# ANATOMICAL CHARACTERISTICS OF SOME WOODY PLANTS OF THE ANGMAGSSALIK DISTRICT OF SOUTHEAST GREENLAND

BY

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WITH 24 FIGURES AND 3 TABLES

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## Abstract

Ten species are represented by the 40 wood specimens collected in 1969 from the Angmagssalik District of S.E. Greenland. Information concerning collection localities, diameter of wood specimens, number and breadth of growth rings and eccentricity is given. A comparison of growth ring observations is made with those made by KRUUSE (1912), in three species from the same area, in relation to their growth form and environment.

An anatomical description of the wood of the 10 species has been made together with an evaluation of some of the anatomical characteristics. Trends towards a modification of the wood due to environmental factors are indicated, but the fact that caution must be exercised when carrying out such an investigation is stressed, with special emphasis on the need for more accurate information regarding environment, the size and age of specimens.



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## Introduction

Following a preliminary investigation of the Angmagssalik District of S.E. Greenland by Dutch botanists in 1966, two expeditions were made to the same area in the summers of 1968 and 1969. Studies were concentrated on the morphological and ecological aspects of the vegetation, with some emphasis on the moss and lichen vegetation. A number of wood samples were collected by F. J. A. DANIËLS, J. G. DE MOLENAAR and H. F. FERWERDA during the last expedition.

The lack of information of the wood anatomy of species growing in this area together with the availability of specimens prompted an investigation into the anatomy and its relationship with the environment.

KRUUSE's (1912) observation of growth rings and the eccentricity of three species found in this area, did not include any attempt to examine the wood anatomy in any detail. FORSAITH (1920) provides some insight into anatomical differences encountered under more extreme conditions but further comparative literature is rather limited.

## Acknowledgements

I wish to express my sincere thanks to Dr. ALBERTA M. W. MENNEGA for her valuable advice and encouragement during the course of this investigation. My thanks are extended to Drs. F. J. A. DANIËLS for providing much information on specimen localities. I am also very grateful for the technical assistance of Mr. A. KUIPER, Mr. A. SCHIPPER and Mr. P. A. VAN DEN BERG.

## Collection localities of the investigated wood specimens

The term "Angmagssalik District" as used in this paper refers to the deglaciated part of the Southeast coast of Greenland between 65°30′ and 66°30′ lat.N. This district constitutes a wild mountainous area deeply cut by numerous fjords.

All the specimens listed in Table 1 (*cf.* Fig. 1), were identified by the collectors and the nomenclature is in agreement with TUTIN *et al.* (1972), and BÖCHER, HOLMEN & JAKOBSEN (1966). For more details concerning localities see DE MOLENAAR (1974).

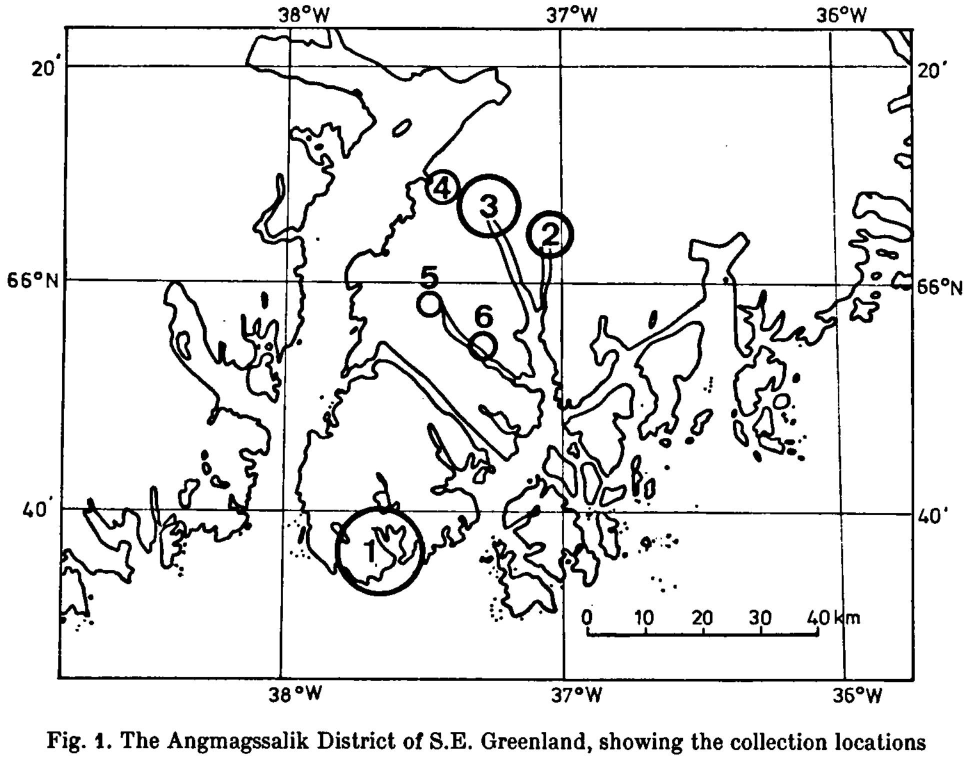


Fig. 1. The Angmagssalik District of S.E. Greenland, showing the collection locations of the wood specimens (cf. Table 1).

Table 1. *Localities, growth rings and diameters of collected specimens*

1. Angmagssalik 65°36′N–37°39′W.
2. Tasîlaq (Tasîssârssik) 66°1′N–37°9′W.
3. Qíngertivaq (Qingorssuaq) 66°7′N–37°16′W.
4. Ilivnera (Itivdleq) 66°9′N–37°22′–29′W.
5. Ikâsaulaq (Ikerasausak) 65°59′N–37°27′W.
6. Ikâsaulaq (Ikerasausak) 65°55½′N–37°20′W.

| Species | Wood collection number | Collection locality | Number of growth rings | Diam. of wood specimen |
|---|---|---|---|---|
| **Cupressaceae** | | | | |
| *Juniperus communis* L. | | | | |
| ssp. *nana* SYME ........ | *Uw 15992 | 6. | 128 | 38 mm |
| | *Uw 16003 | 1. | 91 | 14 |
| | *Uw 16004 | 1. | 98 | 15 |
| | *Uw 16009 | 6. | 45 | 11.5 |
| **Betulaceae** | | | | |
| *Betula nana* L. ........... | *Uw 15999 | 1. | 50 | 7.5 |
| | Uw 16006 | 1. Qortortup imîla | 60 | 17 |
| | Uw 16013 | 3. Falkefjeld | 147 | 24 |
| | Uw 16016 | 3. | 26 | 9.5 |
| | Uw 16022 | 3. | 41 | 14 |
| | *Uw 16023 | 4. | 27 | 9.5 |
| | *Uw 16024 | 1. Qortortup imîla | 60 | 12.5 |
| | Uw 16030 | – | 80 | 13.5 |
| **Empetraceae** | | | | |
| *Empetrum nigrum* L. ssp. *hermaphroditum* (HAGERUP) BÖCHER ................. | *Uw 15996 | 1. | 35 | 5 |
| **Ericaceae** | | | | |
| *Cassiope tetragona* (L). D. DON ................ | *Uw 16028 | 3. Cassiopefjeld 530 m | 23 | 4 |
| *Loiseleuria procumbens* (L.) DESV. ................... | *Uw 16021 | 1. | 55 | 11.5 |
| | Uw 16029 | 1. | 48 | 5 |
| *Rhododendron lapponicum* (L.) WBG. ............... | *Uw 15994 | 2. Valley 800 m | 62 | 8.5 |
| *Vaccinium uliginosum* L. ssp. *microphyllum* LANGE... | *Uw 16017 | 3. | 11 | 5.5 |
| | Uw 16018 | 3. | 11 | 4 |
| **Labiatae** | | | | |
| *Thymus praecox* OPIZ ssp. *arcticus* (E. DURAND) JALAS | Uw 16027 | 1. | 13 | 5 |

(continued)

Table 1. (continued)

| Species | Wood collection number | Collection locality | Number of growth rings | Diam. of wood specimen |
|---|---|---|---|---|
| **Rosaceae** | | | | |
| *Dryas integrifolia* M. Vahl . | Uw 16007 | 1. Sermilikvejen | 60 | 6 |
| | *Uw 16012 | 3. | 62 | 7.5 |
| | Uw 16015 | 2. Valley 810 m | 44 | 4.5 |
| **Salicaceae** | | | | |
| *Salix glauca* L ........... | Uw 15995 | 1. | 12 | 9 |
| | Uw 15997 | 1. | 11 | 7.5 |
| | Uw 15998 | 1. | 12 | 5.5 |
| | Uw 16000 | 1. | 25 | 12 |
| | Uw 16001 | 1. | 26 | 11 |
| | Uw 16002 | 1. | 47 | 11.5 |
| | Uw 16008 | 3. | 89 | 28 |
| | Uw 16010 | 3. | 21 | 12 |
| | Uw 16011 | 4. | 35 | 16 |
| | Uw 16019 | 3. | 13 | 9 |
| | *Uw 16020 | 3. | 19 | 16.5 |
| | *Uw 16025 | 2. Valley 810 m | 43 | 6.5 |
| | *Uw 16026 | 3. | 59 | 34 |
| | Uw 16031 | 5. | 32 | 18 |
| | Uw 16032 | 3. | 41 | 36 |
| *Salix herbacea* L. ......... | Uw 16005 | 1. Sermilikvejen | 34 | 4 |
| | *Uw 16014 | 6. | 26 | 4 |

* These specimens are described.

## Growth ring observations

The term growth ring, although not strictly correct, is unlikely to pass into disuse and it is certainly to be preferred to "annual ring" (JANE, 1970). Generally speaking however, the rings of the north temperate trees can be regarded as annual rings provided care is taken not to include false growth rings (GLOCK & REED, 1940; GLOCK, STUDHALTER & AGERTER, 1960). The growth season in S.E. Greenland is relatively short and the chance of producing false rings is reduced.

The wood specimens and their diameters are listed in Table 1 together with the number of growth rings, while the average, minimum and maximum breadths of their rings are given in Table 2. A note on the eccentricity of the rings is also given as the average measurements are based on the greatest radius.

It can be observed in a number of specimens, that many growth rings are so crowded together that it is very difficult to make a count (Fig. 2). However, on continuing observation whilst rotating the specimen, the rings are seen to widen, making a reasonably accurate count possible.

KRUUSE (1912) examined the growth rings in relation to growth form in three species found during his expedition to East Greenland, namely *Juniperus communis* var. *nana*, *Betula nana* and *Salix glauca*. In *S. glauca* he distinguishes three types: "Krat", an upright growth form;

Table 2. *Breadth of growth rings*

| Species | Average (in $\mu$) | Minimum (in $\mu$) | Maximum (in $\mu$) | Eccentricity |
|---|---|---|---|---|
| *Juniperus communis* L. ssp. *nana* SYME | | | | |
| Uw 15992 | 280 | 25 | 540 | C. Ec. |
| Uw 16003 | 100 | 25 | 470 | Sl. |
| Uw 16004 | 110 | 25 | 225 | Ec. |
| Uw 16009 | 170 | 45 | 370 | Sl. |
| *Betula nana* L. | | | | |
| Uw 15999 | 80 | 20 | 175 | N. |
| Uw 16006 | 160 | 65 | 414 | Sl. |
| Uw 16013 | 95 | 25 | 250 | Sl. |
| Uw 16016 | 160 | 30 | 300 | Sl. |
| Uw 16022 | 170 | 30 | 350 | N. |

Table 2. (continued)

| Species | Average (ii μ) | Minimum (in μ) | Maximum (in μ) | Eccentricity |
|---|---|---|---|---|
| Uw 16023 | 180 | 80 | 350 | N. |
| Uw 16024 | 100 | 30 | 250 | Sl. |
| Uw 16030 | 100 | 25 | 175 | Sl. |
| *Empetrum nigrum* L. ssp. *hermaphroditum* | | | | |
| Uw 15996 | 110 | 40 | 250 | Ec. |
| *Cassiope tetragona* (L.) D. DON. | | | | |
| Uw 16028 | 90 | 45 | 120 | N. |
| *Loiseleuria procumbens* (L.) DESV. | | | | |
| Uw 16021 | 130 | 30 | 250 | Ec. |
| Uw 16029 | 70 | 20 | 130 | Ec. |
| *Rhododendron lapponicum* (L.) WBG. | | | | |
| Uw 15994 | 80 | 20 | 160 | Sl. |
| *Vaccinium uliginosum* L. ssp. *microphyllum* | | | | |
| Uw 16017 | 270 | 160 | 480 | Ec. |
| Uw 16018 | 180 | 60 | 275 | N. |
| *Thymus praecox* OPIZ ssp. *arcticus* | | | | |
| Uw 16027 | 230 | 45 | 380 | Ec. |
| *Dryas integrifolia* M. VAHL | | | | |
| Uw 16007 | 80 | 40 | 280 | C. Ec. |
| Uw 16012 | 110 | 45 | 305 | Ec. |
| Uw 16015 | 50 | 30 | 190 | Ec. |
| *Salix glauca* L. | | | | |
| Uw 15995 | 420 | 65 | 770 | N. |
| Uw 15997 | 360 | 70 | 560 | N. |
| Uw 15998 | 250 | 50 | 350 | N. |
| Uw 16000 | 260 | 30 | 880 | N. |
| Uw 16001 | 170 | 70 | 720 | N. |
| Uw 16002 | 150 | 45 | 240 | Ec. |
| Uw 16008 | 150 | 45 | 380 | N. |
| Uw 16010 | 310 | 60 | 420 | Sl. |
| Uw 16011 | 260 | 75 | 515 | Sl. |
| Uw 16019 | 350 | 80 | 420 | Sl. |
| Uw 16020 | 470 | 140 | 865 | Sl. |
| Uw 16025 | 110 | 30 | 480 | C. Ec. |
| Uw 16026 | 340 | 65 | 720 | Ec. |
| Uw 16031 | 360 | 80 | 500 | Sl. |
| Uw 16032 | 400 | 70 | 740 | N. |
| *Salix herbacea* L. | | | | |
| Uw 16005 | 80 | 45 | 160 | V. Ec. |
| Uw 16014 | 100 | 45 | 190 | Sl. |

N. Not eccentric. Sl. Slightly eccentric. Ec. Eccentric. V. Ec. Very eccentric. C. Ec. Completely eccentric.

"Pilebuskene", a form which grows over the ground, frequently under the leaf layer, with the later formed branches growing upwards, and these branches often not covered with a snow layer; "Espalier", a sprawling form with a short stem and powerful branches that can obtain a more upright position by pushing up over rocks. KRUUSE found that the oldest specimens were mostly of the espalier and pilebuskene type, the stems of which he frequently had to dig up. He reasons that the greater age occurs because the actual stem was examined compared to the krat where only the branches were observed.

In *B. nana* the largest stems were found in the espalier forms, upright forms not being very common. He found that *J. communis* var. *nana* occurred most frequently as espalier forms, growing preferably against upright rocks. It appears from his table that although the amount of wood produced each year is small, this species reaches a comparatively old age.

KRUUSE notes that generally in espalier and the other sprawling forms of all the three species, the stem is eccentric. He states that the eccentricity originates when the weight of the snow forces the upright branches to take up a more procumbent habit, and that this probably causes cessation of growth in the upper part of the branch, sometimes a dying off of that part, while the under part deeper in the snow continues to grow. Such interruptions in growth produce discontinuous growth rings, which were observed by KRUUSE as well as by the present author. These "ramification points", found to be of frequent occurrence in *Juniperus communis* by JAQUIOT (1955), are known to be the result of cambium dormancy (JANE, 1970), thus this reasoning of KRUUSE would appear to be correct, as the chance of these stems or branches obtaining sufficient warmth for growth would be greater closer to the ground or rocks. The varying degrees of eccentricity shown by a great number of the specimens recorded in Table 2, could therefore be explained by the lying heath-like habit adopted by these plants.

The measurements of *J. communis* ssp. *nana* and *B. nana* are closely in agreement with those made by KRUUSE. In *S. glauca* he states that the annual ring breadth is very variable, between 20 and 1500$\mu$. The measurements of the average and maximum breadths found in his table are considerably greater than those found in the present investigation. Obviously with such high maximums the average breadths will also be elevated. According to KRUUSE the broadest rings are to be found in the upright shrubs while the espalier and other low shrub forms have a reduced growth ring thickness. The reduced thickness is to be expected when considering the upper surface of these creeping branches, exposed to the full extreme of the Greenland climate, but the results in Table 2 were based on the greatest radius of the specimen, which is produced under more favourable conditions, and show insufficient evidence to support such a claim.

Many environmental conditions effect the development of plants. FORSAITH (1920) summarized these conditions during his work on the anatomical reduction in Alpine plants. These conditions must therefore be taken into consideration when analysing any growth ring series.

It is perhaps of interest to note, even though the number of wood samples is limited, that the breadth of the growth rings in the *Vaccinium* species is larger than in the other species examined in this family. Within the genus *Salix*, *S. herbacea* shows much narrower rings than *S. glauca*. It is not known however, whether these specimens were growing under optimum conditions.

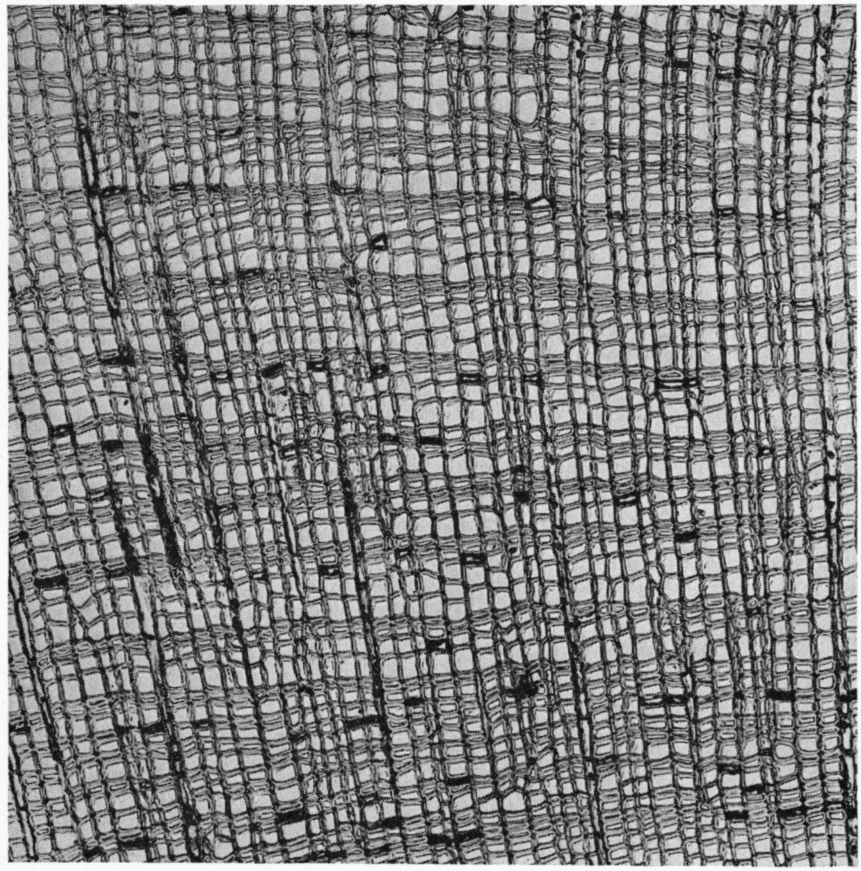

Fig. 2. *Juniperus communis* L. ssp. *nana* SYME. Transverse section showing the many crowded growth rings. ×200.

## Wood descriptions

The 17 specimens studied in this investigation are representative of 10 species. It was thought that no useful purpose would be served in attempting to describe the very small and twisted specimen of *Thymus praecox* OPIZ ssp. *arcticus* (E. DURAND) JALAS, (T. *drucei* RONINGER).

A photograph of the transverse section of each species is included with each description for an easier comparison of the pore distribution. This is accompanied by a photograph of the tangential or radial longitudinal section to clarify the important anatomical characteristics of the wood.

The terminology used in this investigation generally follows that suggested by the Committee on Nomenclature, International Association of Wood Anatomists, Multilingual Glossary of Terms Used in Wood Anatomy (1964).

### Cupressaceae

#### *Juniperus communis* L. ssp. *nana* SYME

Growth rings in all specimens (Uw 15992, Uw 16003, Uw 16004 & Uw 16009) are frequently irregular, generally distinct. Width varies from (2)4–45 cells. Transition from early to late wood is sudden, late wood consisting of (1)2–5(6) rows of flattened tracheids.

*Tracheids* are angular in transverse section, intercellular spaces generally scarce. Specimen Uw 16004 is eccentric, specimen Uw 15992 is markedly so, but tracheid walls do not show usual signs of compression wood. In specimens Uw 16003 and Uw 16009 checking is present even though eccentricity is only slight. Bordered pits arranged mostly in one row on radial walls; on tangential walls pits are smaller, less numerous, especially in early wood. Details of tracheid measurements and pits given in Table 3.

*Wood rays* are uniseriate, only occasionally biseriate or partially biseriate. Cells are mostly procumbent with nodular end walls; square cells found occasionally. Indentures are present but rare. Walls are generally smooth, thickness averaging 1.5 $\mu$. Cross-field pits are cupressoid; 1–2 pits per cross-field, 3–4 pits in marginal cells.

Table 3.

| | Uw 15992 | Uw 16003 | Uw 16004 | Uw 16009 |
|---|---|---|---|---|
| TRACHEIDS | | | | |
| Wall thickness ($\mu$) | | | | |
| Late wood ....... | 2–3 | 2.5–3 | 2–2.5 | 2.5 |
| Early wood ...... | 1.5–2 | 2 | 1.5–2.5 | 1.5–2 |
| Lumen ($\mu$) average | | | | |
| Late wood ....... | 3×12 | 1–5×10 | 4×12 | 2–4×12 |
| Early wood ...... | 14 | 12 | 14 | 12 |
| Length ($\mu$) | | | | |
| Minimum ........ | 400 | 40 | 325 | 325 |
| Maximum ........ | 1600 | 1600 | 1550 | 1450 |
| Average ......... | 1100 | 985 | 1050 | 910 |
| Pit size (average in $\mu$) | | | | |
| Border........... | 14 | 10 | 14 | 10 |
| Aperture ......... | 4 | 4 | 5 | 4 |
| RAYS | | | | |
| Height | | | | |
| Max. no. cells..... | 14 | 9 | 8 | 8 |
| Maximum ($\mu$)..... | 260 | 225 | 160 | 195 |
| Average ($\mu$) ...... per cell | 20.0 | 21.2 | 20.1 | 20.4 |
| Breadth | | | | |
| Average cell ($\mu$) ... | 10.5 | 11.5 | 10.1 | 11.0 |
| Ray height distribution | | | | |
| Frequency % | | | | |
| No. cells high | | | | |
| 1 .......... | 25 | 45 | 40 | 40 |
| 2 .......... | 40 | 35 | 35 | 40 |
| 3 .......... | 15 | 20 | 25 | 20 |
| 4+ .......... | 20 | | | |

*Parenchyma* is relatively abundant for conifers. Strands are (2)5–7(9)-celled, often concentrated concentrically at beginning of late wood. Marked tendency for parenchyma to form in zones, a zone consisting of usually 5–30 rings containing parenchyma, adjacent to a zone of similar size in which it is scarce or even absent. Transverse walls are occasionally nodular. Cells often contain resinous materials.

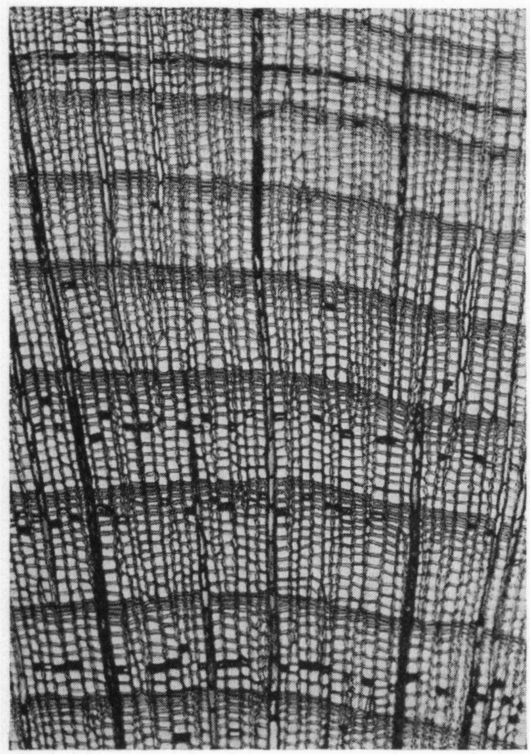

Fig. 3. *Juniperus communis* ssp. *nana*. Transverse section showing parenchyma distribution. ×100.

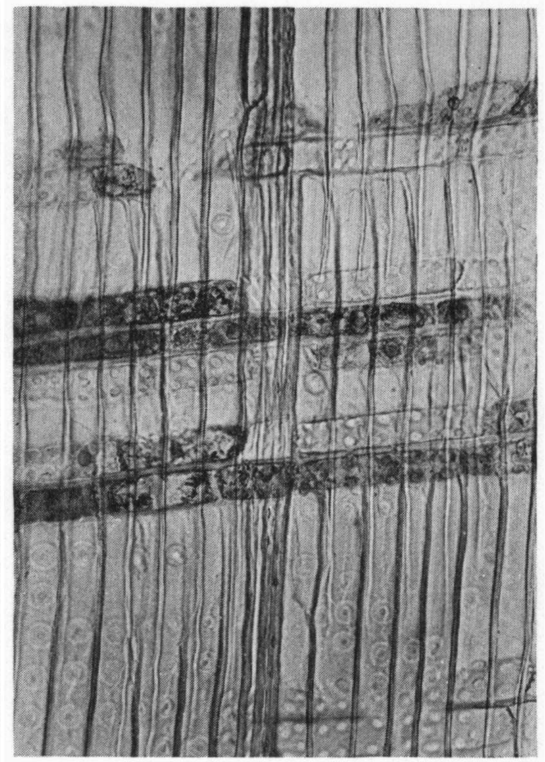

Fig. 4. *Juniperus communis* ssp. *nana*. Radial section showing cross-field pitting ×250.

## Betulaceae

### *Betula nana* L.

Wood in all specimens (Uw 15999, Uw 16023 & Uw 16024) is ring porous.

*Vessels* arranged mostly in radial multiples of 2–6(9), in groups of 2–4(8), occasional solitary. Number: 150–300 per $mm^2$. Pore size: 15–45 μ, average 25–30 μ. Length of vessel members: (100)200–400 (550) μ. Scalariform perforation plates with (10)15–25(40) bars. Intervascular pitting is alternate, sometimes opposite, 2–5 μ.

*Wood rays* are mostly uniseriate, occasional biseriate and partially biseriate, larger multiseriate also occasionally found, heterocellular. Biseriate and larger multiseriate often with 1–6 outer rows of square cells. Height: (1)2–8(30) cells, 25(30)–200(500) μ. Number: 9(12)–15(20) per mm. Pits to vessels are simple, 1.5–3(5) μ.

*Libriform fibres.* Length: (125)250–500(850) μ. Wall thickness in late wood varies little from that in early wood, 1.5–3 μ. Lumen: in early

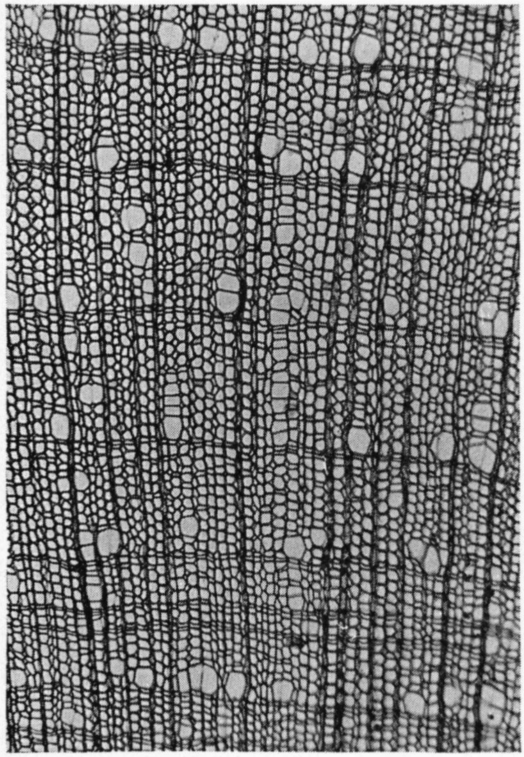

Fig. 5. *Betula nana.* Transverse section: vessels in radial multiples. ×100.

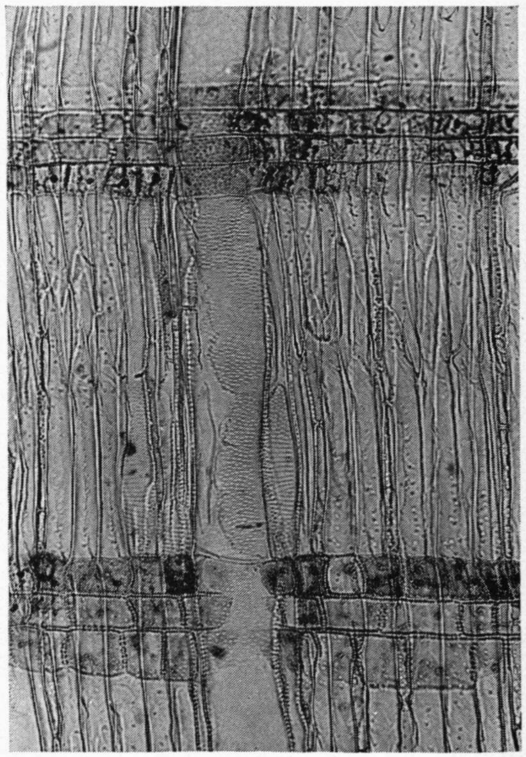

Fig. 6. *Betula nana.* Radial section: scalariform perforations, heterocellular rays. ×250.

wood (4)10–12(20) μ; in late wood (5)10–12(18) μ, but partially radially flattened forming a 1–2 cell wide tangential band. Occasionally fibres with gelatinous walls. Pits slit-like, sometimes slightly oval, most frequent on radial walls, 4–8 μ.

*Parenchyma* is scanty, apotracheal, often associated with terminal growth rings. Strands are (2)3–4(6)-celled. Length: (120)200–460(550) μ. Pits are simple, solitary or in small fields, 1.5–3 μ.

## Empetraceae

### *Empetrum nigrum* L. ssp. *hermaphroditum* (Hagerup) Böcher

Wood of specimen Uw 15996 is ring porous and eccentric.

*Vessels* are frequently solitary, in groups of 2–4(6), occupy most of early wood. Number: more than 500 per mm$^2$. Pore size: (15)25–40(60) μ. Length of vessel members: (115)160–240(375) μ. Scalariform perforation plates with 8–15, average 12 bars, occasional simple perforations. Intervascular pitting is opposite and alternate. Pits with small border vary in shape from oval, slit-like to scalariform, 4–12 μ.

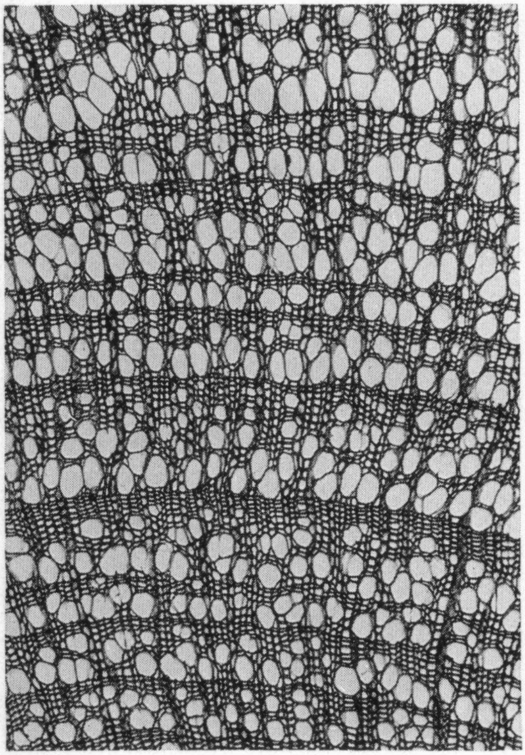

Fig. 7. *Empetrum nigrum* ssp. *hermaphroditum*. Transverse section: showing pore distribution. ×100.

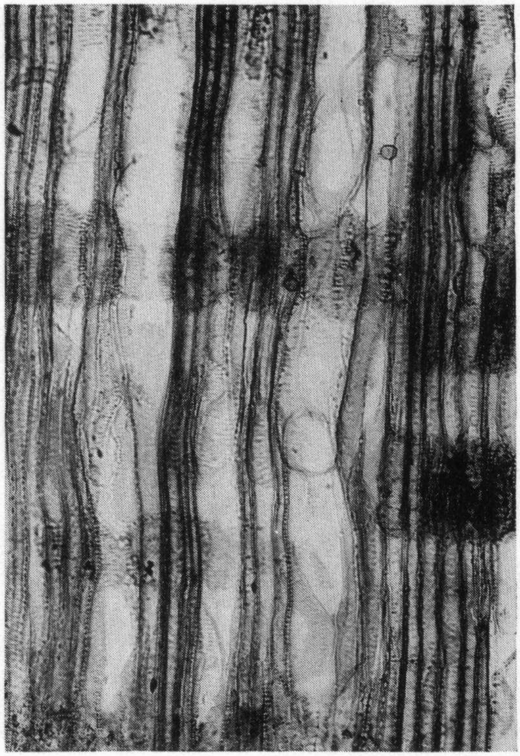

Fig. 8. *Empetrum nigrum* ssp. *hermaphroditum*. Radial section: scalariform and simple perforations. ×250.

*Rays* are uniseriate, occasional partially biseriate, 1–8(12) cells, 40–400(650) μ high, composed of upright cells. Number: (12)15–19(25) per mm. Pits are simple, otherwise similar to intervascular pits.

*Fibre-tracheids*. Length: (120)200–275(400) μ. Wall thickness: 3–5 μ. Lumen: (4)6–8(10) μ. Bordered pits, 3–6 μ, occur on both radial and tangential walls.

*Parenchyma* is rare, apotracheal and paratracheal. Occurs as fusiform cells or 2(3)-celled strands. Length 120–220 μ. Pits are round to oval, occasionally slit-like, smaller than 2 μ.

## Ericaceae

### 1. *Cassiope tetragona* (L.) D. DON.

Wood of specimen Uw 16028 is semi-ring porous.

*Vessels* are generally in groups of 2–4(10), often arranged tangentially at beginning of growth ring, occasionally solitary. Number: more than 800 per mm$^2$. Pore size: (6)12–18(30) μ. Length of vessel members: 80–250 μ, average 150–200 μ. Scalariform perforations with 5–14, average

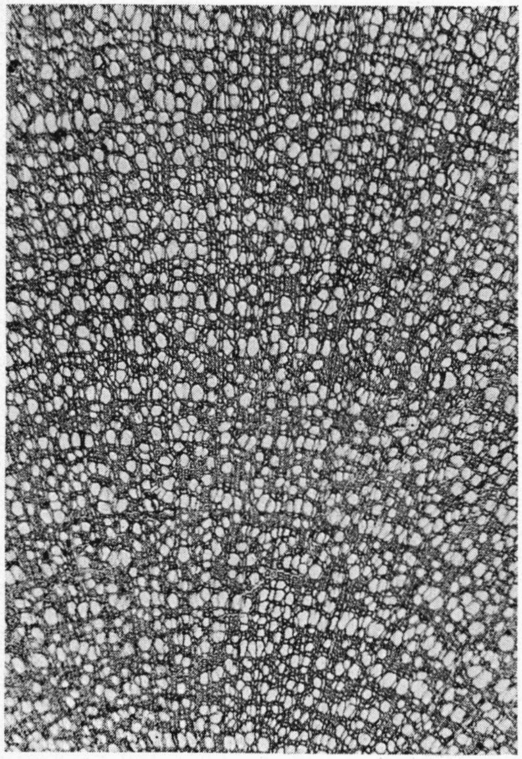

Fig. 9. *Cassiope tetragona.* Transverse section: pore distribution. ×100.

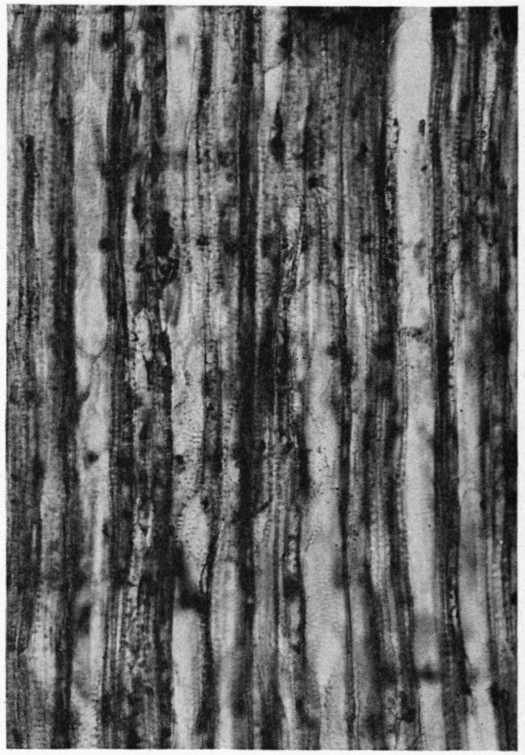

Fig. 10. *Cassiope tetragona.* Radial section: note wide pits of vessels. ×250.

8 bars, simple perforations are very rare. Intervascular pits are slightly bordered, alternate and opposite, 3–5 μ. Larger pits occur with a tendency to form scalariform pitting.

*Rays* are uniseriate, 1–3(5) cells, 40–140(220) μ high, composed of upright cells. Number: (10)12–16(23) per mm. Pits to vessels are simple, smaller than 2 μ.

*Fibre-tracheids.* Length: (120)150–200(275) μ. Wall thickness: 2–4 μ. Lumen: 4–8 μ. Bordered pits, 4–5 μ, occur on both radial and tangential walls.

*Parenchyma* is scanty, paratracheal in incomplete sheaths. Mostly fusiform cells, occasional 2-celled strands. Length: (70)140–200(250) μ. Pits are simple, round to oval or slit-like, smaller than 2.5 μ.

## 2. *Loiseleuria procumbens* (L.) Desv.

Wood of specimen Uw 16021 is semi-ring porous and slightly eccentric.

*Vessels* are solitary and in small groups of 2(3–4), mostly tangentially arranged. Number: 400–500 per mm$^2$. Pore size: 10–40 μ, average 28 μ. Length of vessel members: 80–350 μ, average 200–230 μ. Scalari-

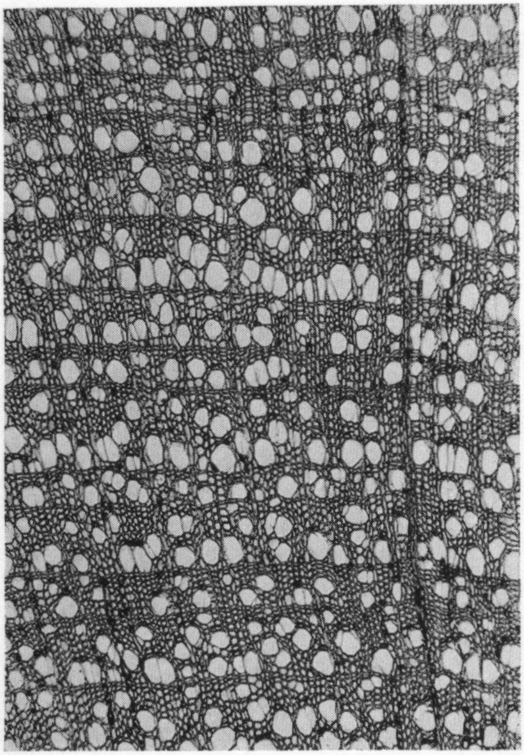

Fig. 11. *Loiseleuria procumbens.* Transverse section. ×100.

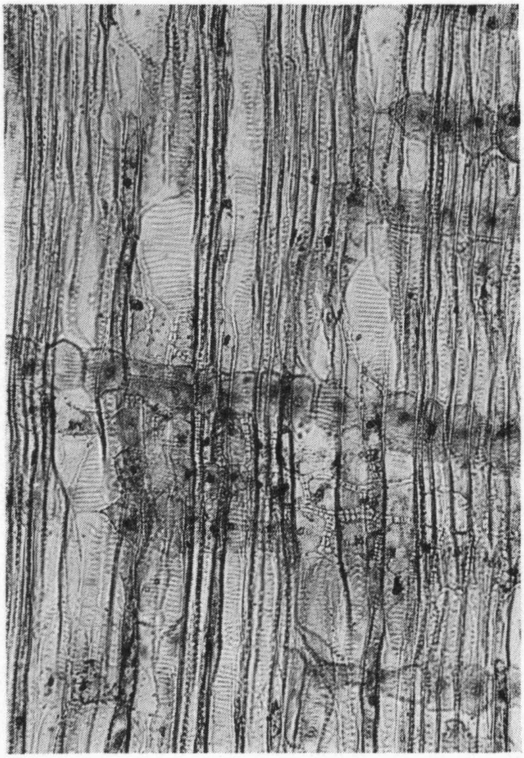

Fig. 12. *Loiseleuria procumbens.* Radial section. ×250.

form perforations, with (10)14–20(30) bars, occasionally perforations are imperfect, simple perforations rare. Intervascular pitting predominantly scalariform, found mostly on radial walls. Other pits with small border, slit-like apertures, 4(7) μ.

*Rays* are uniseriate and biseriate. Mostly uniseriate, 1–4(7) cells, 30–180(275) μ high, composed of square and upright cells. Biseriates, 15–20 μ wide, up to 300 μ but usually 200 μ high, composed of mostly procumbent cells, frequently with 1–3 outer rows of upright cells. Number: 15–35, average 26 per mm. Pits to vessels obscured by brown cell contents, generally appear to be simple, round to oval in form, 2–3 μ × 3–5 μ.

*Fibre-tracheids.* Length: 135–325 μ, average 200–245 μ. Wall thickness: 2–4 μ. Lumen: 5–8 μ. Bordered pits with a slit-like aperture, 2.5–4 μ, occur on both radial and tangential walls. Predominantly found in early wood forming tangential bands.

*Parenchyma* is scanty, apotracheal and paratracheal, mostly in incomplete sheaths. Fusiform cells 120–220 μ long, average 180 μ, often as 2–3(4)-celled strands. Pits are simple, smaller than 2 μ.

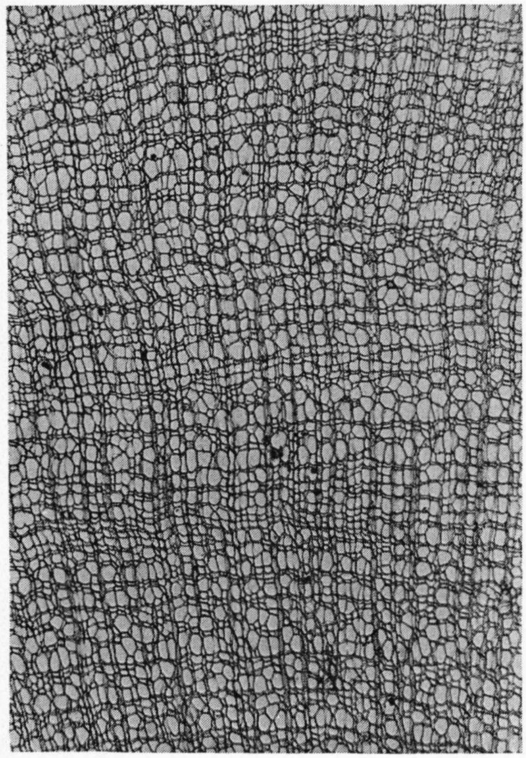

Fig. 13. *Rhododendron lapponicum.* Transverse section: diffuse porous. ×100.

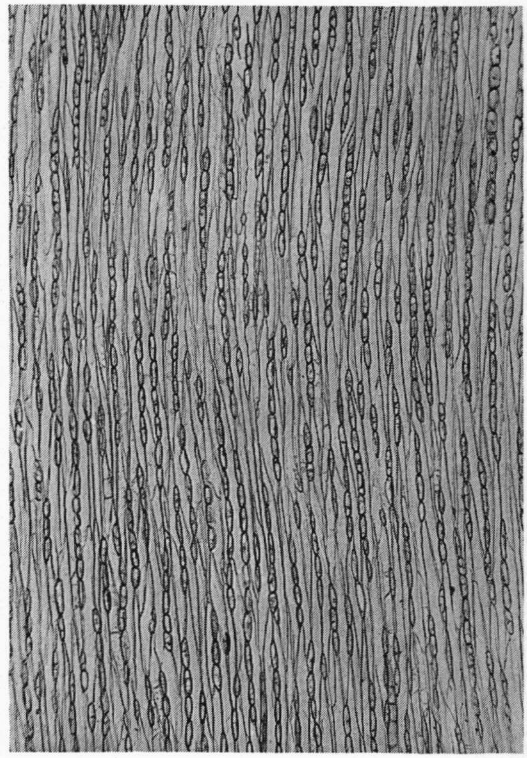

Fig. 14. *Rhododendron lapponicum.* Tangential section: uniseriate rays. ×100.

### 3. *Rhododendron lapponicum* (L.) Wbg.

Wood of specimen Uw 15994 is diffuse porous and slightly eccentric.

*Vessels* distributed more or less evenly, solitary or in small groups. Number: more than 1000 per mm². Pore size: 8–14(22) μ. Length of vessel members: 100–380 μ, average 235 μ. Scalariform perforations, with 5–15, average 10 bars. Intervascular pits are alternate, occasionally opposite, 3–6 μ.

*Rays* are uniseriate, (1)4–8(18) cells, (35)120–300(650) μ high, heterocellular, consisting of square and upright thin walled cells. Number: (20)25–28(35) per mm. Pits to vessels are similar to intervascular pits.

*Fibre-tracheids.* Length: (175)275–325(425) μ. Wall thickness: generally 1–1.5 μ. Lumen: (5)7–8(12) μ. Late wood distinguished mostly by one continuous tangential band. Bordered pits, 3–5 μ, occur on both radial and tangential walls.

*Parenchyma* is scanty, mostly paratracheal. Occasional fusiform cells, generally 2–4(5)-celled strands. Length: (90)160–240(325) μ. Pits are simple, not larger than 2 μ.

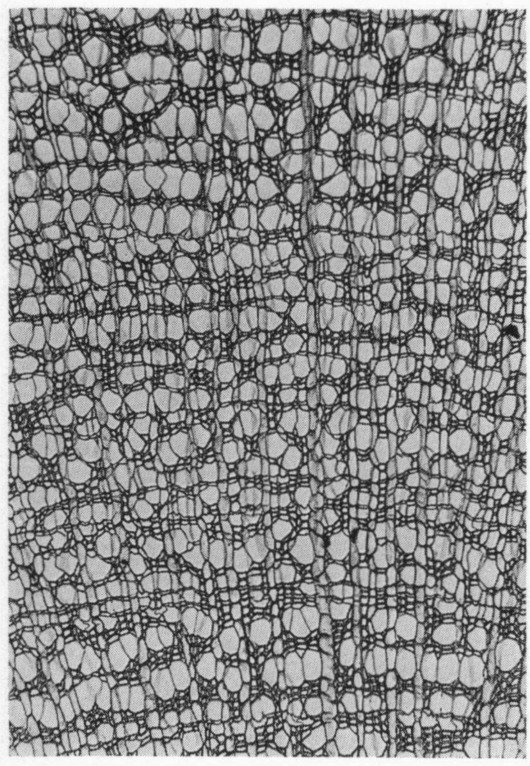

Fig. 15. *Vaccinium uliginosum* ssp. *microphyllum*. Transverse section: pore distribution. ×100.

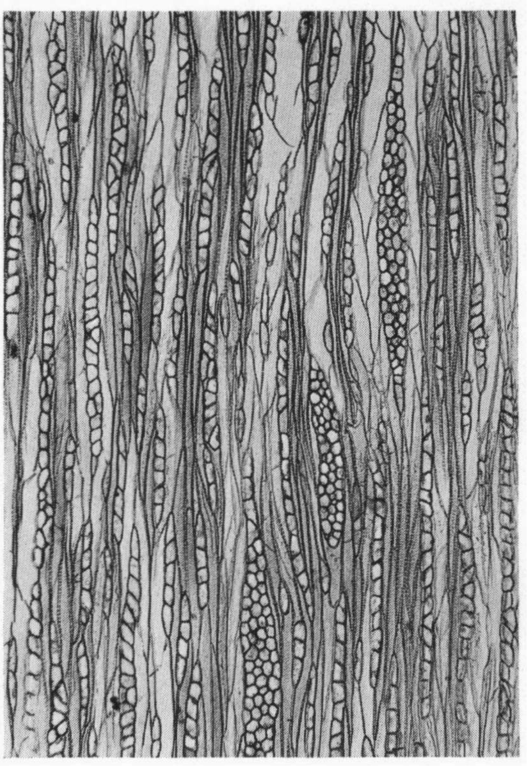

Fig. 16. *Vaccinium uliginosum* ssp. *microphyllum*. Tangential section: uniseriate and multiseriate rays. ×100.

### 4. *Vaccinium uliginosum* L. ssp. *microphyllum* LANGE

Wood of specimen Uw 16017 is semi-ring porous and eccentric.

*Vessels* are solitary or in groups of 2–3(4), sometimes arranged tangentially. Number: more than 500 per mm². Pore size: in outer growth rings 15–50 μ, average 35 μ; in inner growth rings 12–35 μ, average 25 μ. Length of vessel members: 135–375 μ, average 200–275 μ. Predominantly simple perforations, some scalariform with 4–9 bars, occasional reticulate and imperfect perforations. Intervascular pits with small border, alternate, 3–5 μ.

*Rays* are 1– and 3–4(5) seriate. Mostly uniseriate or partially biseriate, 2–30 cells (50–700 μ) high, usually 12–20 cells high, composed of square and procumbent cells. Multiseriate rays, 35–65 μ wide, up to 1800 μ high, heterocellular, often with one row of upright cells. Number: 11–21, average 14 per mm. Pits to vessels are similar to intervascular pits.

*Fibre-tracheids*. Length: 150–550 μ, average 300 μ. Wall thickness: 2–5 μ. Lumen: 6–10 μ. Largest numbers occurring in late wood making up tangential band formations. Many with pointed ends. Many pits on both

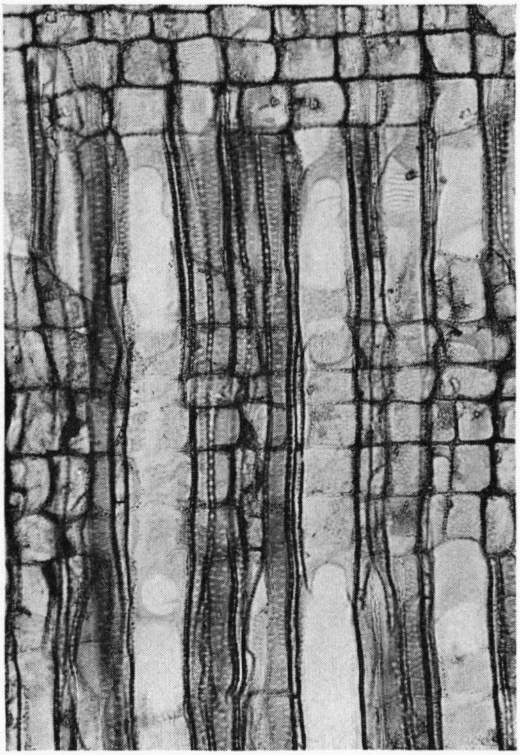

Fig. 17. *Vaccinium uliginosum* ssp. *microphyllum*. Radial section: simple and scalariform perforations. ×250.

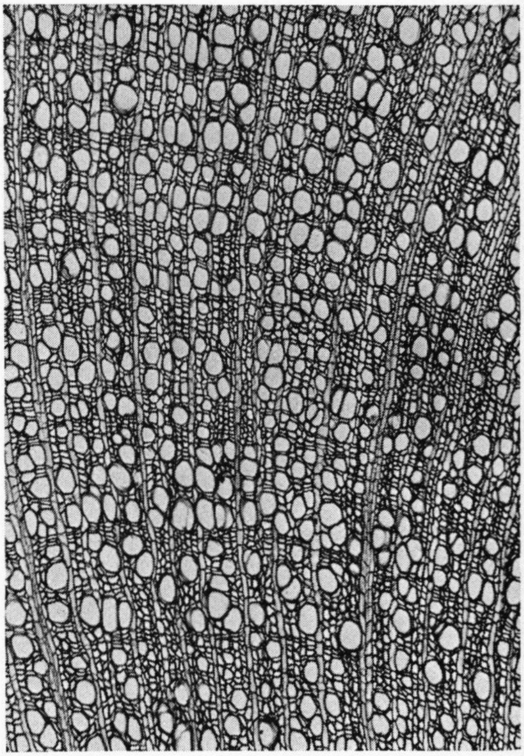

Fig. 18. *Dryas integrifolia*. Transverse section: pore distribution. ×100.

radial and tangential walls, border often distinct, slit-like apertures, 3–4 μ. Occasional septate fibres.

*Parenchyma* is occasional, paratracheal. Fusiform cells, length: 120–300 μ, average 220 μ; 2-celled strands, length: 150–350 μ, average 250 μ, sometimes septate. Pits are simple, approximately 2 μ.

## Rosaceae

### *Dryas integrifolia* M. Vahl

Wood of specimen Uw 16012 is semi-ring porous and eccentric.

*Vessels* are solitary, in small groups of 2–4, and in short tangential rows of 3–6. Number: 350–450 per mm$^2$. Pore size: 12–40 μ, average 25 μ. Length of vessel members: 175–350 μ, average 225 μ. Mostly simple perforations, occasional scalariform perforations with 3–6 bars. Pits are mostly alternate, occasionally opposite, with small border, often slit-like, 3–5 μ. Tendency for some pits to become scalariform.

*Rays* are 1- and 2–3(4) seriate. Mostly multiseriate, 18–30(35) μ wide, (450)550–900(1200) μ high, heterocellular with 1–6(20) outer rows of upright cells. Uniseriate and partially biseriate mostly consisting of

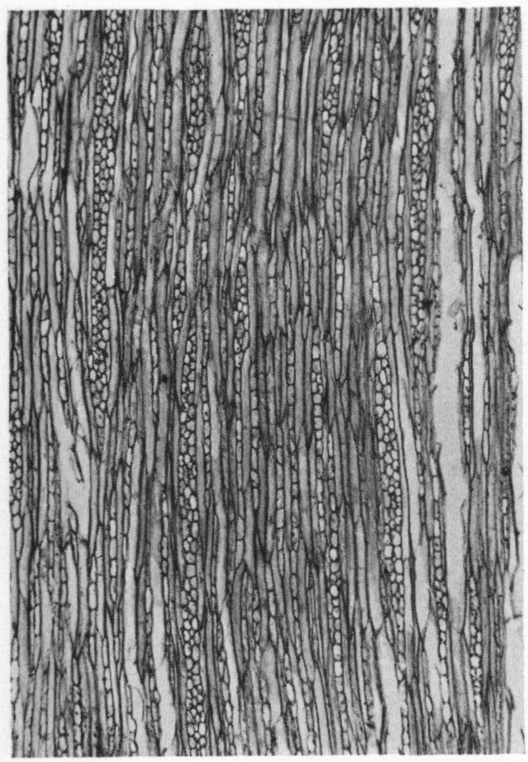

Fig. 19. *Dryas integrifolia.* Tangential section: storied structure of fibre-tracheids. ×100

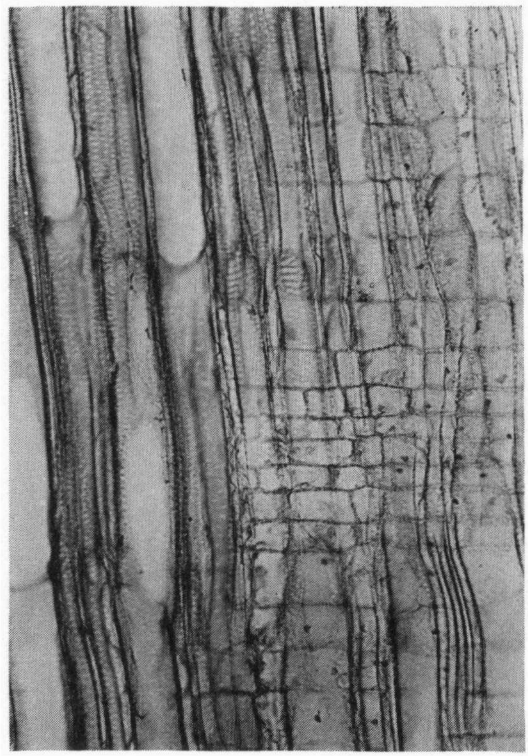

Fig. 20. *Dryas integrifolia.* Radial section: showing upright cells. ×250.

upright cells, (3)4–10(18) cells, (80)140–300(500) μ high. Pits to vessels are simple, 2–4 μ.

*Fibre-tracheids* show storied structure. Length: mostly 250–350 μ. Wall thickness: 1–2 μ. Lumen: (6)7–10(14) μ. Some radial flattening in late wood. Pits are bordered, apertures 2–4 μ.

*Parenchyma* is scarce, apotracheal and paratracheal. Fusiform cells and 2(3)-celled strands. Length: (180)220–270(300) μ. Pits are simple, oval, 4–5 μ.

## Salicaceae

### 1. *Salix glauca* L.

Wood of specimens Uw 16020, Uw 16025 & Uw 16026 is semi-ring porous and varies in eccentricity.

*Vessels* occur in radial multiples of 2–4(6), groups of 2–6, occasional solitary. Number: 150–250 mm$^2$. Pore size: 12–50 μ, average 35 μ in smallest specimens, up to (20)40–70(115) μ in largest specimen. Length of vessel members: (225)300–450(600) μ. Simple perforations. Intervascular pits are alternate, bordered, 6–10 μ, with apertures 2–5 μ.

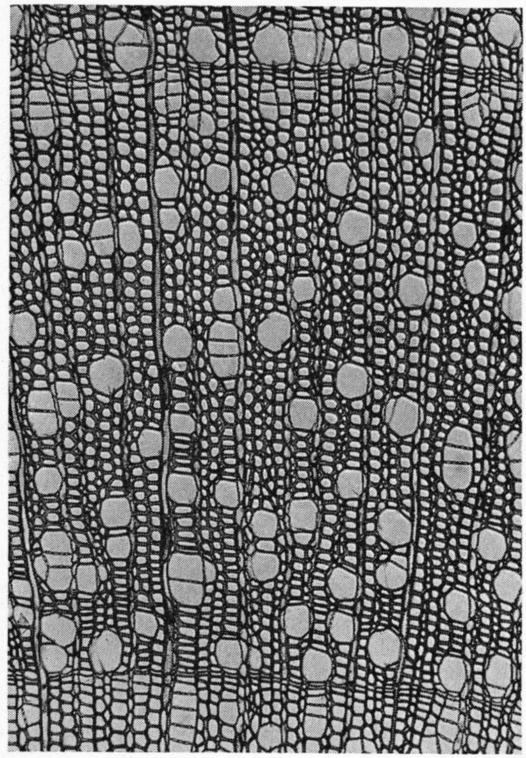

Fig. 21. *Salix glauca.* Transverse section: pore distribution. ×100.

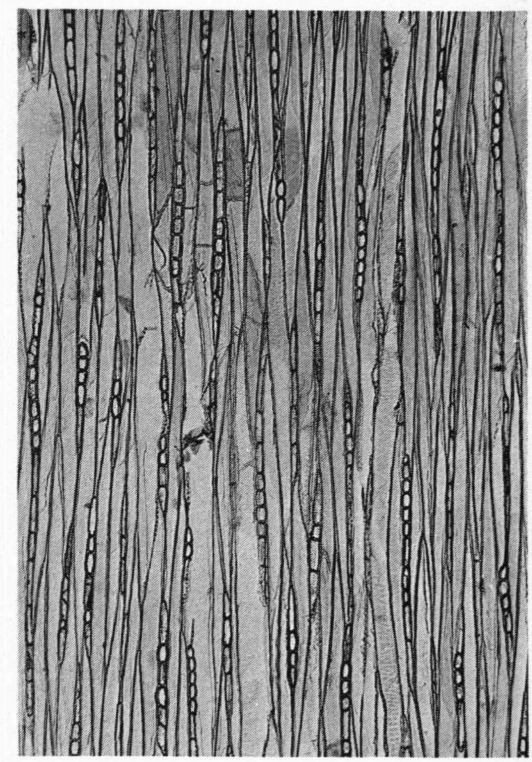

Fig. 22. *Salix glauca.* Tangential section: uniseriate rays. ×100.

*Rays* are mostly uniseriate, occasional partially biseriate or biseriate, latter more frequent in larger samples. Heterocellular, (2)7–16(28) cells, 80–680 μ, average 230–350 μ high. Number: (7)9–13(16) per mm. Only square and upright cells contain pits to vessels. Pits are simple, 6–10(12) μ, arranged in 3–8 rows of 2–8 pits per row.

*Libriform fibres.* Length: (300)450–650(850) μ. Wall thickness varies little from early to late wood, 1.5–4 μ. Lumen: in late wood (8)12–15(25) μ, sometimes radially flattened to 1–3 cell wide band where growth ring terminates, then lumen averages 6 μ; in early wood (5)12–15(25) μ. Many gelatinous fibres, frequently in early wood. Occasional septate fibres. Pits are narrow slit-like, 3–8 μ.

*Parenchyma* is scanty, paratracheal and apotracheal, often confined to termination of growth ring. Occasional fusiform, mostly 2–3(4)-celled strands. Length: (200)300–460(600) μ. Pits are simple, round to oval, 2–4(7) μ.

## 2. *Salix herbacea* L.

Wood of specimen Uw 16014 is semi-ring porous and slightly eccentric.

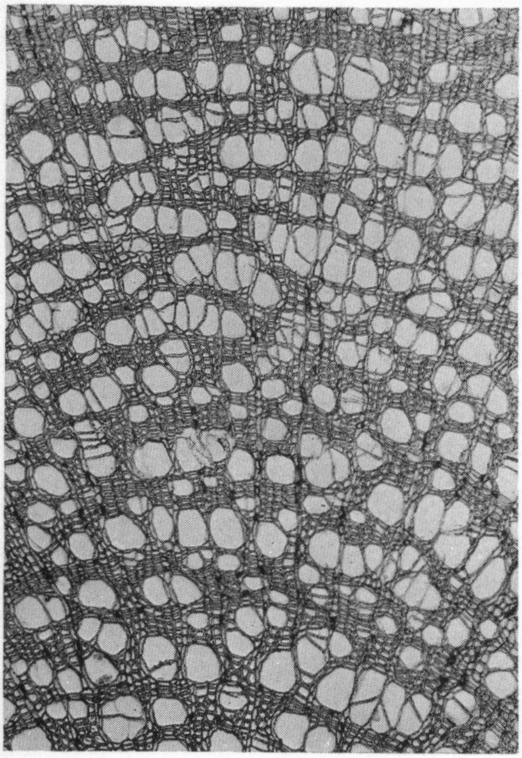

Fig. 23. *Salix herbacea.* Transverse section: pore distribution. ×100.

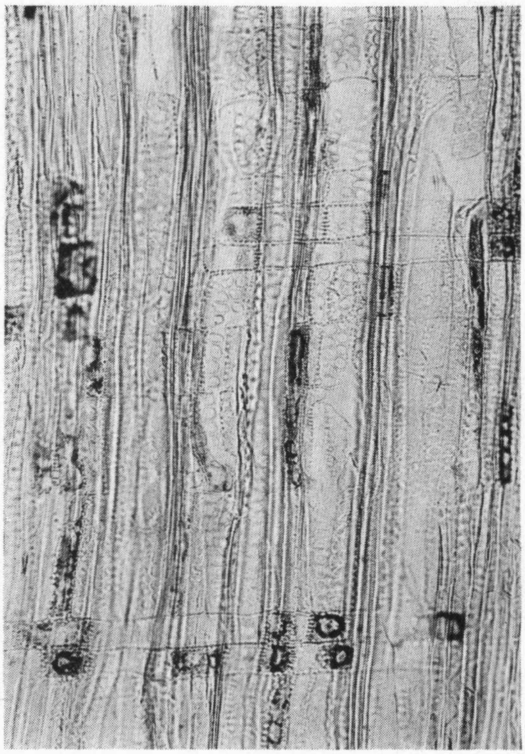

Fig. 24. *Salix herbacea.* Radial section: showing typical pitting in ray cells to vessels. ×250.

*Vessels* are often solitary, many in small groups of 2–4, occasional radial multiples of 2–4. Length of vessel members: (180)250–325(450) μ. Simple perforations. Alternate intervascular bordered pits, 6–8(10) μ with apertures 4–6 μ. Small part of specimen contains traumatic tissue where vessels are filled with tyloses; wall thickness variable, 1.5–5 μ, unpitted.

*Rays* are uniseriate, occasionally partially biseriate, (1)5–12(40) cells, (50)200–400(1200) μ high, heterocellular. Number: (10)15–18(23) per mm. Pits are simple, irregular in shape, 5–8 μ, arranged in 2–8 rows of 3–6 pits per row.

*Libriform fibres.* Length: (250)350–450(650) μ. Wall thickness: in late wood 1.5–3 μ; in early wood 1–1.5 μ. Lumen: in late wood 3–10 μ radially, 10–12 μ tangentially; in early wood 5–12 μ radially, 8–15 μ tangentially. Gelatinous fibres occur in early wood. Occasional septate fibres. Pits are slit-like, 4–5 μ.

*Parenchyma* is scarce, apotracheal, paratracheal. Fusiform cells, 2–3(4)-celled strands. Length: (200)300–425(500) μ. Pits are simple, round to oval in form, 4–6 μ.

## Evaluation of anatomical characteristics

An evaluation of the various anatomical characteristics found during this investigation should be made bearing in mind the environmental conditions under which the described species grew. This is best attempted by examining those features which are relatively stable and therefore of taxonomic importance, as well as the more flexible features which together may add to a better understanding of the phylogenetic sequence.

The samples of *Juniperus communis* ssp. *nana* SYME show very little variation in structure with the exception of the degree of eccentricity which has already been described in a preceeding chapter. The average and maximum tracheid lengths appear to be somewhat longer than those of the same species found in the more temperate climates (MILLER, 1974). Although longer tracheids are considered to be of a more primitive nature (BAILEY & TUPPER, 1918; FROST, 1930), the general description is however, in agreement with that of *J. communis* (GREGUSS, 1955; MILLER, 1974).

*Betula nana* illustrates, qualitatively at least, a typical example of the Betulaceae. The vessels, with scalariform perforations, are arranged in radial multiples, and the scanty apotracheal parenchyma is frequently associated with the late wood. GREGUSS (1959), METCALFE & CHALK (1950) report, for *B. nana*, rays up to 4, occasionally 5 cells wide and mention that in Betulaceae rays tend to be homogeneous. FORSAITH (1920) notes for the dwarfed alpine birch, *Betula glandulosa* MICHX., an increase in uniseriate rays, and after a comparison with a lowland form, *Betula alba* var. *papyrifera* (MARSH.) SPACH., with its many multiseriate rays, suggests a modification. Using the argumentation of HOAR (1916) and BAILEY (1912), he states that the results obtained from his study of *B. glandulosa*, may be applied equally as well to *Betula alba* var. *cordifolia* (REGAL) FERNALD., which also shows an increase in the number of uniseriate rays and is indigenous to high altitudes. The large number of uniseriate rays found in *B. nana* in this investigation, by the same token, may be considered to be a further modification under the arctic conditions, while the heterocellular nature of the rays may well represent a more primitive stage (CARLQUIST, 1961).

The description of *Empetrum nigrum* L. ssp. *hermaphroditum* (HAGERUP) BÖCHER is generally in agreement with METCALFE & CHALK'S

(1950) description of *E. nigrum*, which in turn appears to have been based on GREGUSS (1945). The present author notes the occurrence of simple perforations as well as scalariform perforations. Simple perforations in *E. nigrum* are not mentioned either by the above authors or by GREGUSS (1959). This more specialized anatomical feature (FROST, 1930), might be regarded as characteristic of this subspecies or it may be considered to be a part of the plant's environmental adaptation. However, either hypothesis will be best supported after a comparison has been made with the same subspecies from the temperate zones.

The wood of *E. nigrum* ssp. *hermaphroditum* characterized by uniseriate rays of upright cells, relatively small but numerous vessels with both scalariform and simple perforations, together with scarce parenchyma which is often present as fusiform cells, does show a remarkable resemblance to some members of the Ericaceae.

COX (1948b) gives some measurements for *Cassiope tetragona*. The pore diameters and vessel lengths are in close agreement with those of the present author; the average number of bars in the scalariform perforations is lower. COX notes, however, that the exact source of the material is not known. COX (1948a) examined the wood of *Rhododendron lapponicum* and found pore diameters and vessel lengths with measurements which do not appear to be significantly different from those found in this investigation. COX notes that 25 % of the vessels contain simple perforations, but again the origin of the material is not known.

The vessels of all four species of Ericaceae examined in this investigation show both simple and scalariform perforations. METCALFE & CHALK (1950), and GREGUSS (1959), note the presence of simple perforations only in *Vaccinium*. Throughout the Ericaceae the rays appear to be variable. In *Loiseleuria procumbens* (L.) DESV. not only uniseriate but biseriate rays with procumbent and upright cells are seen. The biseriate rays were not previously reported. The rays of *Rhododendron lapponicum* are uniseriate, which is in agreement with FORSAITH (1920), whereas generally in the Ericaceae, including some species of *Rhododendron*, rays of up to 5 cells wide are to be found. FORSAITH (1920) considers *Rhododendron* to be among the well advanced members of its genus because of the reduction in width of its rays. The loss in number of either uniseriate or multiseriate rays being associated with advancement (KRIBS, 1935; CARLQUIST, 1961).

Of the species examined in this family, the wood of *Vaccinium uliginosum* L. ssp. *microphyllum* LANGE appears to be the least typical. GREGUSS (1959) reported in *V. uliginosum* multiseriate rays as being rare, but in this subspecies relatively large numbers occur. *V. uliginosum* ssp. *microphyllum* shows a predominance of simple perforations with occasional reticulate perforations, occasional septate fibres and the occurrence of septate cells in the axial parechyma. METCALFE & CHALK (1950) do in fact place this genus in an apart family the Vacciniaceae, (according BENTHAM & HOOKER in *Genera Plantarum*).

In the wood of *Dryas integrifolia* M. VAHL the multiseriate rays are more frequent than in *Dryas octopetala* L. (GREGUSS, 1959), The rays too occur with many outer rows of upright cells compared to *D. octopetala*, a feature considered as primitive (KRIBS, 1935). However, the fibre-tracheids show a tendency to form a storied structure, a feature regarded by METCALFE & CHALK (1950) to be associated with a high level of specialization.

Very little difference is to be found between the woods of *Salix glauca* L. and *Salix herbacea* L. The simple perforations and the numerous large pits occurring in the square and upright cells of the rays adjoining the vessels, typify this family. Septate fibres were occasionally observed in both species, a feature previously reported by SOLEREDER (1908) in *Salix alba* L., but not reported by METCALFE & CHALK (1950). Tension wood, as indicated by the frequent occurrence of gelatinous fibres in the specimens examined of both *S. glauca* and *S. herbacea*, is commonly found in branches and leaning trunks and is often associated with an eccentric pith. ROBARDS (1965) showed, in *Salix fragilis* L., a positive correlation between the degree of eccentric growth of the wood and the quantity of gelatinous fibres found. Tension wood is usually found therefore, on the upper side above the pith, where the growth rings are wider than elsewhere (JANE, 1970).

Uniseriate rays are believed to be typical of the wood of Salicaceae, although biseriate rays have been reported in *Populus alba* L. (HERMANN, 1922). GREGUSS (1959) states that about 1 $^0/_0$ of the rays are partially biseriate in Salicaceae. Present observations show some variation in the presence of biseriate and partially biseriate rays. Frequently large areas of the tangential sections were found to contain only uniseriate rays. Although so relatively little material was examined, even though tangential sections of other specimens were seen (Uw 16008 and Uw 16019), it would appear that the occasional presence of biseriate rays also typifies the wood of Salicaceae. However, considering the numerous publications concerning the stability of anatomical structures after reaching a certain age, and especially taking into consideration the argumentations of CARLQUIST (1961, 1962) concerning ray development and juvenilism, the author feels that he cannot ignore the possibility of a modification of this wood under the arctic conditions.

During the author's study of comparative literature, there has been an increasing awareness of the lack of information, especially regarding the environment, the size and the age of the specimens described. GREGUSS's (1959) reason for not noting the presence of simple perforations in *Empetrum nigrum*, for example, may be due to the fact that the wood was still immature (11 growth rings counted in his photograph).

It may have become obvious to the reader of the author's reluctance to discuss the many quantitative features. Many variations in measurements may be the result of different environmental conditions, but without the above mentioned information the significance of such features as pore diameters and number of pores per square mm, cannot be appreciated. In the investigation of *Vaccinium uliginosum* ssp. *microphyllum* for example, the pore sizes were greater in the outer growth rings than in the inner growth rings.

The comparative anatomy of woods under different environmental conditions has frequently been conducted on different species from the same genus (FORSAITH, 1920). When studies of somewhat variable qualitative characteristics are concerned, an accurate analysis should only be attempted when the wood from different environments is of the same species. This emphasis should be even greater when considering quantitative characteristics.

Although VERSTEEGH (1968) made a series of studies on wood obtained from species growing at different altitudes, the comparison unfortunately was not made using the same species. However, his conclusion that possibly species in mountain areas, possess one or more "less specialized" anatomical characteristics, may well be true. The statement of CHALK (1962), "From the taxonomic point of view the great importance of this (referring to the work of Bailey) has been that it is now clear that some of the more obvious differences between woods, such as the occurrence of simple and scalariform perforation plates, represent only different degrees of specialization and may have nothing to do with phylogenetic affinity", should also be treated with great caution, even though some of the findings of the present study may give that impression. Whichever view one takes and whatever word is used, such as "advanced", "specialized", "modified" or "adapted", the ice is still rather thin.

If greater "specialization" is to be related to more extreme environments as proposed by FORSAITH (1920), it may be worth considering that if woods show paedomorphosis, they are not really comparable, phylogenetically to truly adult woods (CARLQUIST, 1962). Similarly if characters considered to be more primitive are found, especially in the presence of what may be considered more advanced features, heed should be given that specimens have reached maturity.

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