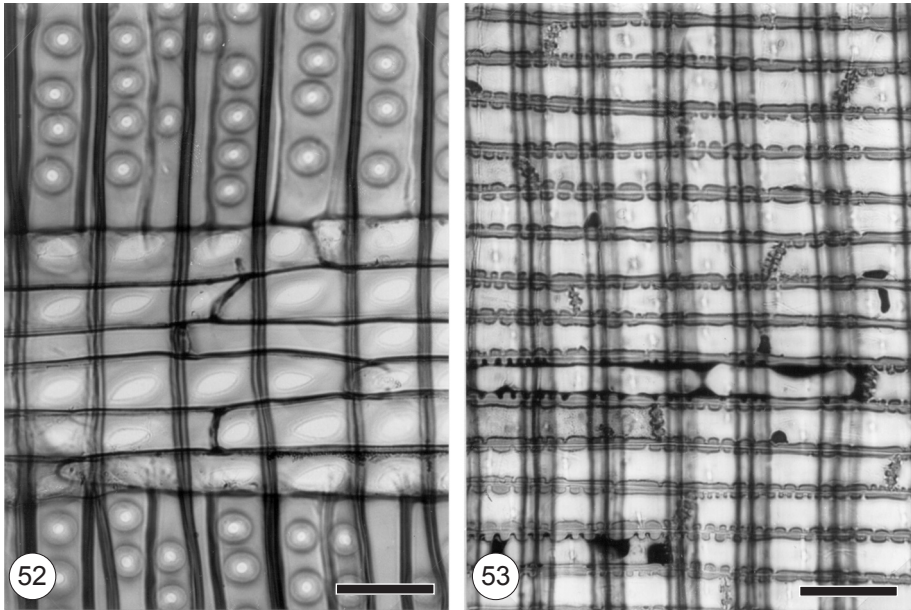


Fig. 52 & 53. Horizontal walls of ray parenchyma cells, radial sections. – 52: Horizontal walls smooth (feature 87), as are end walls (feature 85). *Sciadopitys verticillata*. – 53: Horizontal walls distinctly pitted (feature 88), and end walls nodular (feature 86). *Abies alba*. — Scale bars for 52 & 53 = 50 µm.

HORIZONTAL WALLS OF RAY PARENCHYMA CELLS

87. Smooth (unpitted)

88. Distinctly pitted

Upper and lower horizontal walls of ray parenchyma cells can be either smooth (unpitted) or distinctly pitted. Pitted horizontal walls of ray parenchyma cells appear to be restricted to a few genera of Pinaceae, e.g., *Abies* (fig. 53), *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Pseudotsuga*, and *Tsuga*. Most other coniferous taxa have smooth horizontal walls (fig. 52).

Caution:

The character state “distinctly pitted” should be coded and used for identification only when well developed, e.g., in *Abies* spp.

INDENTURES**89. Present***Definition:*

Indentures = Depressions in horizontal walls of ray cells at their junction with vertical end walls as seen in the radial plane (fig. 48). Indentures, a term coined by Peirce (1936), appear as very small, pit-like hollows in the horizontal walls intersecting with the vertical walls. They are observed in all conifer families except Araucariaceae; in Podocarpaceae only in *Podocarpus salignus* and *Dacrycarpus (Podocarpus) dacrydioides* (Phillips 1948). According to Yatsenko-Khmelevsky (1954), indentures are poorly developed or absent in *Cedrus*, *Keteleeria* and *Pinus* (Pinaceae) but considered of some diagnostic importance in Cupressaceae s.l. (sensu Farjon 2001), viz. *Thuja plicata*, *T. occidentalis*, *Juniperus*, *Taxodium*, and *Cryptomeria japonica* (Core et al. 1979). They are also reported to be abundant and conspicuous in *Taiwania cryptomerioides* (Peirce 1936).

Cautions:

To avoid misidentifications, this character should be used with great care and not in cases when indentures are poorly defined and rare.

For microscopic observation, sections should be cleared of extraneous materials with an appropriate bleaching agent such as sodium hypochlorite or eau de javelle.

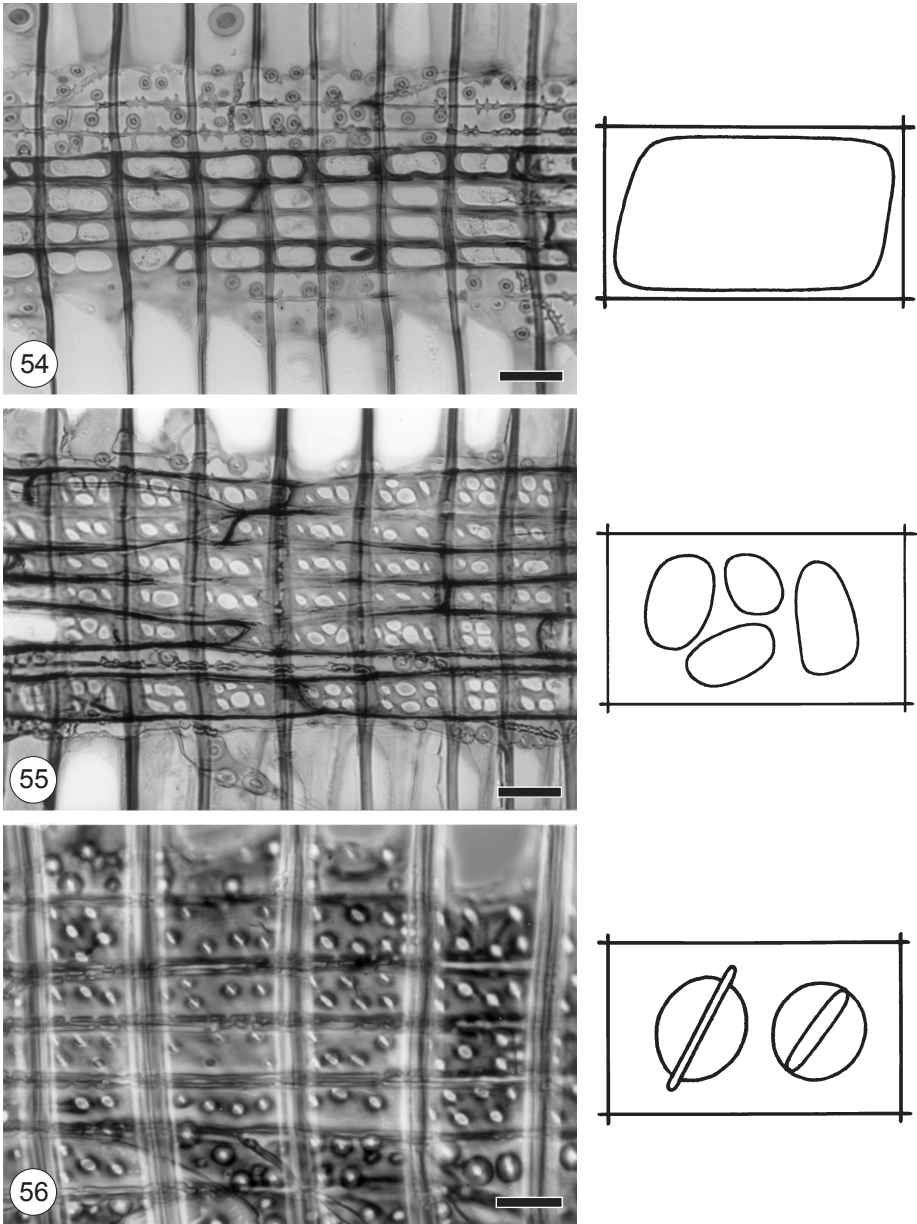


Fig. 54–56. Cross-field pitting, radial sections. — 54: “Window-like”, fenestriform (feature 90). *Pinus sylvestris*. — 55: Pinoid (feature 91). *Pinus ponderosa*. — 56: Piceoid (feature 92). *Picea abies* (phase contrast). — Scale bars for 54 & 55 = 50 μm ; for 56 = 20 μm .

CROSS-FIELD PITTING

CROSS-FIELD PITTING (according to Phillips 1948, amended by Vogel 1995)

90. “Window-like” (fenestriform)

91. Pinoid

92. Piceoid

93. Cupressoid

94. Taxodioid

95. Araucarioid

Definition:

Cross-field = the area bounded by the intersecting walls of a single longitudinal tracheid and a single ray parenchyma cell. Cross-field pitting = pits occurring on these areas of contact between ray parenchyma cells and axial tracheids (cross-fields), to be observed only in earlywood and throughout the ray (body and marginal cells).

Types:

The cross-field pitting is crucial to the identification of coniferous woods. Cross-field pit features include frequency, arrangement, form, size and/or position of the apertures relative to the border of the pits. For this IAWA character list the categories recommended by Phillips (1948) have been adopted and amended by one additional type (“araucarioid”) already used by Barefoot & Hankins (1982) and re-evaluated by Vogel (1995). The following types of cross-field pitting are proposed for description and identification of coniferous woods:

“Window-like” = with usually 1–2 large simple or apparently simple cross-field pits (fig. 54). Such large, square or rectangular pits occupying nearly the entire cross-field can be observed in the sections *Sylvestris* and *Strobus* of the genus *Pinus* (Pinaceae). According to Rol (1932), *Pinus kesiya* and *P. merkusii* would have to be included as examples for taxa with window-like pits although cross-fields with more than two large and simple (or nearly so) pits occur in these species. Additional examples listed by Phillips (1948) are *Lagarostrobos* (*Dacrydium*), *Sundacarpus amarus* (Podocarpaceae), *Phyllocladus* (Phyllocladaceae) and *Sciadopitys* (Sciadopityaceae).

“Pinoid” = cross-field pits 1–6 pinoid, 3 or more pits common (fig. 55). Such pits are small to fairly large depending on the number per cross-field, simple or with reduced borders, and often of irregular shape as opposed to the more or less rectangular “window-like” pits. They can be found in all sections of *Pinus* except those with the large, “window-like” type.

“Piceoid” = cross-field pits piceoid (fig. 56). Piceoid pits have borders much wider than the narrow, slit-like and often extended apertures as, for instance, in *Larix* spp., *Picea* spp., *Pseudotsuga* spp. and *Tsuga* spp. (Pinaceae). This type can also be observed in *Cedrus* spp. (Pinaceae). Great care is needed here with specimens which have compression wood (Ilic 1995).

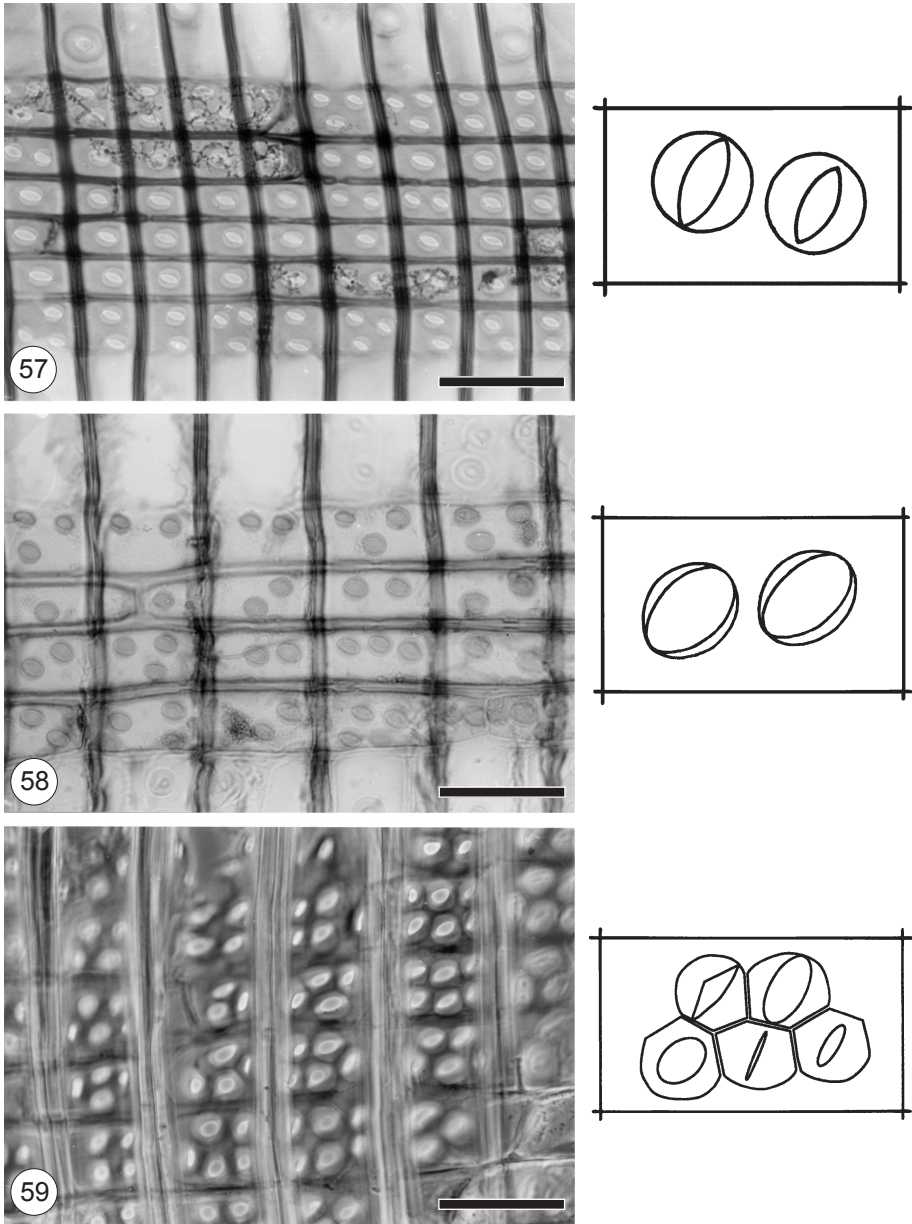


Fig. 57–59. Cross-field pitting, radial sections. — 57: Cupressoid (feature 93). *Juniperus communis*. — 58: Taxodioid (feature 94). *Taxodium distichum*. — 59: Araucarioid (feature 95). *Araucaria araucana* (phase contrast). — Scale bars for 57–59 = 50 μm .

“Cupressoid” = cross-field pits cupressoid (fig. 57). Cupressoid pits have elliptical apertures included within the limits of the pit border (contrary to the often extended piceoid pits); apertures are definitely narrower than the border. The long axis of the apertures varies in position from vertical to horizontal even within a single specimen. This type of pitting is characteristic of most Cupressaceae (*Thuja* is one exception), and also occurs in some Podocarpaceae and Taxaceae.

“Taxodioid” = cross-field pits taxodioid (fig. 58). Taxodioid pits have large, oval to circular, included apertures; the aperture exceeds the width of the border at its widest point. Taxodioid pitting can be found in most taxa of former Taxodiaceae (now Cupressaceae), but also in the genera *Abies*, *Cedrus* (Pinaceae), *Thuja* (Cupressaceae) and in several species of Podocarpaceae. In certain Cupressaceae, particularly *Sequoia* and *Taxodium*, the cross-field pits are commonly arranged in rows of two to three (rarely up to five) pits per cross-field except in marginal cells.

“Araucarioid” = cross-field pits araucarioid (Barefoot & Hankins 1982; Vogel 1995) (fig. 59). The individual pits are predominantly cupressoid (pit aperture elliptical, included, definitely narrower than the border, Ilic 1995), but their arrangement in the cross-field is distinctive. The pits are arranged in alternate rows of usually three or more with a tendency for crowding; individual pits often have a polygonal outline similar to the alternate intertracheary pitting in Araucariaceae. Araucarioid cross-field pitting is restricted to Araucariaceae (*Agathis*, *Araucaria*, *Wollemia*).

Comment:

Useful information on the differentiation of taxa is also reported for certain quantitative cross-field pit characters not adopted for this IAWA list of characters. According to Chavchavadze (1979) the number of pit rows per cross-field may be employed as a diagnostic feature in some Cupressaceae, e.g., up to 5 rows in *Sequoia*, up to 4 rows in *Metasequoia* and *Taxodium* spp., up to 3 rows in *Sequoiadendron*.

Cautions:

Pit apertures can be considerably modified in compression wood: cross-field pits in Araucariaceae may occasionally be less crowded and then correspond to the cupressoid type, although the latter have a more regular outline. Always observe a large number of earlywood cross-fields to determine the most common type of cross-field pitting.

Intergrading between pit types occurs especially between “piceoid” and “cupressoid” and also between “cupressoid” and “taxodioid” pits.

NUMBER OF PITS PER CROSS-FIELD (earlywood tracheids only)**96. ... < number per crossfield >***Procedure:*

The number of pits per cross-field must be determined in the earlywood, and based on at least 25 (preferably more) counts. The values entered should represent the most common occurrence in a given taxon.

Examples:

One pit per cross-field is most common in *Pinus*, sections *Sylvestris* (e.g., *P. densiflora*, *P. nigra*, *P. resinosa*, *P. sylvestris*) and *Strobus* (e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. strobus*) (Pinaceae), in *Phyllocladus* (Phyllocladaceae), and in several taxa of Podocarpaceae, e.g., *Lagarostrobos*, *Manoao*, *Microstrobos* and *Sundacarpus* (*Podocarpus*) *amarus*.

Two pits per cross-field are most common in *Chamaecyparis*, *Cryptomeria* and *Cunninghamia* (Cupressaceae), and *Taxus* (Taxaceae).

Three to four pits per cross-field are common in *Sequoia* and *Taxodium* (Cupressaceae), *Torreya* (Taxaceae), and *Pinus*, sections *Ponderosa* (e.g., *P. contorta*, *P. patula*, *P. pinaster*, *P. ponderosa*, *P. radiata*) and *Sula* (e.g., *P. canariensis*, *P. halepensis*, *P. leucodermis*, *P. longifolia*) (Pinaceae).

Four and more pits per cross-field are most common in *Pinus*, section *Taeda* (e.g., *P. banksiana*, *P. caribaea*, *P. echinata*, *P. palustris*, *P. taeda*) (Pinaceae), *Agathis* and *Araucaria* (Araucariaceae).

Caution:

These distinctions are of a gradual nature. Base your decision on observation of as many cross-fields as possible. Make sure that the number of cross-field pits represents the majority of cross-fields in a given taxon or specimen.

NUMBER OF PITS PER CROSS-FIELD (earlywood only - categories)**97. (large window-like) 1–2****98. 1–3****99. 3–5****100. 6 or more**

RAY SIZE

Note:

All features referring to ray height and width exclude rays containing intercellular canals (“fusiform rays”) unless otherwise specified.

AVERAGE RAY HEIGHT

101. ... < μm >*Procedure:*

The ray height (in μm), is determined from tangential sections. At least 25 randomly selected rays should be measured calculating the mean, standard deviation and range.

Comment:

In several taxa, for example *Abies* spp., a larger number of particularly high rays is considered taxon specific (see, for instance, Greguss 1955). If the presence of such high rays is not adequately expressed by the numerical data (mean and range) this particular feature should be recorded in a corresponding comment.

Caution:

Do not measure ray height in wood from young stems, since these rays tend to be much lower.

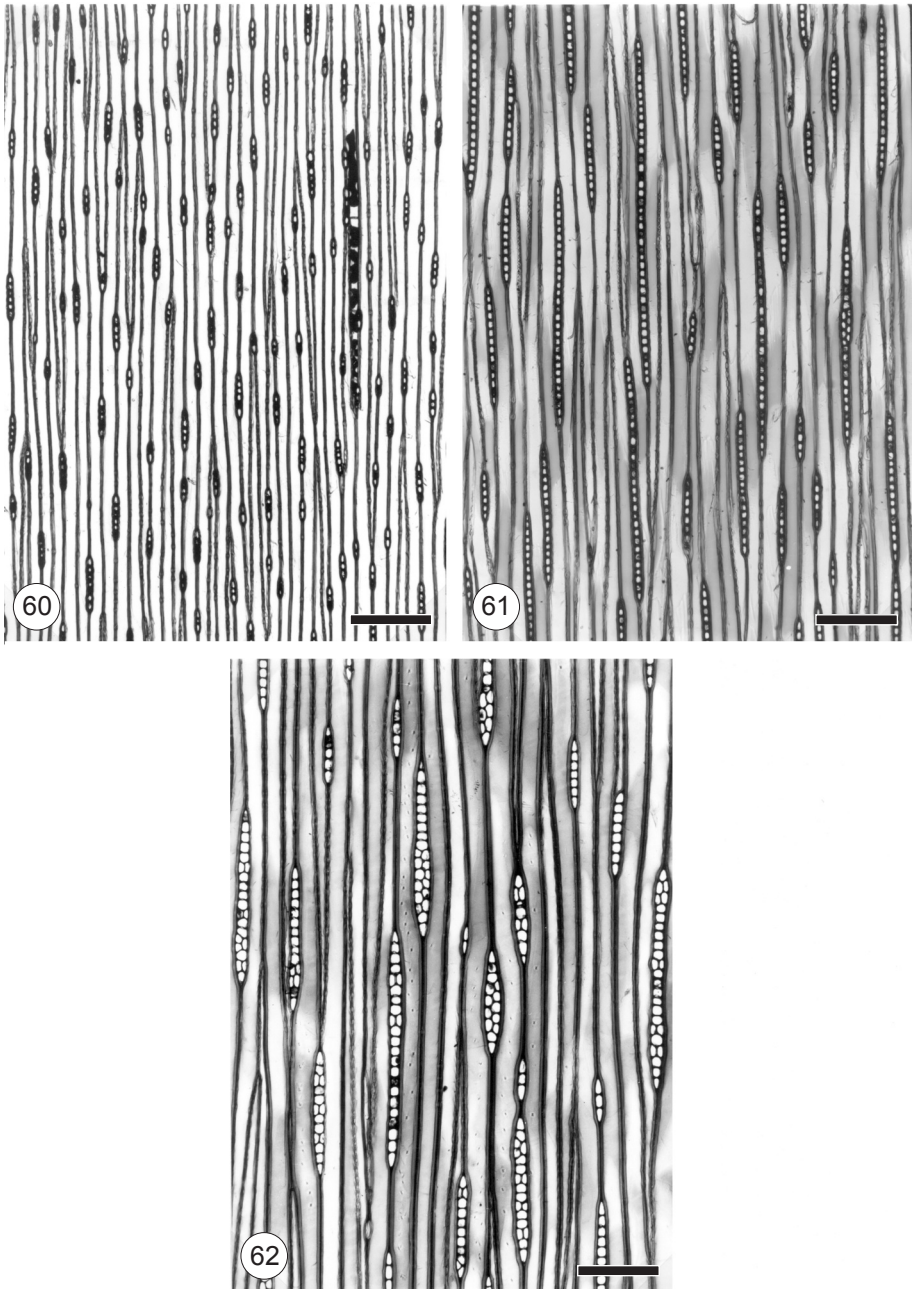


Fig. 60 & 61. Ray size, tangential sections. — 60: Rays very low (up to 4 cells - feature 102). *Chamaecyparis thyoides*. — 61: Rays very high (more than 30 cells - feature 105). *Cedrus deodara*. — Fig. 62. Rays 2-3-seriate in part (feature 108), although only up to biseriate here, note also fine bordered pits in tangential walls of tracheids. *Sequoia sempervirens*. — Scale bars for 60-62 = 200 μ m.

AVERAGE RAY HEIGHT (number of cells)**102. Very low (up to 4 cells)****103. Medium (5 to 15 cells)****104. High (from 16 to 30 cells)****105. Very high (more than 30 cells)***Comment:*

Figures 60 and 61 are examples for very low rays (feature 102) and very high rays (feature 105).

Caution:

Check information from the literature and old keys carefully to ensure that only data on **average** ray height are entered in the respective categories.

AVERAGE FUSIFORM RAY HEIGHT**106. ... < μm >***Procedure:*

Rays that contain radial intercellular canals are called fusiform because of their shape in tangential sections: The ray height (in μm), is determined from tangential sections. At least 25 randomly selected fusiform rays should be measured calculating the mean, standard deviation and range. Ensure that the entire ray is measured, including the uni-seriate extensions at both ends of the ray.

Comment:

In some taxa, for example *Pinus* spp., particularly the white pines (sect. *Strobus*, e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. strobus*; Pinaceae), the uni-seriate extensions at both ends of the ray may be very high. If the presence of such high rays is not adequately expressed by the numerical data (mean and range), this particular feature should be recorded in a corresponding comment.

Caution:

Do not measure ray height in wood from young stems, as these rays tend to be much lower.

RAY WIDTH (cells)**107. Exclusively uniseriate****108. 2–3-seriate in part***Definitions:*

Exclusively uniseriate = as for feature descriptor (including the very sporadic occurrence of partially biseriate rays).

2–3-seriate in part = approximately 10% of the larger rays should be at least biseriate over nearly the full height (fig. 62).

Comment:

Although rays in most coniferous woods are uniseriate (including the very sporadic occurrence of partially biseriate rays), some possess a fair number of bi- and triseriate

rays (in addition to uniseriate ones), e.g., *Sequoia sempervirens* and *Cupressus macrocarpa* (Cupressaceae) (Phillips 1948). Peirce (1937) describes biseriate rays also in *Fitzroya*, *Thujopsis*, and *Calocedrus* (Cupressaceae).

Note:

The outline of ray cells in cross section, as seen in the tangential plane, can vary and has been used by several authors (Core et al. 1979; Roig 1992) to distinguish between otherwise very similar taxa. This feature has not been included in this list. However, information on cell shape may be recorded and documented in a respective comment.

INTERCELLULAR CANALS

Definitions:

Intercellular canal = a tubular intercellular duct lined by an epithelium, conducting secondary plant products secreted by the epithelial cells. The nomenclature for softwood intercellular canals (synonyms: resin ducts, resin canals) is clarified in Wiedenhoft & Miller (2002). The epithelium is the single layer of cells adjacent to the canal. The remaining parenchyma and included or strand tracheids outside the epithelium are subsidiary cells. The entity as a whole – canal, epithelium and subsidiary cells – is the resin canal complex. Intercellular canals may be oriented axially (axial/vertical intercellular canal), or radially (radial/horizontal intercellular canal, within a ray). Axial and radial canals are usually interconnected in a three-dimensional network.

In conifers the presence of normal intercellular canals is restricted to several genera of Pinaceae, i.e., *Keteleeria* (only axial), *Larix*, *Picea*, *Pinus*, and *Pseudotsuga* (both radial and axial). Traumatic intercellular canals (axial and/or radial) may occur in these and in a number of other taxa of Pinaceae.

AXIAL INTERCELLULAR (RESIN) CANALS

109. Present

Comments:

In Pinaceae from regions with a pronounced seasonal climate, axial canals are found mainly (but not exclusively!) in the latewood. In subtropical and tropical taxa they are more evenly distributed. Axial canals are mostly single (solitary) but occasionally also occur in pairs (e.g. in *Pseudotsuga* and in many species of *Larix*) or small tangential groups (fig. 63–66).

As regards the morphology of epithelial cells (see corresponding character), two types of canals are distinguished: narrow canals mainly with thick-walled epithelial cells, as in *Pseudotsuga*, *Picea*, *Larix*, and wider canals with thin-walled epithelial cells, as in *Pinus* (Grosser 1977).

Caution:

In many instances, archaeological material may only consist of ‘toothpick’ size specimens. These specimens often comprise only one or a part of a growth ring, and therefore axial resin canals may not be observed if they are uncommon. Hence, always examine the tangential sections for fusiform rays with radial canals. If radial canals are present,

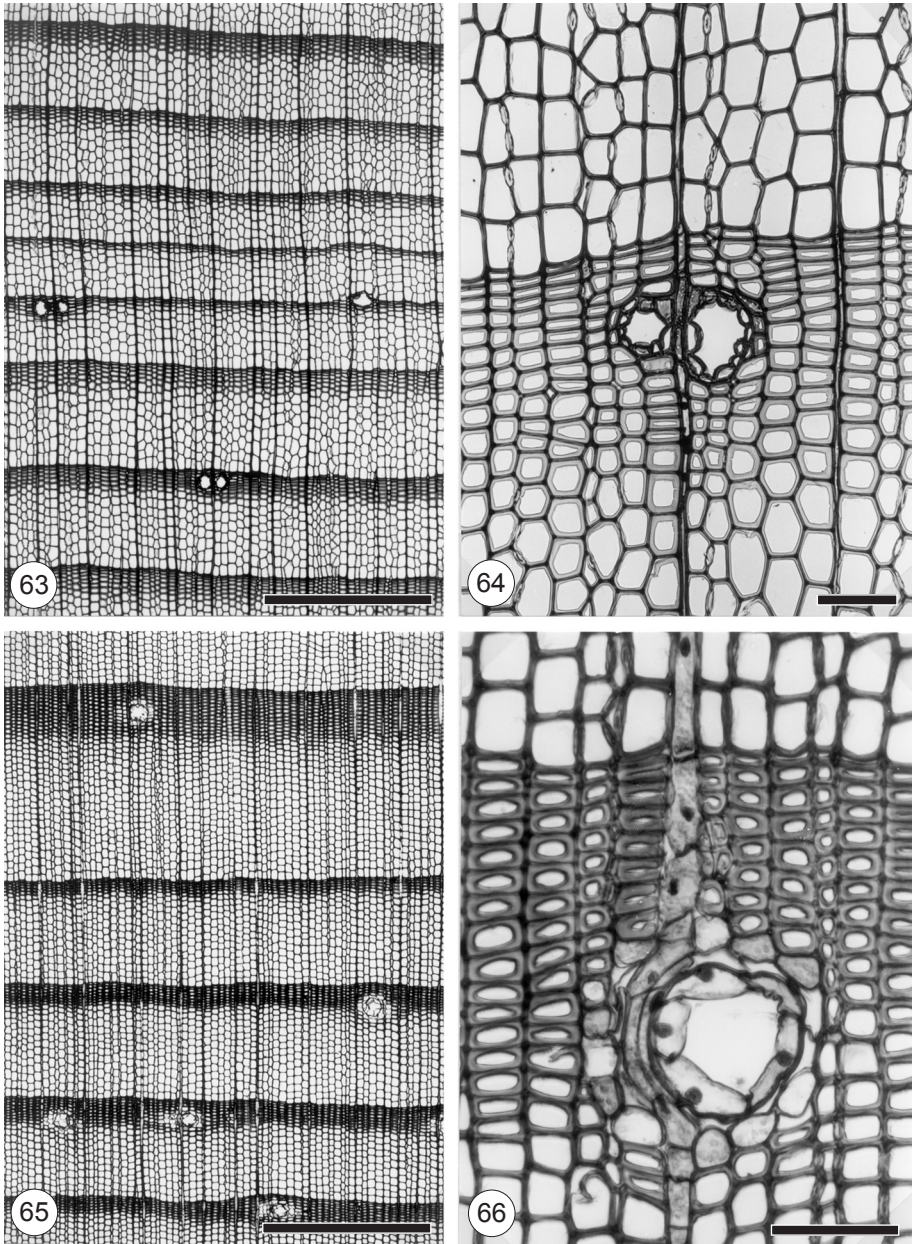


Fig. 63–66. Axial intercellular (resin) canals, cross sections. – 63: Axial intercellular canals present (feature 109). *Larix decidua*. – 64: Epithelial cells of the canals thick-walled (feature 116). *Larix decidua*. – 65: Axial intercellular canals present (feature 109). *Pinus sylvestris*. – 66: Epithelial cells of the canals thin-walled (feature 117). *Pinus sylvestris*. — Scale bars for 63 & 65 = 1 mm; for 64 & 66 = 100 μ m.

then “axial intercellular canals present” can also be provisionally recorded and used for identification.

RADIAL INTERCELLULAR (RESIN) CANALS

110. Present

Radial canals are located exclusively within the rays (fig. 67). Rays containing intercellular canals are called fusiform rays because of their shape in tangential sections. In Pinaceae, the genera *Larix*, *Picea*, *Pinus*, and *Pseudotsuga* possess radial intercellular canals in addition to axial canals. No coniferous taxon is known to have exclusively radial canals.

TRAUMATIC (RESIN) CANALS (axial, radial)

111. Present

Definitions:

Traumatic resin canals usually are large in diameter, of irregular outline, and frequently tangentially fused.

Traumatic resin canals are formed in taxa with normal canals as well as in many taxa in Pinaceae and other families that normally do not have them.

According to Engler (1954), Phillips (1948), and Bannan (1936), resin canals in Pinaceae may occur in the following combinations: *Larix*, *Picea*, *Pinus* and *Pseudotsuga* form normal axial and radial resin canals and, under external disturbance, also traumatic axial (fig. 69) and radial resin canals. *Keteleeria* forms only axial resin canals, both normal and traumatic. *Cedrus* may form both axial and radial resin canals which, due to their irregular form and large size (fig. 68 & 70), are considered to be of traumatic origin (Pearson & Brown 1932). *Abies* and *Tsuga* do not have normal canals but may very occasionally form traumatic axial resin canals. Bailey & Faull (1934) have reported the occasional presence of traumatic resin canals in *Sequoia sempervirens* (Cupressaceae).

AVERAGE DIAMETER OF NORMAL AXIAL INTERCELLULAR CANALS

112. Tangential diameter, delimited by epithelial cells (Method A) < μm >

113. Tangential diameter of entire resin canal complex (Method B) < μm >

114. Radial diameter, delimited by epithelial cells (Method C) < μm >

Procedures:

The diameter of axial intercellular canals is measured in transverse sections. Canals are selected for measurement with care not to bias the selection towards the larger or smaller ones.

For method A, the tangential diameter of the resin canal, including the epithelial cells, is measured at the widest part of the opening. This is the method that is assumed to be used in most references to date (e.g. Greguss 1955; Panshin & DeZeeuw 1980).

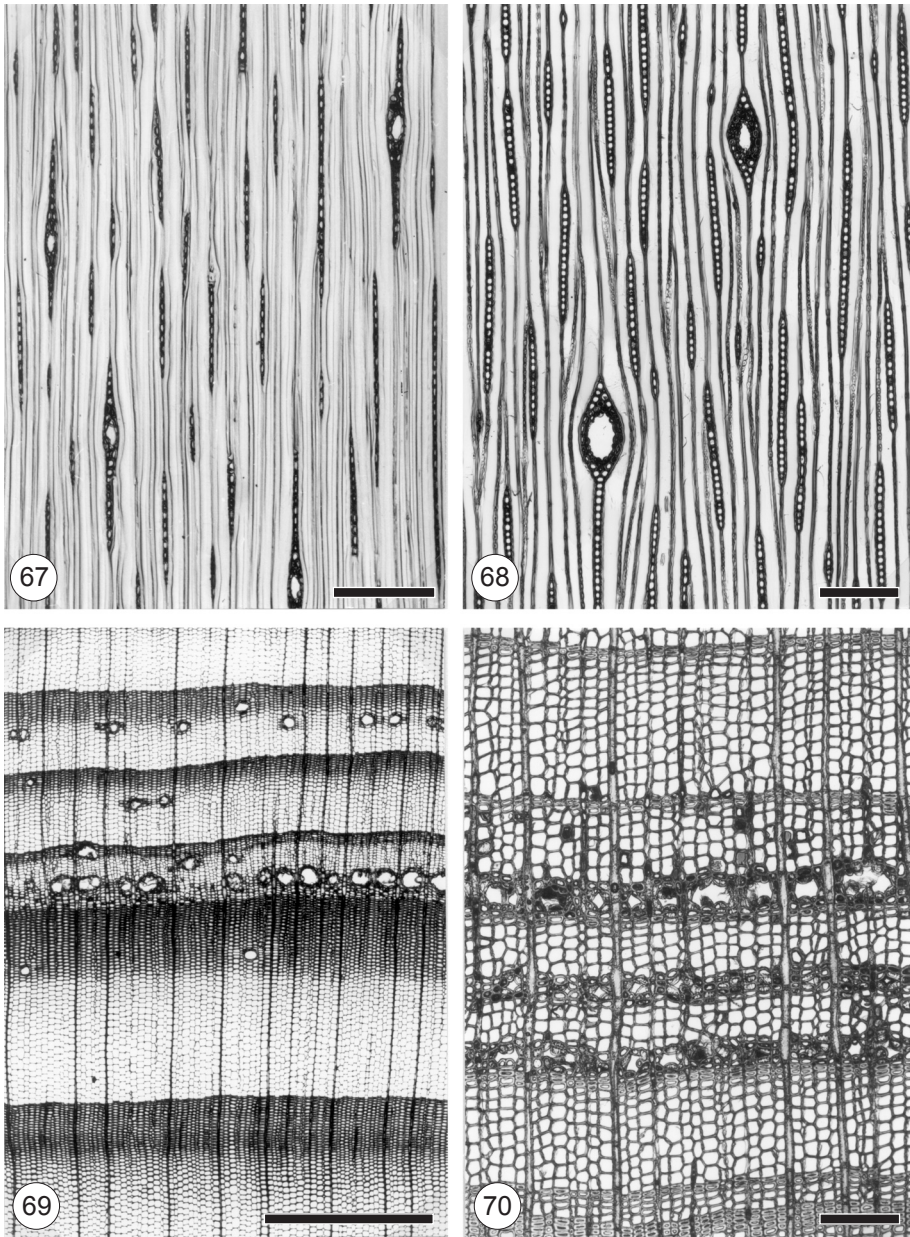


Fig. 67. Normal radial intercellular (resin) canals (feature 110) in *Larix decidua*. — Fig. 68. Traumatic radial (resin) canals (feature 111) in *Cedrus libani*, tangential section. — Fig. 69. Traumatic axial canals in tangential rows in *Pseudotsuga menziesii*, cross section. — Fig. 70. Three tangential rows of traumatic axial canals in *Cedrus libani*. — Scale bars for 67, 68 & 70 = 200 μ m; for 69 = 1 mm.

For method B, the tangential diameter of the entire resin canal complex is measured at the widest point. This measurement includes all components of the axial resin canal complex as differentiated from the axial tracheids.

For method C, the radial diameter of the canal complex, including the epithelial cells, is measured at the widest point.

At least 10 (preferably more) canals should be measured. It is recommended to enter the average and range of values, e.g., 30–**50**–75 μm .

Comments:

The diameter of normal axial resin canals (measured by any of the three methods) varies considerably between and within taxa as a function of canal type (epithelial cells thin-walled vs. thick-walled) and growth conditions (primarily site, and natural stand or plantation-grown). In most general terms, axial canals are smallest (c. 40–100 μm by method A) in taxa with thick-walled epithelial cells, e.g., *Larix*, *Picea* and *Pseudotsuga*. Medium-sized (c. 100–170 μm by method A) are common in *Pinus*, e.g., *P. nigra*, *P. sylvestris*. Large canals (c. 170–300 μm by method A) are characteristic of *Pinus*, sections *Strobus* (white pines, including *P. cembra* and *P. strobus*) and *Taeda* (southern yellow pines, including *P. banksiana*, *P. palustris*, and *P. taeda*) as well as in plantation-grown *Pinus radiata*, *P. merkusii*, and others.

AVERAGE DIAMETER OF NORMAL RADIAL INTERCELLULAR CANALS

115. ... < μm >

Comment:

Intercellular canals in fusiform rays tend to be smaller than corresponding axial canals. Panshin & DeZeeuw (1980) consider the diameter of radial canals diagnostic and have included this feature in their softwood key. Examples: average diameter 45 μm for *Pinus contorta*, 30–35 μm for *P. banksiana*, less than 35 μm for *Picea sitchensis*, less than 25 μm for *Pseudotsuga menziesii*.

Procedures:

The diameter of radial intercellular canals is measured in tangential sections. Canals are selected for measurement with care not to bias the selection towards the larger or smaller ones. The diameter of the canal lumina plus the epithelial cells, is measured at the widest part. At least 10 (preferably more) canals should be measured.

It is recommended to enter the average and range of values, e.g., 25–**35**–60 μm .

EPITHELIAL CELLS (of intercellular canals)

116. Thick-walled

117. Thin-walled

Definitions:

Epithelial cells are specialised parenchyma cells that surround an intercellular canal. More specifically, the term “epithelial cells” applies only to the cells facing the resin

canals. It does not apply to other axial parenchyma cells forming part of a multilayered sheath around the canals (Werker & Fahn 1969; Kibblewhite & Thompson 1973; LaPasha & Wheeler 1990). Resin is produced in the epithelial cells and secreted into the canal.

Epithelial cells are usually square to sometimes rectangular in shape, forming a continuous interior lining of the canal (epithelium). They are usually thick-walled and rather rigid in *Keteleeria*, *Larix* (fig. 64), *Picea*, and *Pseudotsuga* (possibly also in *Cedrus*, see feature 111, traumatic resin canals present) and typically thin-walled in all species of *Pinus* (fig. 66).

Comments:

Individual taxa within Pinaceae are often distinguished by the number of epithelial cells of horizontal/radial resin canals. Bosshard (1974), for instance, reports that 6 or fewer epithelial cells are characteristic of radial canals in *Pseudotsuga*, 7–9 epithelial cells of *Picea*, and up to 12 epithelial cells of *Larix* (for further information on the number of epithelial cells see also Barefoot & Hankins (1982) and Sudo (1968)). The number of epithelial cells in large traumatic resin canals is much higher, e.g., from 30 to 60 cells per canal, and usually it is not taken into account as a diagnostic feature. The number of (thick-walled) epithelial cells surrounding radial resin canals appears highly variable (e.g., 5–14 in *Picea* - Sudo 1968), and has therefore not been included in this character list. All information on this feature should be carefully documented in a respective comment.

The clear division between thick- and thin-walled epithelial cells is occasionally obscured because the thick-walled epithelial cells, e.g., in *Larix* and *Picea*, may sometimes be mixed with thin-walled cells.

Note on tylosoids:

Tylosoids are defined as “a proliferation of a thin-walled epithelial cell into an inter-cellular canal; a tylosoid differs from a tylosis in that it does not pass through a pit cavity” (IAWA Committee 1964). Tylosoids may occur in all taxa with thin- or relatively thick-walled epithelial cells, e.g., *Pinus*, and do not have a significant diagnostic value.

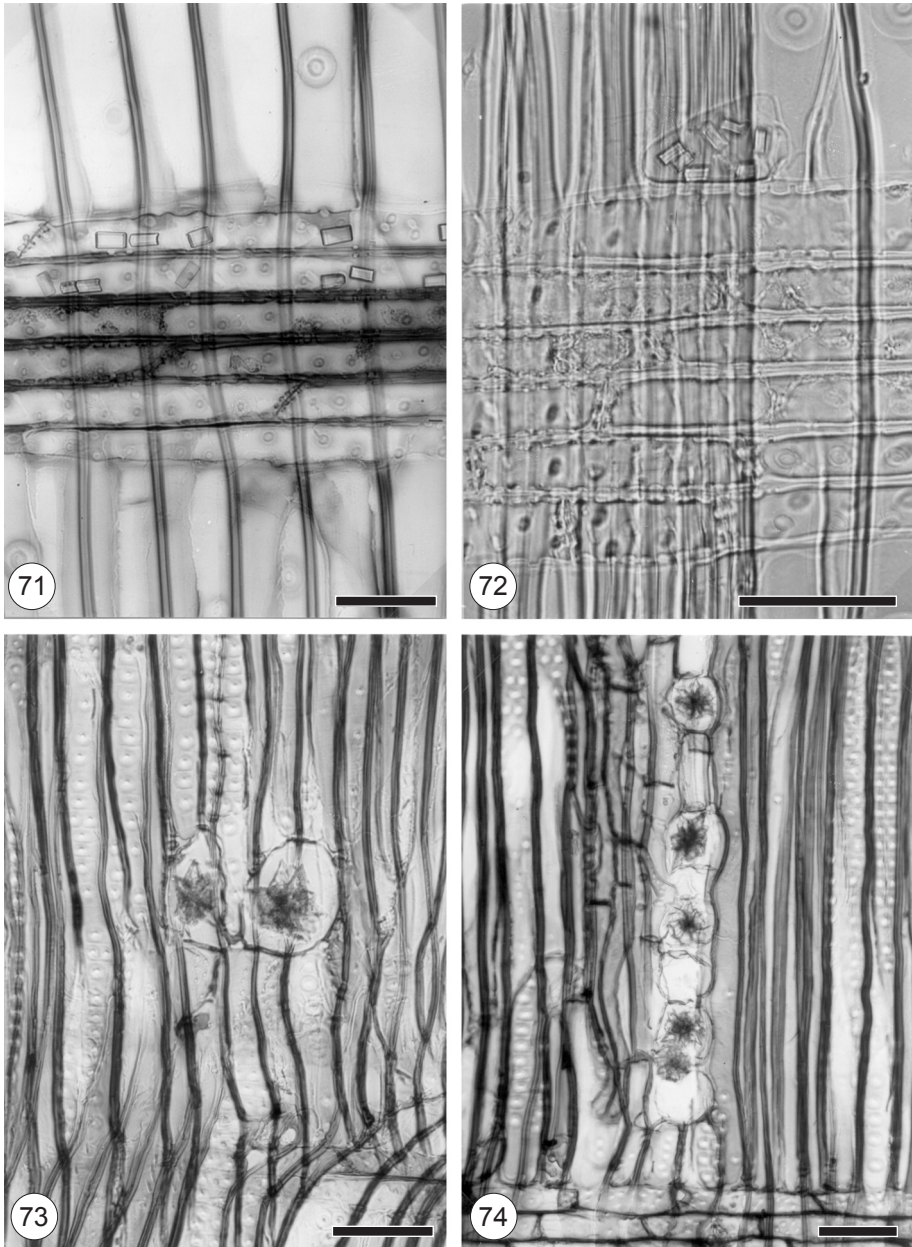


Fig. 71–74. Crystals (feature 118), radial sections. – 71: Prismatic crystals in rays (features 119 & 122). *Abies alba*. – 72: Prismatic crystals in an enlarged ray cell (features 119 & 122). *Abies lasiocarpa*. – 73: Druses in axial parenchyma cells (features 120 & 123). *Ginkgo biloba*. – 74: Druses in axial parenchyma cells (features 120 & 123). *Ginkgo biloba*. — Scale bars for 71 & 72 = 50 μm ; for 73 & 74 = 100 μm .

MINERAL INCLUSIONS

CRYSTALS

118. Present

Crystals of calcium oxalate are rare in coniferous woods. Thus their regular occurrence, e.g., in species of *Abies*, *Picea* (prismatic crystals), in *Ginkgo biloba* (druses), and *Pinus flexilis* (small styloid crystals in epithelial cells) is of considerable diagnostic significance. Calcium oxalate crystals are birefringent and can be most readily observed under polarised light.

TYPE OF CRYSTALS

119. Prismatic**120. Druses****121. Other forms (specify)***Definitions:*

Prismatic crystals = solitary rhombohedral or octohedral crystals composed of calcium oxalate (fig. 71 & 72).

Druse = a compound crystal of calcium oxalate, more or less spherical in shape, in which the many component crystals protrude from the surface giving the whole structure a star-shaped appearance, e.g., *Ginkgo biloba*, Ginkgoaceae. Synonym: cluster crystal (fig. 73 & 74).

Other types = any type of crystal other than prismatic crystals and druses (specify) (fig. 75 & 76).

CRYSTALS LOCATED IN

122. Rays**123. Axial parenchyma****124. Cells associated with intercellular canals***Comments:*

Crystals in conifers appear to occur only in a single cell type in a given taxon. Prismatic crystals are more or less common in the marginal and submarginal ray cells of some species of *Abies*, *Cedrus*, and some species of *Picea* (all Pinaceae). These cells are not subdivided and one or more crystals may be found in any single cell (fig. 71 & 72).

Druses have been observed in axial parenchyma (idioblasts) of *Ginkgo biloba*, Ginkgoaceae (fig. 73 & 74).

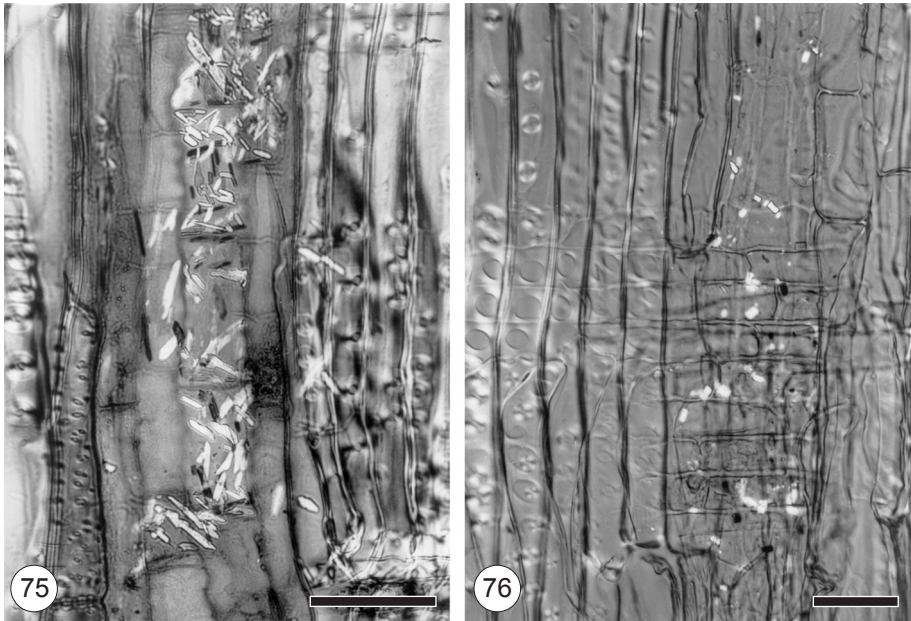


Fig. 75 & 76. Crystals (feature 118), radial sections. – 75: Small styloid and elongated crystals in resin canal complex (features 121 & 124). *Pinus pinaster* (polarised light). – 76: Small cubic crystals in resin canal complex (features 121 & 124). *Pinus flexilis* (polarised light). — Scale bars for 75 = 100 μm ; for 76 = 50 μm .

Kellogg et al. (1982) report that in one species of the “soft pines” group, *Pinus flexilis*, small styloid crystals can be observed in the resin canal complexes. Very small styloid and spindle-shaped crystals were also described for bristlecone pines (*Pinus longaeva*, *P. balfouriana*, *P. aristata* (often considered a synonym of *P. longaeva*) (Baas et al. 1986). Due to their small size, observation of these crystals requires polarised light and a magnification of at least $\times 500$ under the light microscope (fig. 75 & 76).

Organic crystalline deposits have been observed in axial tracheids of *Tsuga heterophylla* (Krahmer et al. 1970), *Callitris endlicheri* (Ilic 1994), and *Torreya yunnanensis* (Kondo et al. 1996). Though of an organic nature and not to be considered “mineral”, such crystalline deposits should be reported here and documented in a respective comment.

Information on size and number of crystals per cell should also be reported and documented.

Caution:

The absence of crystals is not diagnostic.

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