ON THE ANATOMY OF ARAUCARIAN WOOD

by

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Contents.

CHAPTER I.

INTRODUCTION.

1. Aim of the paper.

The opinions regarding the origin of the Coniferae largely differ, while, moreover, the relations of the subgroups (families) in this class should be called entirely uncertain.

In order to examine into the relationsship between the groups of plants mutually, various methods may be made use of (comparative morphology, comparative anatomy, phylogeny, palaeontology etc.).

Up till now comparative morphology has been made most use of.

In the following treatise, I have tried to write on one of the groups of the Coniferae according to comparative anatomy. In order to apply comparative anatomy successfully, it is necessary to give precise anatomical descriptions of the organ, which one wants for this purpose and not to pay attention to a few characteristics only.

The secondary xylem has been chosen for material in this work, while at the same time the primary xylem has been described as much as possible. These parts have been chosen, because they are perhaps most characteristic of the plant. Moreover, they have the advantage that after the dying-off of the plant, they change little, while in fossils the structure remains very well intact.

The Araucariaceae family has been chosen, because the latter — generally being looked upon as the most primitive family —, is of great importance for the origin of the Coniferae in general, whereas in the literature short and incomplete descriptions, often only concerning one single species, were to be found.

2. Material.

In order to make the description as complete as possible, it was desirable to collect material of as many species as possible. The chief interest could only be the secondary wood, preferentially of the stem and of the root and at different ages. It was in itself very difficult to collect this material, since the Araucariaceae are mostly tropical trees and the only extra-tropical forms are met with on the southern hemisphere. But for one or two exceptions, it was impossible to get them from their natural habitats. Nevertheless, I have finally been successful in obtaining a number of species, both of the Araucaria and of the Dammara genus, for which I thank all those who have contributed to it. Especially to Prof. Dr. Docters van Leeuwen my thanks are due. In the first place for the great amount of material which he most kindly sent me from Buitenzorg and Tjibodas and secondly for the fact that during his expedition through New Guinea he even found an opportunity to collect Araucaria-material, which he forwarded to me later on. This was the more valuable to me, because it came from its natural habitat.

Eight species of the Araucaria genus were finally examined:

1. Araucaria araucana Koch (syn. imbricata Pavon), found in Chile and Argentinia.
   Material from Holland.
2. Araucaria Bidwillii Hook.
   (Queensland). Material chiefly from Buitenzorg.
3. Araucaria angustifolia Berteloni (syn. brasiliana Rich) (Brazil). Material from Brazil.
4. Araucaria Cunninghamii Sweet.
   (New South-Wales and Queensland) Material from Buitenzorg.
5. Araucaria excelsa R. Br.
   (the Norfolk-Isles). Material from Buitenzorg.

6. Araucaria Cookii R. Br.
   (New Caledonia) Material from Buitenzorg.
7. Araucaria Rulei F. Muell.
   (New-Caledonia) Material from Buitenzorg.
8. Araucaria species. [1])
   (New-Guinea) Material from New-Guinea.

Two species of the Dammara genus were examined; (Dammara Rumph 1741, syn. Agathis Salisbury 1807)

1. Dammara alba Lam. 1786 (syn. Agathis alba (Lam.) Foxworthy; Ag. loranthifolia Salisbury 1807; Agathis Dammara Lamb. 1826).
   Found in the East Indies and the Phillippine Islands. Material from Buitenzorg.
2. Dammara australis Lamb. (syn. Agathis australis Steud.)
   New-Zealand. Material from Buitenzorg.

For a more detailed indication about origin, see the separate descriptions.

3. Way of describing.

From the species mentioned above, a description was given of the secondary xylem, if possible of parts of different ages. For the sake of completeness the primary xylem was in most cases described afterwards. If root-wood was present it was likewise carefully examined as far as it concerned the secondary xylem. As a rule no primary xylem was to be found here.

The descriptions were made in the same manner as was done by Moll and Janssonius in their works. [2]) The following principles, which I cite verbally from their „Penportraits" [3]) have therefore been followed in the present

[1]) This material was collected during Dr. Docters van Leeuwen's expedition in New-Guinea 1926 and was not yet determined. At Buitenzorg it is known under no. 10576.

[2]) Moll and Janssonius, Mikrographie des Holzes.
„ „ „ Botanical Penportraits.

[3]) Botanical Penportraits p. 21—22.

paper as well." Sections according to the three directions of space were used for building up the perspective descriptions. In all descriptions the dimensions of several parts have been given as often as possible. They are always mentioned at the outset and expressed in micromillimeters (μ).

Since three dimensions are noticed, it was necessary to mention the direction of each. For this purpose, however, abbreviations were introduced, while the directions mentioned must be understood as recorded with respect to the whole organ of which the structure is described (stem or root) the following abbrevations were used;

L. in a longitudinal direction, i. e. in the direction of an axis uniting the organic base and apex.

R. in a radial direction, i. e. transverse or at a right angle to the longitudinal direction and at the same time extending from the centre to the periphery.

T. in a tangential direction i. e. transverse and at the same time at a right angle to the radial direction.

In a certain number of cases it is impossible to make use of the abbrevations mentioned above for instance"..... (in the present paper in the case of the pores of the pits, which are generally stretched in an oblique direction). „In such cases no abbrevations have been used, but instead of them the words length, width etc."

„The measures were taken either by choosing what seemed to be a mean value, or a minimum, or maximum value. They are also to be considered as rough statistical evaluations". „They are also only mentioned to give an idea of the shape of an element, which will be completed by adding some descriptive term such as, prism, cylinder etc."

In order to get a surveyable whole, a description of the wood of the Araucaria genus, as a whole, was given first and afterwards the separate descriptions of the various

species. The description of the genus, as a whole, was obtained by a mutual comparison of the species.

A description of the wood of Dammara genus as a whole was not given for want of material (see p. 561). Only the species of this genus present were described separately.

Finally a summarizing description was given of the wood of the Araucariaceae family, in which the various resemblances and differences were at the same time discussed.

Since the pits of the Araucariaceae play a leading part in the literature existing and in this treatise much attention has always been paid to the pits, it seems desirable to look closely at the structure of these bordered pits, before passing on to the descriptions proper.

A bordered pit is generally built in such a way that a closing membrane, mostly with a thickened part the so-called „torus", is found in the middle of the pits. On both sides of it is the border, an infundibular widening of the pit-canal. This border is covered on the side opposite the closing membrane, with a membrane, which has been formed by an excrescence of the primary cell-wall. On the side towards the interior of the cell this membrane is covered with the secondary thickening layers. Shape and origin of the membrane mentioned, have first been described by Sanio (1873/74) [1]) and by him it has been called „the membrane covering the border" [2]) or occasionally „the primary border membrane" [3]). The latter name will also be used by me in the following treatise.

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[1]) See further for the structure of the bordered pits: C. Sanio, Bot. Zeitung 1860 p. 193, and for the development of the bordered pits C. Sanio, Jahrb. f. Wissensch. Bot. Bd. 9, p. 73—89.

[2]) l.c. p. 80.

[3]) l.c. p. 81.

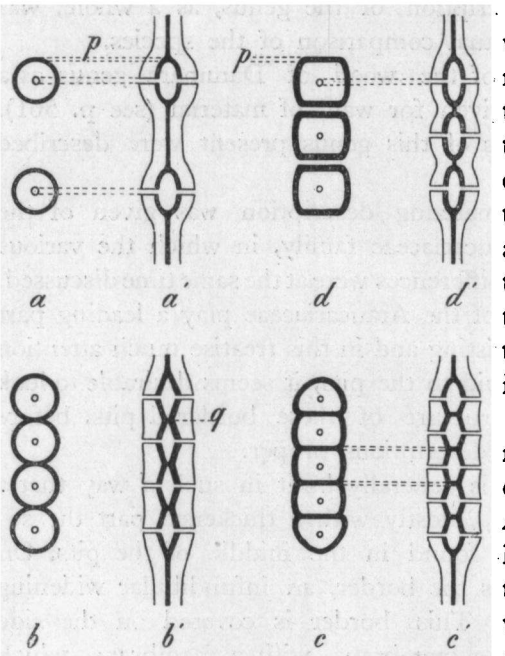

Fig. 1. Schematic figure showing bordered pits in front-view and in section. Closing-membranes left out. *a*, a^1, general type of bordered pit; *b*, b^1, araucarioid pitting, pits touching hardly; *c*, c^1, araucarioid pitting, pits touching and flattening each other; *d*, d^1, way of pitting in Pinus sylvestris, pits standing closely together.

If a colouring with ruthenium red [1]) is applied to certain preparations, in which bordered pits occur, the result will be a reddening of: *a.* the middle-lamella, the separation between two adjoining cells; *b.* the primary border membrane *c.* the closing membrane. As all these parts have arisen from the primary cell-wall, the colouring comes up entirely to what one expects.

The parts mentioned may be best observed in pits in longitudinal sections (fig. 1 a'; d'; cf. fig. 2).

If the bordered pits are looked in front view, it will be seen that the border is bounded by an annular band of measurable thickness, so that we can distinguish again between two demarcations, namely an inner and outer circle. This is caused owing to the circumstance that the middle-lamella has a measurable thickness, where it passes into

[1]) For the treatment see p. 497 of the present treatise.

the primary border membrane. In future I shall call this annular band, „the pectic annulus", because, just like the middle-lamella, it contains many pectin substances and therefore it colours red, when treated with ruthenium red. [1]) (fig. 1*a*, compare fig. 3).

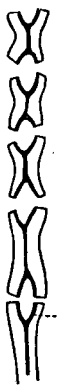

Fig. 2. Pinus sylvestris. Pits in section. × 420.

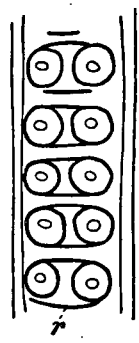

Fig. 3. Pinus sylvestris. Pits in front-view; r, rim of Sanio. × 420.

If we look at the bordered pits of the Araucariaceae, it will be seen that they largely come up to the structure described above. Here too, the border is covered with the primary bordered membrane. Both in front-view and in longitudinal section of the pit, we have the same appearance, if the pits stand separate. However, this is mostly not so on the radial walls. Here the pits stand so close together that they touch. It is this touching, which causes the characteristic appearance of the „Araucarioid pitting" and it happens as follows:

The pectic annuli of two pits touching one another coalesce on the points of touching, so that no normal middle-lamella is formed. If the pits remain circular in shape, the coalescing takes place over a very short distance only (fig. 1*b*, compare fig. 4).

The pits are mostly flattened at the same time and the coalescing takes place then over a short or great distance

[1] In this fig. 1 and all further figures the ring has been drawn as a wide black band; owing to reasons of a technical nature, it could not be represented by two outlines, even though this would have offered certain advantages.

(dependent upon the flattening) and in that case the pectic annuli have a straight common part (fig. 1 *c*. compare fig. 5). In consequence of this, the Araucarioid pitting in front-view has a characteristic appearance.

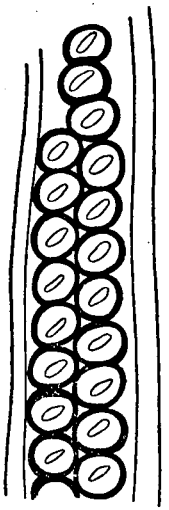

Fig. 4. Araucaria Bidwillii. Pits in front view. × 660.

Likewise the pits show a characteristic aspect in longitudinal section. For, whereas in the separate pits the primary border membrane passes, after the pectic annulus, into the middle-lamella, forming the boundary between two fibres, in the araucarioid pitting, no normal middle-lamella is formed. From the point of touching the pectic annulus diverges to two sides, namely: towards one side it passes into the primary border membrane of the pit lying above that point; towards the other side it passes into the primary border membrane of the pit lying under that point (fig. 1 *b'*, at *q*). The pieces formed through this, consisting of a lower, respectively an upper half of a primary border membrane, united by the common part from the pectic annuli, have a peculiar X-shape in optic section.

This may still be emphasized owing to extension of the common part of the pectic annuli, in a direction perpendicular to the closing membrane, so that a small plane is formed (fig. 1 *c'*).

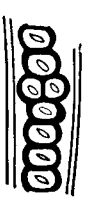

Fig. 5. Araucaria araucana. Pits in front view. × 420.

Besides the parts arisen from the primary cell-wall, the secondary thickening layers have a characteristic shape, owing to the small influence of the presense of these pits upon the shape of these layers.

The secondary layers practically run on in a straight line and do not swerve between two succeeding pits (fig. 1 *b'*; c'; compare fig. 6).

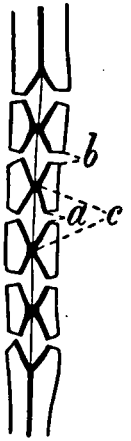

Fig. 6. Araucaria. Pits in section; a, primary border membrane.

If in connection with the above described „araucarioid pitting", we consider the „modern pitting", as it has been called by Potonié-Gothan, for instance in Pinus sylvestris, it strikes one in the first place that the pits are generally wider apart, as fig. 1 *a; a'*; represents. Some fibres in the stem-xylem and especially those in the root-wood, do have the pits very close together, however, even so much that here too, the border is flattened above and below. In this case touching is out of the question. Hence the pectic annulus of each pit below and above does have a straight part (fig. 1 *d*; compare fig. 7 and 8), but round about, it remains free from the nearest pit.

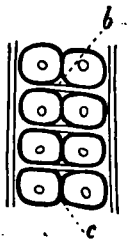

Fig. 8. Pinus sylvestris Pits in front view, non touching above and below, sometimes touching on the sides, if two pits are on one primary pit-area, for instance at c; b, rim of Sanio. × 260.

In longitudinal section there is no typical shape of the araucarioid pitting either, because the pectic annuli are constantly free from each other and remain separate by a little part of the middle-lamella (fig. 1 *d'*; compare fig. 2).

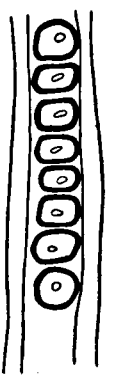

Fig. 7. Pinus sylvestris. Pits in front view, non touching but flattened above and below. × 260.

The secondary thickening layers are influenced by the presence of the pits and form and undulating line.

In very rare cases only, an actual touching and coalescing

of the pectic annuli issuing from this, may occur, namely if two or more pits have been formed on one „Primordialtüpfel".

As this number is never more than four in the case of Pinus, the touching will only be possible over short distances, i. e. between two pits at most (fig. 8 at *c*).

CHAPTER II.

DESCRIPTIONS OF THE WOOD OF THE ARAUCARIA GENUS.

1. Summarizing description of the wood of the Araucaria genus.

Secondary xylem.

Topography: Growth rings sometimes very clear, sometimes nearly or entirely wanting. Very well developed in Araucaria angustifolia and Araucaria araucana, which had, however, grown under conditions, different from those of the others i. e. in a climate highly conducive to periodicity.

Wood chiefly consisting of fibre-tracheids only, arranged in radial rows. Wood parenchyma rare or entirely wanting, if present scattered among the fibre-tracheids.

Medullary rays numerous and generally of a simple structure [1]) usually one cell broad, locally two at most and in the latter case these cells nearly as broad as the ray-cell lying over or under it (fig. 38), for long distances seldom two cells broad and somewhat irregular (fig. 46 p. 552), few cells deep (1—10), sometimes more, down to 40, more or less dependent upon the age.

Intercellular spaces between the fibre-tracheids fairly

[1]) Deviations from this normal type only on definite spots, namely where a leaf-trace penetrates into the wood and in the neighbourhood of the primary xylem (see p. 499).

general, especially in the neighbourhood of medullary rays.

Elements: I Fibre-tracheids: R. 10—65 μ, T. 15—50 μ, L. 1200—1300 μ, forming tetragonal-hexagonal prisms, less frequently elliptical or circular cylinders. Walls thick 4—15 μ [1]), sometimes the radial walls a little thicker than the tangential ones. Tangential walls perceptibly thicker at a medullary ray than elsewhere. Walls lignified, middle-lamella well developed (1—2 μ measured double), at the angles forming gussets, often not solid.

Pits: Between the *fibre-tracheids mutually* bordered pits, especially on the radial walls, less frequently on the tangential ones.

On the radial walls pits in long contiguous rows, generally in one, sometimes in two series, in the older stem and especially in the root now and then in three rows, mostly touching each other and flattening in the places of contact, namely above and below, (fig. 5 p. 492). If in two or more rows, the pits generally alternate, and owing to flattening, somewhat hexagonal in shape (fig. 9).

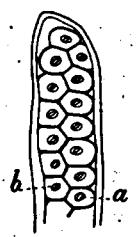

Fig. 9. Araucaria araucana. Pits, vertically alternate; *b*, inner aperture, less strongly slit-like than the outer aperture (*a*). × 260.

Deviations from this normal type numerous, for instances the pits not alternate, but opposed and consequently tetragonal in shape (Araucaria species a.o. fig. 49, p. 553), or touching little, and therefore not being flattened, and the round shape practically preserved Araucaria Bidwillii (fig. 4, p. 492). (For this see also the separate detailed descriptions with the figures belonging to them). Dimensions: Border L. 8—10 μ, R. 12—15 μ, in the mature wood often somewhat larger L. 12—15 μ, R. 14—18 μ. Pore more or less slit-

[1]) The dimensions of the walls all denote the wall of a single element, unless expressly stated otherwise.

like and in that case sinistrorse, length 5—8 μ, seldom up to 15 μ, width 1—4 μ, rarely entirely circular 2—4 μ.

On the tangential walls, pits far less numerous than on the radial ones, nevertheless sometimes in fairly large numbers. Generally not in contiguous rows, but separate and then circular in shape, smaller than those on the radial walls. L. 5—10 μ, T. 5—8 μ; pore more or less slit-like, length 3—4 μ, width about 2 μ. Rarely in contiguous rows and if so, entirely of the same shape and size as those on the radial walls.

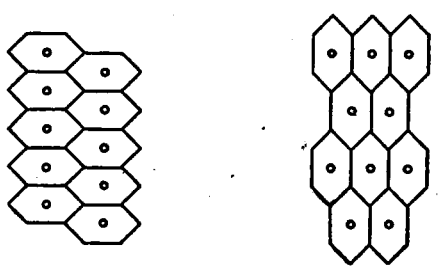

Fig. 10. Schematic figure showing *a*, pits vertically alternate; *b*, horizontally alternate.

In accordance with Gerry (1913) no rims of Sanio observed anywhere.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, always in groups on the rhomboid bordering plane, as a rule in two or more vertical rows, sometimes slightly irregular seldom one row, for instance in distinctly visible autumn wood. The rows sometimes vertically alternate, but more frequently horizontally alternate [1]), or even opposed. In the two former cases the touching pits more or less hexagonal in shape, in the latter case tetragonal; frequently pits hardly touching,

[1]) In both cases the pits are alternate and as far as is known to me no distinction is made in the literature. Nevertheless, there is a clear difference and for this reason, both terms were introduced. In the case of a vertical alternate position, the pits stand in alternate vertical rows. This position is particularly adapted to long distances, and is therefore especially met with in the pits between the fibre-tracheids mutually (fig. 10*a*).

In the case of a horizontal alternate position, the pits stand in

and not flattenning each other, consequently more or less circular in shape. The pits mostly smaller than those of the fibres mutually L = R 6—12 μ, pore generally more slit-like, length 5—10 μ, width 1—2 μ, seldom nearly circular. (Araucaria Cookii a.o.).

Between *fibre-tracheids* and *woodparenchyma* unilateral bordered pits, mostly in single rows, touching harly or not at all, seldom side by side. Border L. = R. 9—10 μ, pore elliptical, length 6—10 μ, width 2—5 μ.

Between the *first fibre-tracheids* of *the secondary xylem* and *medullary ray cells* unilateral bordered pits entirely of the same structure as in the case of the primary xylem (see p. 504).

Contents of the fibres generally small. In some species, especially in the neighbourhood of the medullary rays, some resin, in others some starch, or both at the same time. Here and there trabeculae.

Intercellular spaces, rather frequent in general, especially in the neighbourhood of the medullary rays, partly longitudinal, arisen owing to the hollow quality of the gussets (fig. 13, p. 505), partly horizontal, owing to thed ivergence of the tangential walls (fig. 14 p. 506).

II. Woodparenchyma fibres very rare. If present scattered among the fibre-tracheids. running lengthwise and divided by septa. [1]) Fibres sometimes single, often

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alternate horizontal rows. This is less adapted to long distances. It is therefore only locally met with in the fibre-tracheids mutually, but very frequently on the rhomboid bordering plane between fibre-tracheid and medullary ray cells. (fig. 10*b*).

[1]) This parenchyma may be best observed in preparations treated with ruthenium-red owing to which the walls, like those of the medullary ray cells, become red. The preparations were treated in the same way as was indicated by Strasburger-Koernicke (1913) p. 281, in so far that it was advisable to leave the sections for about sixteen hours in ammonia and likewise a proper time in a ruthenium-red solution, generally for about 4 to 5 hours. After L. Mangin

two, side by side. R. about 30 μ, T. 10—14 μ, total length difficult to state, septations L. 55—245 μ, Walls mostly thin, about 1μ, without pits, neither, on the side of an adjoining fibre, nor between two septations mutually. Sometimes walls thick, about 6—7 μ, with numerous simple pits, both on the side of the fibre-tracheids and between the cells mutually (fig. 17, p. 508).

III. Medullary ray cells.

1. Procumbent cells. R. generally about 40—140 μ (dependent on the age, in very old stems much larger, for instance in Araucaria angustifolia, Bidwillii and species, measured up to 250—400), T. 10—30 μ often about 15—20 μ, L. 15—40 μ, forming elliptical to circular cylinders to almost tetragonal prisms with radially directed axis. Walls mostly thin, generally 1—2 μ, somewhat lignified (slight wood-reaction in phloroglucin and hydrochloric acid), a small cellulose content (becoming hardly blue in potassium iodide odine and sulphuric acid 75 %), especially containing pectin-substances (colouring deeply red in ruthenium red). No pits, neither on the side of the fibre-tracheids, nor between the cells mutually (see also the fibre-tracheids p. 496).

In one species thick-walled medullary ray cells, scattered among the thin-walled ones, R. 140—240 μ, T. 18—22 μ, L. 25—35 μ. Walls of those cells frequently irregularly thickened, about 5—12 μ, rather lignified (less strongly than those of the tracheidal medullary ray cells), having

p. 653 a 5 ‰ watery solution was used for the colouring. The solution was constantly refreshed in small quanties, as the watery solution is little durable l.c. p. 654.

This woodparenchyma is not very clear in ordinary preparations, partly so, because it rarely occurs. In connection with this, it goes without saying that these elements are nowhere found indicated in the literature, at least with regard to the stem. Even for Dammara, where it occurs much oftener, the various indications do not agree (see for this Dammara p. 581).

simple pits, both on the side of the fibre-tracheid and on the side of the adjoining ray cells. The former in diameter 2—5 μ, the latter larger 9—12 μ. (fig. 27 and 29, p. 528). Contents of both usually rich in protoplasm with distinct nuclei, often a good deal of starch and in some species great quantities of resin.

Intercellular spaces between medullary ray cells and fibre-tracheids generally numerous, especially in radial direction. Owing to this sometimes distinct connecting frames on the radial walls of the ray cells (fig. 35, p. 534). In various species also intercellular spaces between the ray cells mutually. Sometimes the ray cells more or less prismatic and consequently little development of the intercellular spaces (fig. 38, p. 541), seldom solid gussets between ray cells and fibre-tracheids (fig. 28, 30, p. 530).

2. Upright cells, always in the neighbourhood of and within the primary xylem, higher than the procumbent cells and irregular in shape, giving rise to vertical connections between the medullary rays lying above one another. Dimensions of these cells very different, R. 15—55 μ, T. not measured, L. 40—150 μ (fig. 22, p. 515, and 42, p. 544). Walls and contents like those of the procumbent cells. Here no discernible pits either (see also the tracheid of the primary xylem p. 504).

3. Tracheidal ray cells scattered among the thin-walled procumbent cells in various medullary rays, not generally, limited to the rays in neighbourhood of a leaf-trace, running through the wood, usually not extending farther than 1,5 mm from the leaf-trace, but in some cases to 8 mm or perhaps still more from it. Sometimes a shifting of the fibre-tracheids is connected with it. In that case tracheidal ray cells numerous in the places of shifting. In cases without shifting tracheidal ray cells only in the immediate neighbourhood of the leaf-traces or even wanting there. (fig. 11 and 12). In other places these elements

probably absent. [1]) Dimensions: R. 20—250 μ, sometimes up to 300 μ, T. 12—35 μ, mostly about 25 μ, L. 15—30 μ, rarely larger, up to 60 μ; cells generally forming nearly circular cylinders, with radially directed axis, sometimes

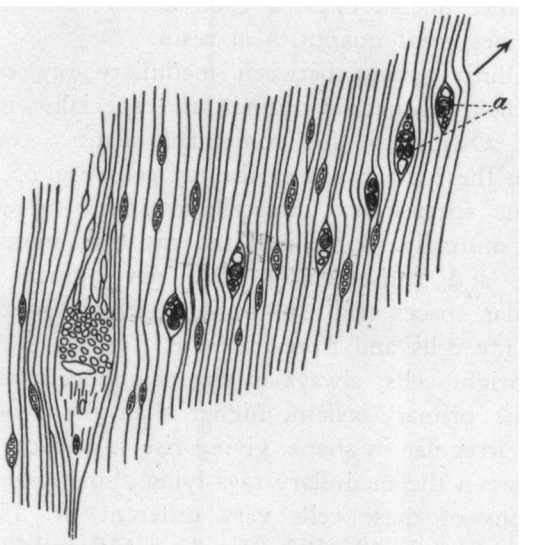

Fig. 11. Araucaria species. Tangential section of secondary xylem, showing a leaf-trace and a shifting of fibre-tracheids. *a*, tracheidal ray cells. Pits of the radial walls left out. × 60.

fairly irregular in shape. Walls 6—10 μ in thickness, strongly lignified, becoming red in pholoroglucin and hydrochloric acid, remaining intact in case of maceration, often thickened very irregularly and consequently, the interior wall provided

[1]) Only once a tracheidal ray-cell was observed in a medullary ray, in which case there was no leaf-trace in the immediate neighbourhood; as it was, however, the first one that was found, the possibility of the presence of a leaf-trace was not considered. The absence of the latter organ in the preparation may be well accounted for, since it concerned a radial section.

with a great many small dentations, sometimes of two opposite walls, touching each other and filling up the whole cell more or less. On the side of the fibre-tracheid bilateral bordered pits. Number of pits far less numerous

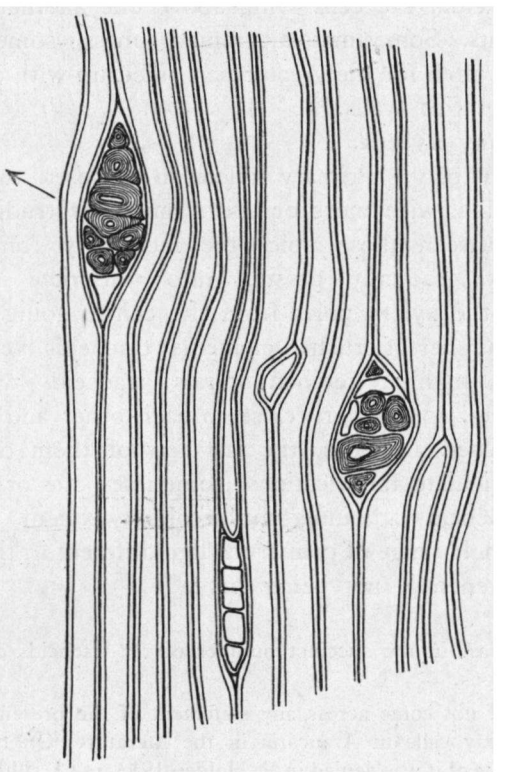

Fig. 12. Showing a part of fig. 11 under higher magnification. × 165.

than in the thin-walled ray cells, only one or two in a whole cell (fig. 54, p. 558), border circular about 12 μ, pore small on the side of the medullary ray about 1 μ, larger on the side of the fibre-tracheid (fig. 31). On the side of the adjoining medullary ray cells unilateral bordered pits

(fig. 54, 55), border circular 7—10 μ, pore small about 1 μ. On the tangential walls no pits observed. [1])

Intercellular spaces between tracheidal ray cells and fibre-tracheids mostly little developed, wanting between two tracheidal ray cells lying above one another.

Contents. Sometimes a granular mass, sometimes no contents, often for the greater part filled up with dentations of the lignified walls. [2])

Primary xylem.

Topography. Primary xylem in a closed tube round the medulla, with more or less strongly protruding xylem poles, between those poles the medullary commissures, outwardly gradually passing into uniseriate medullary rays. At the xylem poles from the centre going outward: a small number of crushed elements; tracheids, very narrow and with highly stretched spirals; tracheids with spiral sculpturing, spirals very close to each other and evidently not stretched anymore, the last few of them often with a few reticulate ramifications; sometimes one or two reticulate tracheids adjoining the secondary xylem.

The whole range of primary xylem different in the various species, generally not being large. [3])

[1]) At least in the succinct number of ray-tracheids observed in radial sections.

[2]) I did not come across any statement of the presence of these tracheidal ray cells in Araucaria in the literature. On the contrary the existence of it was denied in R. Holden 1913, p. 61. The absence of it was even alleged as a proof that the Araucariaceae should have sprung from the Abietineae before the Cretaceous.

[3]) Generally about $^1/_{30}$ of the branch, only much smaller in Araucaria Bidwillii, A. Cunninghamii and A. excelsa ($^1/_{60}$—$^1/_{80}$ there), in most species medulla larger ½—¼ of the branch, only much smaller in Araucaria Bidwillii and A. excelsa resp. $^1/_{14}$ and $^1/_{10}$. In order to trace these proportion minutely, it would be desirable to compare homogeneous material, for instance the two year-old top of the main stem. This was not possible for me. In most cases,

Elements. I. Spiraltracheids protoxylem R-T 6—8 μ, sometimes up to 10 μ, L. difficult to measure [1]) probably about 700—800 μ, cylinder shaped. Sculpturing on wall one to two spirals, less frequently three, irregularly stretched, mostly continued over the whole length, thick 1—2 μ in diameter, rarely thicker (Araucaria araucana 2—3 μ), angularly circular in section, wall between the spirals thin. Interstices irregular.

II. Tracheids metaxylem. Spiraltracheids, with thin spirals, very close to each other, outwardly gradual occurrence of reticulate ramifications, passing into reticulate tracheids; R-T 10—12 μ, sometimes up to 20 μ from within outward, L. difficult to state for the same reason as above, if measured 700—1200 μ, [2]) cylinder-shaped. Spirals usually 3—6 in number, very close to each other, mostly continued over the whole length, 1—2 μ in thickness, sometimes oblong in section, mostly with narrowed foot. Interstices small, mostly about 1 μ, seldom up to 2 μ. Wall in these interstices thin.

Pits. Between the last few tracheids mutually bilateral bordered pits, mostly confined to those with reticulate sculpturing of the walls, also sometimes in the last few spiral tracheids. Those pits mostly in single rows, seldom in two (Araucaria species), in the latter case alternate or opposed, in neither of the two cases touching each other. Pits smaller than in the secondary wood, border circular, 6—8 μ in diameter, often about 6 μ, pore likewise circular 1—2 μ.

I could only dispose of side-branches. The proportion found by me are therefore drawn up according to measurings on unselected two-year-old branches.

[1]) In macerating they generally break.

[2]) In a few cases I have succeeded in removing the entire tracheids by carefully macerating on a cover.

Between tracheids and medullary ray cells, unilateral bordered pits, very numerous in connection with the increased height of the medullary rays. The pits in 1—2 long rows, opposed, or somewhat alternate with little narrowed pit-canal and therefore the pore nearly as big as the border. Both horizontally elliptical, their respective sizes largely different.

III. Medullary ray cells. Exclusively upright cells of the same structure as in the beginning of the secondary xylem and already described there (p. 499).

2. Araucaria araucana Koch.

(syn. Araucaria imbricata Pavon).

A. Stem.

Material. 1. The entire tree, about twenty-seven years old with side-branches and roots, grown in the garden of Villa „Volonté" near Groningen (Holland). The tree frozen to death in the severe winter of 1922—'23.

The material, already dead was preserved in alcohol.

2. A side-branch about nine years old of an old tree, 6 m. high and about thirty years old, grown in the Arboretum at Wageningen (Holland). The material, received in a fresh condition was preserved in alcohol.

Description secondary xylem made after preparations of adult wood from the stem about 27 years old, to which that of the 5- to 6-year old stem was compared.

Topography. Growth rings clear about 3—5 mm, the inner ones wider than the outermost ones 1—3 mm, under a wreath of side-branches wider than anywhere else, 7—12 mm, in connection with the locally thickened condition of the stem; boundaries formed by the widening of the elements; difference in thickness of wall between early and late wood slight. Irregularities of radial arrangement abundant.

Fibre-tracheids constituting the bulk of the wood.

Woodparenchyma fibres scarce, scattered among the fibre-tracheids.

Medullary rays very numerous (30—80, usually 60—70 per sq. mm) separated by 2—7 rows of tracheids, mostly uniseriate, sometimes locally biseriate, the two cells not much broader than one cell lying above them, 1—16 cells in depth, sometimes down to 20. In generally no ray-tracheids, except in the neighbourhood of a leaftrace penetrating into the wood (see p. 499), no irregular bounding up or down, save directly near and within the primary xylem, where irregularly-shaped upright cells give rise to mutual commissures between the medullary rays.

Elements. I. Fibre-tracheids: R. 15—35 μ, the last few rows of a growth ring smaller about 10 μ, T. 20—30 μ, rarely up to 35 μ, L. 1200—2200 μ, below a ramification wider, R. up to 40 μ, T. 35—40 μ, forming tetragonal or hexagonal prisms, the lumen more or less cylinder-shaped (fig. 13). The outer ends of the tracheids usually pointed, if touching upon another tracheid or upon a medullary ray flattened and pitted. In touching a medullary ray, fibre-tracheids often diverted from their longitudinal course and accompanying the medullary rays for some distance. Sometimes the fibre-tracheids apparently septated, owing to secretion of resin-plates.[1])

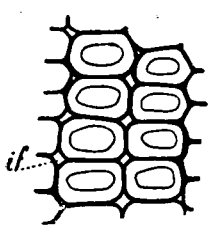

Fig. 13. Araucaria araucana. Transverse section of wood; if intercellular spaces at the corners. × 315.

Walls, early wood R. 5—5.5 μ, T. 4.5—5.5 μ, late wood R. 6—6.5 μ, T. 4.5—5.5 μ (in most cases tangential walls thinner than the radial ones), lignified, becoming red in phloroglucin and hydrochloric acid. Middle-lamella colouring more intensely, therefore very distinct, 1—2 μ (double), forming gussets at the corners, not always entirely solid

[1]) S. Record p. 61.

(fig. 13) Secondary thickening layers strongly developed, colouring little or not at all in sulphuric acid 75 % and potassium iodide iodine. Tangential walls somewhat thicker at the medullary rays and often diverging little (fig. 14). Radial walls, in connection with the inflated medullary rays, strongly bent inward there, especially clear in maceration preparations. Especially in the late wood, the walls with a distinct sinistrorse spiral striation (fig. 15).

Fig. 14. Araucaria araucana. Radial section; if, intercellular spaces between the tangential walls, due to divergence. × 195.

Pits. Between the *fibre-tracheids mutually* bordered pits, especially on the radial walls, or on those nearly radial, less frequently on the tangential walls.

On the radial walls pits in most cases in one or two rows, touching and therefore somewhat flattened above and below, for the rest border more or less circular in outline. If in two rows, the pits mostly alternate. The structure of the pits entirely as described at the beginning of this thesis (p. 489). The pore slit-like and sinistrorse. Difference in pits between early- and late wood slight, occurring in both in the same way, chiefly at the outer ends of the fibre-tracheids. Dimensions border L. 8—12 μ, R. 12—16 μ, pore length 6—8 μ, width 2—4 μ.

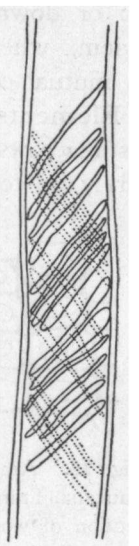

Fig. 15. Araucaria araucana. Fibre-tracheid with spiral-striation. × 358.

No rims of Sanio.

On the tangential walls the pits separate or in groups together, but not touching, not in a straight line either and smaller than those on the radial walls. Border circular, L. T. 5—6 μ, pore slit-like sinistrorse, length

3—4 μ, width about 1 μ. Rarely pits in a contiguous row, in this case similar to those of the radial walls.

Between *fibre-tracheids* and *medullary raycells* unilateral bordered pits, always in groups on the rhomboid bordering plane. Sometimes in one, but mostly in two rows, if two rows, pits generally opposed (fig. 16*a*, *o*), or horizontally alternate (fig. 16*a*, *ha*), but also, especially in the adult wood, vertically alternate (fig. 16*b*). Border feebly developed, circular in shape, sometimes tetra-or hexagonal flattened, R-L 10—12 μ. Pore slit-like, more so than in the fibre-tracheids mutually, length 6—9 μ, width 1—2 μ. Number of pits on a bordering plane variable, largely dependent on the size of that plane.

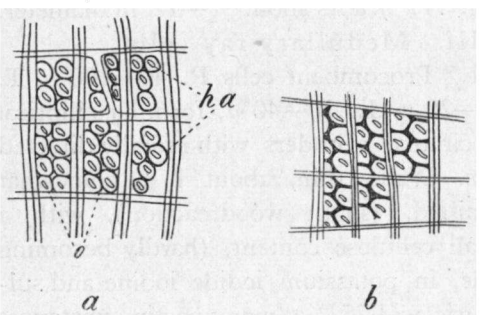

Fig. 16. Aracaria araucana. Pits on the rhomboid bordering planes between fibre-tracheids and ray cells. *a*. *o*, pits opposed; *ha*, pits horizontally alternate. × 260. *b*. pits vertically alternate. × 260.

Between the *first few fibres of the secondary xylem* and *the medullary ray cells*, unilateral bordered pits, entirely of the same structure as those in the primary xylem (see p. 511).

Between *fibre-tracheids* and *woodparenchyna fibres*, unilateral bordered pits, in single rows, touching hardly or not at all. Border circular R-L 9—12 μ, pore elliptical, length 6—10 μ, width 2—5 μ.

Contents of the fibre-tracheids nihil.

Intercellular spaces between the fibre-tracheids especially in the neighbourhood of the medullary rays, arising partly owing to the unsolid gussets (fig. 13), partly to the divergence of the tangential walls (fig. 14).

II. Woodparenchyma fibres. Mostly scarce, more numerous in the neighbourhood of leaf-traces, if present R. about 30 μ, T. 10—14 μ. Total length difficult to measure, septations L. 180—200 μ, thin-walled and unpitted, sometimes thick-walled 6—7 μ and in that case with numerous simple pits, both on the side of the fibre-tracheids and between the cells mutually. (fig. 17) [1]). Pits about ½—1 μ in diameter.

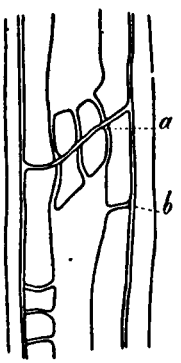

Fig. 17. Araucaria araucana. Thick-walled woodparenchyma fibre with simple pits; *a*. pits in co-operation; *b*. non-co-operation. × 500.

III. Medullary ray cells.

1. Procumbent cells R. 40—100 μ, T. 15—20 μ, L. 20—40 μ, forming elliptical to circular cylinders with radially directed axis. Walls thin, about 1 μ, somewhat lignified, (slight woodreaction), with a small cellulose content, (hardly becoming blue, in potassium iodide iodine and sulphuric acid 75 %), many pectin substances (colouring deeply red in ruthenium red). No pits, neither on the side of the fibre-tracheids, nor between the cells mutually (see also the fibre-tracheid p. 507).

Hardly any or no intercellular spaces at all between ray cells and fibre-tracheids. None at all between the medullary ray cells mutually. Contents: small, sometimes a brownish mass, sometimes nihil. [2]) Seldom a single grain of starch, likewise very little resin.

[1]) Whereas the pits of two septations mutually correspond, it was to be expected that the simple pits of the thick-walled woodparenchyma would communicate with the unilateral bordered pits in the adjacent fibre-tracheids, but there is no co-operation between them (fig. 17).

[2]) This was probably owing to the fact that the tree had been dead for more than three years. In a living branch about nine years old, from the Arboretum at Wageningen, I found, as I did in the other species, a rich protoplasmatic contents with distinct nuclei.

2. Upright cells. Only in the neighbourhood of and within the primary xylem, not strongly developed, rather irregular in shape, R. 30—50 μ, T. not measured, L. 45—100 μ Walls and contents like those of the procumbent cells. Here no pits either (see for the rest the tracheids of the primary xylem p. 511).

3. Tracheidal ray cells, fairly profusely in the neighbourhood of the leaf-traces (see p. 499), especially downwards and upwards and to a considerable distance (about 1.5 mm), rarely near the sides. R. not measured, T. 17—20 μ, L. about 17 μ, forming circular cylinders with radially directed axis. Wall 4—5 μ, lignified, (becoming yellow in hydrochloride of aniline), sometimes irregularly thickened and consequently the inner wall provided with many small dentations, sometimes occupying the entire cell, with a small number of bilateral bordered pits on the side of the fibre-tracheids. Border circular, about 7 μ in diameter, with a strongly narrowed pit-canal on the side of the medullary ray cell. Pore 1—2 μ in diameter.

Intercellular spaces between the tracheidal ray cells and fibre-tracheids little developed or entirely absent.

Contents: sometimes a granular mass, sometimes nihil.

The wood of thin branches, for instance about two-years old, practically agrees in structure with that of the older stem. As minor points of difference might be mentioned the following: the first annual bands indistinct and the medullary rays still more homogeneous, all uniseriate and 1—3 cells deep, rarely 4, very numerous 80—140 per sq. mm. The various elements too, agreeing in structure with those of the older stem. Fibre-tracheids R. 15—20 μ, in the last few rows of an annual band, sometimes 10 μ or less T. 15—20 μ, L. 1000—2200 μ. Also the pits between the fibre-tracheids mutually agree with those of the adult wood, generally standing in one row here. Between fibre-

tracheids and medullary ray cells, unilateral bordered pits, agreeing with those already described in the adult wood.

The medullary ray-cells thin-walled and the walls somewhat less lignified than those of the older stem. In most cases becoming blue in potassium iodide iodine and sulphuric acid 75 %. Pectin substances too very profuse (colouring deeply red in ruthenium red.)

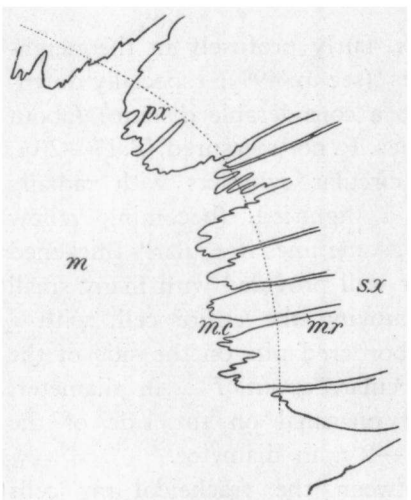

Fig. 18. Araucaria araucana. Transverse section of stem, showing the pith, surrounded by the primary xylem (*p.x*): Dotted line, boundary between primary- and secondary xylem; *m*, pith; *m.c.*, medullary commissures; *m.r.*, medullary ray; *p.x.*, primary xylem; *s.x.*, secondary xylem. × 30.

Primary xylem observed on a branch, about two years old being the top of a seven year old side-branch.

Topography. Primary xylem in a closed tube round the medulla, with numerous protruding xylem-poles (fig. 18). Between the xylem-poles the medullary commissures, from within outward passing into uniseriate medullary rays. From the centre going outward: at the tops a slight number of flattened elements; next very narrow tracheids provided with strongly irregulary stretched spirals; then tracheids with spiral sculpturing on wall, close to each other, sometimes with a few reticulate ramifications; one or two reticulate tracheids, adjoining the secondary xylem.

The whole range of primary xylem 200—250 μ, medulla very extensive about 3 mm; diameter of the entire branch about 7 mm.

Elements. I. Spiraltracheids protoxylem. R-T 6—8 μ, L. difficult to measure, cylinder-shaped. Sculpturing on wall one to two spirals, stretched irregularly. Spirals 2—3 μ thick, interspaces irregular, 4—5 μ. Wall between the spirals thin.

II. Tracheids metaxylem. R-T 12—20 μ, L. 1000—1200 μ, cylinder-shaped, sculpturing on wall, chiefly spirals, the outermost with indistinct reticulate sculpturing. Number of spirals often three, sometimes 4—6, and these spirals running from one end to the other without interruptions. Spirals close together. In section sometimes circular, but mostly with narrowed foot. Spirals and interspaces the same dimensions 1—2 μ.

Pits. In the reticulate tracheids, just as in the last few spiraltracheids, between the tracheids mutually bordered pits in simple non-touching rows. Border 6—8 μ, pore about 2 μ, both circular in shape.

Between the tracheids and medullary ray cells unilateral bordered pits, very numerous in connection with the extension of the medullary rays, mostly in one row, but sometimes in two or more. The border horizontally elliptical, the pit-canal little narrowed, owing to this a large pore, likewise horizontally elliptical.

III. Medullary ray cells. Upright cells only, entirely of the same structure as in the beginning of the secondary xylem and already described there (p. 509).

B. Root.

Material. A disk of a root, about ten years old from the same specimen, as the wood of the stem (see p. 504).

Secondary xylem. The root-wood largely agrees with the stem-wood, so that a short description will suffice.

Topography. Growth rings distinct, 1—2 mm broad, the outermost a little broader, boundaries as in the stem.

Fibre-tracheids the bulk of the wood. Wood-parenchyma

rare, scattered among the fibre-tracheids, more frequently occuring than in the stem. Medullary rays of the same shape, less frequent locally two cells broad.

Elements. Fibre-tracheids R. early wood 45—60 μ, late wood 20—35 μ, T. 20—30 μ, L. generally 1400—2400 μ, sometimes very short ones 600—800 μ, on an average longer than in the stem. Especially early wood very irregular, both in shape and in arrangement, therefore, the structure entirely unlike the regular structure of other Coniferae. The late wood more regular, the fibre-tracheids mostly forming tetragonal prisms, both if radially opposed (fig. 19*a*) and if radially alternate (fig. 19*b*) [1]) The radial arrangement too, more regular than in the early wood. Walls R. early wood 4—5 μ, late wood 5—5½ μ, T. early wood 4—5 μ, late wood 4—5 μ. Here too the tangential walls slightly thinner than the radial ones. For the rest walls and intercellular spaces like those in the stem.

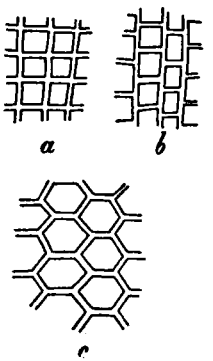

Fig. 19. Schematic figure to show the way of alternating of the fibre-tracheids *a*, radially opposed; *b*, radially alternate, fibre-tracheids tetragonal; *c*, radially alternate, fibre-tracheids hexagonal.

Pits. Between the *fibre-tracheids mutually* bordered pits of the same structure as those of the stem (see p.506) mostly standing in one row, sometimes in two, seldom three, often alternate but not unexceptionally opposed or sub-opposed, consequently all kinds of transitions (fig. 20). In most cases open spaces between the pits. Dimensions border R-L 10—12 μ, pore slit-like, length 6—8 μ, width 2—4 μ.

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[1]) In the latter case they get in Pinus a hexagonal prismatic shape (fig. 19c).

No rims of Sanio.

No pits on the tangential walls, occasionally on walls nearly tangential, consequently in tangential sections cut somewhat obliquely, and then pits of the radial type.

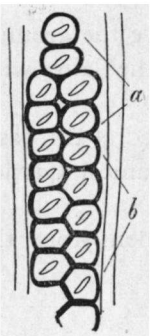

Fig.20. Araucaria araucana. Root; radial wall of a fibre-tracheid with pits touching and flattening each other; *a*, opposed and horizontally alternate; *b*, vertically alternate. × 420.

Between *fibre-tracheids* and *medullary ray cells*, unilateral bordered pits, position like that of the stem (see p. 507), sometimes more separate, dimensions the same.

Contents of the fibres small, no resin or starch. Here and there long rows of trabeculae. (fig. 21).

II. Woodparenchyma fibres. Scattered among the fibre-tracheids small in number, shape and structure similar to that of the stem. Contents generally a brownish mass.

III. Medullary ray-cells.

1. Procumbent cells R. 100—200 μ, T. 15—32 μ, L. 20—40 μ. Walls thin, 1—2 μ, firmer than in the stem. [1])

2. Upright cells absent, no tracheidal ray cells either.

Fig. 21. Araucaria araucana. Root, fibre-tracheids with trabecula. × 260.

Just like the medulla, the primary xylem is so little developed that it is hardly to be observed or not at all. For this reason it is not described.

[1]) Remain intact in sections, which is of course promoted by the thinner walls of the fibre-tracheids.

3. Araucaria Bidwillii Hook.

A. Stem.

Material. 1. A disk of a stem, 8 m. above the ground, and a second one 16 m. above the ground, the latter with branch-occulation.

Both disks of an old tree, which had decayed at the base. All this material from the Governmental Botanical Garden of Buitenzorg (Java).

2. A two year old branch of a specimen from the Botanical Garden at Groningen.

All the material was preserved in alcohol.

Description secondary xylem, made after preparations of adult wood from the disk of a stem 8 m. above the ground, about 50 c.m. in diameter.

Topography: Growth rings not clear; sometimes macroscopically something of the kind to be observed, microscopically very indistinct; formed by few thin-walled layers, alternated by several thick-walled ones, passing into each other without clearly marked boundaries.

Fibre-tracheids the bulk of the wood, irregularities in the radial arrangement fairly frequent, no woodparenchyma. Medullary rays far less numerous than those of Araucaria araucana, yet fairly well represented 10—60 per sq. mm, usually 30—40, mutually separated by 2—5 rows of fibre-tracheids, 2—17 cells in depth, generally uniseriate, seldom locally biseriate, the two cells having about the same breadth as one cell lying over it (see f.i. fig. 38). The upper and the lower boundaries of the medullary rays straight, except within and near the primary xylem due to irregularly-shaped upright cells, forming commissures between the medullary rays mutually (fig. 22). Tracheidal ray cells generally wanting.

Elements. I. Fibre-tracheids R. 25—55 μ, generally 35—50 μ, T. 35—45 μ, L. 3200—5500 μ, mostly

forming tetra- to hexagonal prisms, sometimes more or less circular cylinders. The outer ends usually pointed, except when touching upon another fibre-tracheid or upon a medullary ray, in that case flattened and pitted. Sometimes fibre-tracheids apparently septate owing to resin-plates. Spiral striation not observed. Walls R-T 2—5 μ. T. walls thicker at a medullary ray, up to about 6 μ. Walls lignified, becoming red in phloroglucin and hydrochoric acid. The middle-lamella colouring more intensely and therefore very conspicuous (1—2 μ double); at the corners the gussets, generally solid. Secondary thickening layers little developed (remaining unstained in potassium iodide iodine and sulphuric acid 75 %). At a medullary ray the radial walls bent inward a little (narrow medullary rays), owing to which the medullary ray entirely enclosed.

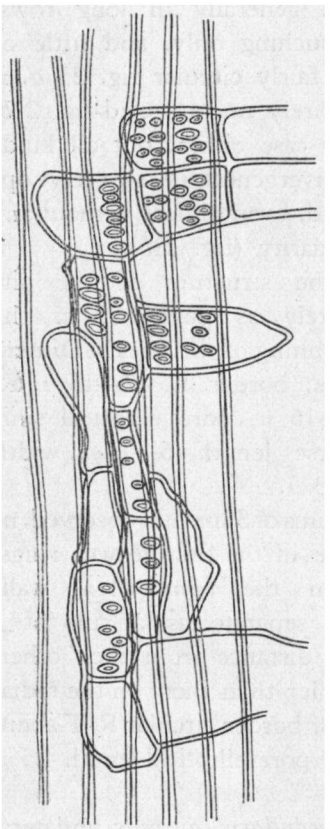

Fig. 22. Araucaria Bidwillii. Radial section of the stem, showing upright medullary ray cells, near the primary-xylem (to the left). × 260.

Pits. Between the *fibre tracheids mutually* bordered pits, especially on the radial walls, or nearly radial ones, chiefly crowded at the outer ends, therefore the middle part with considerable vacant pieces. On the tangential walls pits comparatively rare, sometimes

a long row, but then cut obliquely and probably on a wall of radial origin.

On the radial walls, pits generally in long rows, sometimes one, oftener two, touching only, and little or no flattening, therefore border fairly circular fig. 23 *a*, if in two rows, even the two entirely unconnected-fig. 23*b*. Not entirely alternate in every case either, but all kinds of divergences i.e. two rows opposed, even almost without any regularity (fig. 23*b*).

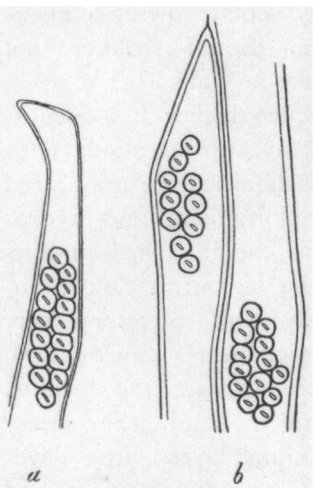

Fig. 23. Araucaria Bidwillii. Radial section. *a*, pits opposed. × 260. *b*, pits irregular. × 260.

The structure of the pits entirely as described at the beginning of this thesis. Dimensions: border L. 12—15 μ, R. 14—16 μ, pore elliptical sinistrorse length 6—7 μ, width 2—3 μ.

Rims of Sanio not observed, no more in the first growth rings.

On the tangential walls pits separate as a rule at a fair distance from each other, smaller than those on the radial ones, border circular R-T about 9 μ, pore elliptical length 4,5 μ, width about 2 μ.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, invariably fairly large in number on the rhomboid bordering plane between fibre-tracheids and medullary ray cell, generally in two rows, seldom one or three, mostly opposed, sometimes horizontally alternate seldom vertically alternate. Border very indistinct mostly circular (pits little flattening each other). L-T about 10 μ. Pore slit-like, more so than between the fibre-tracheids mutually.

Between the *first fibre-tracheids* of the secondary xylem and *medullary ray cells* unilateral bordered pits entirely of the same structure as on these spots in the primary xylem (see p. 522). Contents of the fibre-tracheids small, in the neighbourhood of the medullary ray a good deal of resin, often T-shaped; once or twice trabeculae observed.

Intercellular spaces fairly frequent, especially near the medullary rays, at the corners, due to unsolid gussets or between the tangential walls owing to divergence of those walls.

III. Medullary ray cells.

1. Procumbent cells. R. 190—400 μ, T. 15—25 μ L. 30—35μ, length greatest in the middle of a cell, at the tangential separating walls lower, generally 20—25 μ there. Walls thin 1—1,5 μ, generally breaking by sectioning, not becoming blue in potassium iodide iodine and sulphuric acid 75 %, somewhat lignified and especially containing pectin substances (becoming deeply red in ruthenium red). No pits, neither on the side of the fibre-tracheids, nor between the cells mutually (see for the rest the fibre-tracheid p. 516). Contents: much protoplasm with distinct nuclei and usually a fair quantity of resin, very rarely a single grain of starch.

Intercellular spaces between fibre-tracheids and medullary ray cells badly developed. On these spots large gussets in the mature wood. (see also p. 531, fig. 31).

2. Upright cells. Only in the neighbourhood of and within the primary xylem, rather strongly developed. Cells fairly irregular in shape. R. 15—30 μ, L. 40—80 μ (fig. 22). Wall and contents like those of the procumbent cells. Here no pits either (see for the rest the tracheid of the primary xylem p. 524).

3. Tracheidal medullary ray cells, occurring very rarely, and if at all in the inmediate neighbourhood of a leaf-trace. L. 35—40 μ, T. about 28 μ, R. not measured, forming

circular to elliptical cylinders, with radially directed axis. Wall about 5 μ, strongly lignified. Little to be seen of pits in those few cases in which observed at all.

Contents none. Intercellular spaces fairly well developed between the tracheidal ray cells and fibre-tracheids.

By way of comparison the wood of the disk of the stem 16 m. above the ground was observed.

The latter differs little in structure from the first.

Topography entirely agreeing with that of the preceding disk.

Elements. I Fibre-tracheids, somewhat wider on an average. R. normal 45—55 μ, sometimes still larger 40—85 μ, T. 35—45 μ very rarely only less wide 20—30 μ. Wall mostly somewhat thicker 4—6 μ. For the rest entirely like the preceeding one. The pits of the same structure too, but generally closer to each other. Dimensions of the border L. 12—15 μ, R. 15—17 μ, pore elliptical, sinistrorse, length 4—6 μ, width 3—2 μ, or entirely circular, about 4 μ in diameter.

Between fibre-tracheids and medullary ray cell unilateral bordered pits, arranged in the same way as in the preceding one. Diameter of the border about 10 μ, pore length 5—7 μ, width 1—2 μ, so more slit-like than between the fibre-tracheids mutually. No resin observed. Intercellular spaces like those above.

II. Medullary ray-cells.

1 Procumbent cells R. 160—330 μ, T. 15—25 μ, L. 25—35 μ at least in the middle of a cell, far less high at the tangential separating walls 18—25 μ. Walls entirely like those above; contents no resin [1]), a great deal of starch, however.

Intercellular spaces in radial direction far better developed

[1]) So this in contrast with the lower disk of the stem.

than in the older stem, both on the sides, and above and below. Here and there solid gussets.
2. Upright cells } entirely like those in the older
3. Tracheidal ray cells } stem.

Finally the young wood on a living two year old branch was observed. The wood was of a specimen from the Botanical Garden at Groningen.

This wood too, was little different from that of the older stem and a short description will therefore be sufficient here.

Topography. First growth rings, macroscopically rather indistinct, microscopically several thin-walled layers to be seen alternating with a few thick-walled ones. Yet slightly clearer than in the older stem, perhaps in connection with the different conditions of life. The bulk of the wood formed by fibre-tracheids. Wood-parenchymafibres scarce, scattered among the fibre-tracheids. Medullary rays 50—80 per sq. mm, few cells deep (1—3), and one cell broad, generally with straight boundaries below and above, except near and within the primary xylem, once or twice in the middle of the secondary xylem.

Elements. I. Fibre-tracheids, less wide, than in the adult wood, R. 15—20 μ, T. 15—20, L. 800—2100 μ, mostly about 1400 μ, forming tetragonal to hexagonal prisms with rounded ribs. Walls in the thin-walled layers 4—4½ μ, in the thicker-walled ones 5—5,5 μ, for the rest in shape and constitution as in the adult wood.

Pits. Between *fibre-tracheids mutually* bordered pits, entirely agreeing in shape and structure with those of the adult wood, standing often in two rows, sometimes even close to the primary xylem. [1]) Diameter of border 8—10 μ, pore slit-like, sinistrorse, length about 4μ, width 2 μ.

No rims of Sanio.

---

[1]) More frequently in two rows than in Araucaria araucana.

Between *fibre-tracheids* and *medullary ray cells*, like in the adult wood, unilateral bordered pits, in groups together on the rhomboid bordering plane. Pits sometimes in one row, in the thick-walled layers, sometimes in two, mostly opposed or horizontally alternate. Border in diameter about 6 μ, pore slit-like length 4—5 μ, width about 1 μ, in the late wood pore much more slit-like.

No contents in the fibre-tracheids observed. Intercellular spaces like those in the older stem.

II. Woodparenchyma. Sometimes wood parenchyma-fibres observed here, namely as simple vertical septated fibres, partly thin-walled and unpitted, partly thick-walled and then with simple pits, both on the side of the fibre-tracheids and between the septations mutually. R. about 30 μ, T. not measured, L. septations 55—200—245 μ.

III. Medullary ray-cells.

1. Procumbent cells R. 40—100 μ, T. 7—15 μ, L. 15—20 μ. Walls thin 1—2 μ (double) remaining unstained in potassium iodide iodine and sulphuric acid 75 %, somewhat lignified (slight wood-reaction), but especially pectin-substances (colouring red in ruthenium red). Here no pits either (see further fibre-tracheids p. 520).

Contents: Cells rich in protoplasm with distinct nuclei, besides some resin.

Intercellular spaces little developed comparatively, cells practically filling up the entire room. No solid gussets, like in the older stem.

2. Upright cells: *a.* close to and within the primary xylem, agreeing entirely with those described in the older stem (see p. 517, fig. 22).

b. also in a few other places, and there too forming connections between the medullary rays mutually (fig. 24). Shape and dimensions practically agreeing with those mentioned under *a.* R. 15—35 μ, L. 45—100 μ.

Contents and walls like in the procumbent cells.
3. Tracheidal ray cells not observed here.

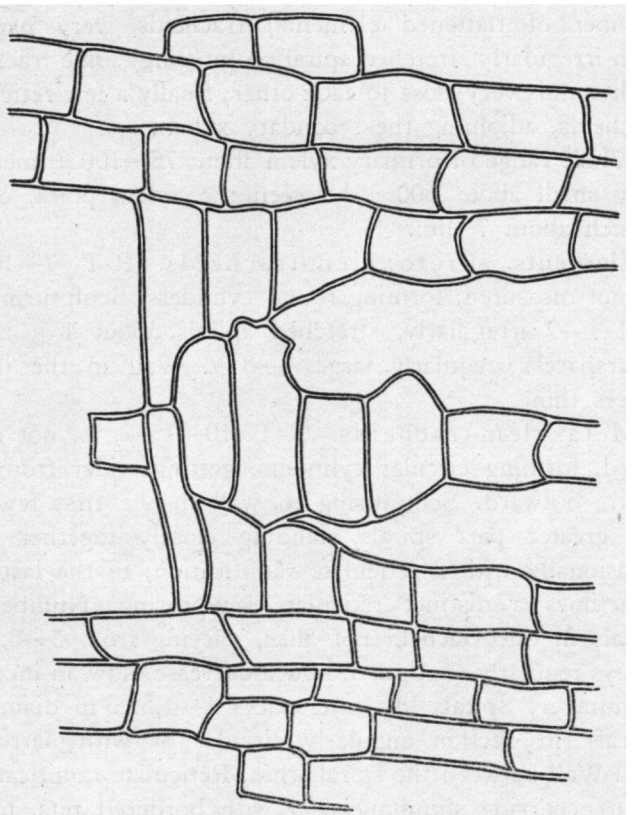

Fig. 24. Araucaria Bidwillii. Radial section of the stem, showing upright medullary ray cells which are in the first years growth, but not in the neighbourhood of the primary xylem. × 260.

Description Primary xylem. Observed on a branch about two years old, coming from the Botanical garden at Groningen.

Topography. Primary xylem in a closed tube round

the medulla, with protruding poles; between them medullary commissures, gradually passing into uniseriate medullary rays. Going from the centre outward at the poles: a slight number of flattened elements; tracheids, very narrow, with irregularly stretched spiral sculpturing; some tracheids with spirals very close to each other; finally a few reticulate tracheids, adjoining the secondary xylem.

Whole range of primary xylem about 75—100 μ, medulla very small about 500 μ between the xylem poles, entire branch about 7 mm.

Elements. Protoxylem-tracheids. R-T 7—10 μ. L. not measured, forming round cylinders. Sculpturing on wall 1—2 irregularly, stretched spirals, about 1 μ thick. Interspaces irregularly large 4—8 μ. Wall in the interspaces thin.

Metaxylem-tracheids. R-T 10—15 μ, L. not measured, forming circular cylinders, getting wider from the centre outward. Sculpturing on wall in the first few for the greater part spirals, standing closely together very occasionally with a reticulate ramification; in the last few sometimes a distinct reticulate sculpturing. Number of spirals in one tracheid not alike, varying from 3—6, not always regularly continued, now a decrease, now an increase in number. Spirals like interspaces 1—1,5 μ in diameter. Spirals in section angularly circular or with narrowed foot. Wall between the spirals thin. Reticulate ramifications often occurring simultaneously with bordered pits, to be found in the last few tracheids. Pits standing in long rows, hardly touching each other or not at all. Border circular, 5—6 μ in diameter. Pore circular, rather large about 2 μ. Between tracheids and medullary ray-cells unilateral bordered pits, very numerous in connection with an increasing depth of the medullary rays (fig. 22), often in one row, but occasionally in two or three. Border horizontally slit-like, pore likewise slit-like, practically horizontal, pit-canal

little narrowed and therefore pore and border nearly coinciding.

Medullary ray-cells. Upright cells only, numerous and irregular in shape, for the rest entirely like those described in the secondary xylem (see for this p. 517) fig. 22.

B. Root.

Material. A disk of a well developed root, about 8 cm. in diameter, grown excentrically (exc. ⅓), from Tjibodas.

Description Secondary xylem.

Topography. Growth rings macroscopally clearer than in the stem, microscopally indistinct, formed by a few rows of thick-walled tracheids alternated by several thin-walled ones, without formation of well marked boundaries. Bulk of the wood formed by fibre-tracheids. Woodparenchyma as a few scattered woodparenchyma-fibres, occurring very rarely.

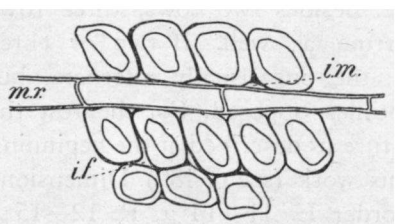

Fig. 25. Araucaria Bidwillii. Transverse section of root, showing a medullary ray with adjoining fibre-tracheids; *m.r.*, medullary ray; *i.m*, intercellular spaces between medullary ray and fibre-tracheid; *i.f.*, intercellular spaces between fibre-tracheids mutually. × 195.

Medullary rays, 20—60 per sq. mm., 2—17 cells deep, mostly uniseriate, bounded straight above and below. No tracheidal medullary ray-cells.

Elements. Fibre-tracheids. R. normally 30—45 μ, but owing to irregularities much varying (17—75 μ), T. normally 25—40 μ, strongly varying too (15—65 μ), L. 1150—2900 μ. Especially along the medullary rays, radially small and tangentially broad fibre-tracheids, having their largest tangential breadth not perpendicular but obliquely to the medullary ray (fig. 25). Fibre-tracheids forming polygonal prisms with pointed outer ends. Radial

arrangement with many irregularities. Walls everywhere practically equally thick 3—5 μ, tang. walls along the medullary rays often somewhat thicker only, lignified, becoming yellow in hydrochloride of aniline, middle-lamella rather thin 0,5—1 μ (double), with gussets at the corners. Secondary thickening layers little developed, hardly colouring blue in potassium iodide iodine and sulphuric acid 75 %. Radial walls comparatively little bent inward at the medullary rays (narrow medullary rays).

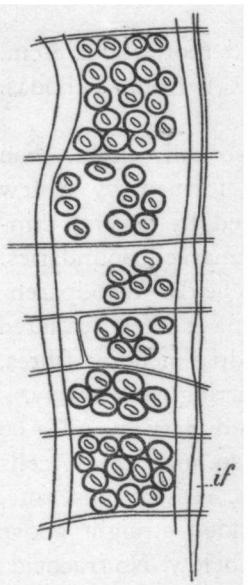

Fig. 26. Araucaria Bidwillii, radial section of root, showing pits on the bordering planes between fibre-tracheids and ray cells. *i.f.*, intercellular spaces. × 260.

Pits. Between *fibre-tracheids mutually* bordered pits, about the same as in the stem, perhaps closer to each other and therefore oftener hexagonal in shape. Besides two rows, three rows occurring as well. If two or three rows, the pits usually alternate, but sometimes opposed. For the rest the structure as described at the beginning of this work (see p. 489). Dimensions of border L. 11—14 μ, R. 12—15 μ. Pore elliptical length 6—8 μ, width 2—3 μ. Pits the same in early and late wood. No rims of Sanio.

Between *fibre-tracheids and medullary ray-cells* unilateral bordered pits, always in groups together on the rhomboid bordering plane, in number rather varying and fairly irregularly arranged (see fig. 26). Border fairly distinct, more or less circular about 8 μ in diameter. Pore slit-like length 5—7 μ, width 1—2 μ.

Between *woodparenchyma fibre* and *fibre-tracheid* unilateral bordered pits, in single rows, mostly touching

hardly or not at all, rarely two rows, border circular 9—10 μ, pore slit-like length about 6 μ, width about 2 μ.

Contents of the fibre-tracheids small; locally, namely in the neighbourhood of the medullary rays, a good deal of resin.

Intercellular spaces not numerous; if present at the corners and likewise between the tang. walls owing tod ivergence (see fig. 25), both in the neighbourhood of medullary rays.

II. Woodparenchyma-fibres occurring rather rarely, nevertheless regularly scattered among the fibre-tracheids, mostly by two's or three's together, but occasionally separate. Fibres thin-walled and unpitted, running on lengthwise, and divided by partition walls. Thick-walled septations not observed here. R. 25—30 μ, sometimes up to 40 μ, T. 12—25 μ, L. of the septations 120—300 μ. Total length difficult to measure (fall asunder in maceration).

III. Medullary ray-cells.

1. Procumbent cells R. 110—270 μ, T. 10—20 μ, L. 15—40 μ, in the middle of a cell perceptibly longer than at the tangential separating walls, for instance (26—37—26); (17—20—17); (15—30—17) etc. Walls like those in the stem; thick 1—1½ μ, having no pits, neither on the side of the fibre-tracheids nor between the cell mutually (see for the rest the fibre-tracheids p. 524).

Contents of the cells locally much resin, in other parts much starch.

Many intercellular spaces between medullary ray cells and fibre-tracheids, likewise between the cells mutually

2. upright cells
3. tracheidal cells } absent here.

The primary xylem is so little developed that it is not to be found again in the older root and will therefore be left out of discussion.

4. Araucaria angustifolia Bertoloni. (Syn. Ar. brasiliana Rich.).

Material. A piece of wood of an evidently fairly big tree from Brazil. For the rest age and origin unknown.

Description secondary xylem, made after preparations of adult wood, made of the above-mentioned block of wood.

Topography. Growth rings macroscopally particularly clear, very regular, at a mutual distance of 2—6 mm., microscopically also very clear. Boundaries formed by a great difference in thickness of wall, elements somewhat narrowed at the end of a period, with a sudden transition into the new period.

The bulk of the wood formed by fibre-tracheids. No woodparenchyma fibres. Medullary rays not numerous, 10—50 per sq. mm., all of them uniseriate 2—10 cells deep, usually separated by 3—6 rows of fibre-tracheids. Tracheidal ray cells in special cases only, chiefly near a leaf-trace penetrating into the wood, and even there, not numerous, but extending to a fair distance up to about 1.8 mm. Upper and lower boundaries straight, at least within the secondary xylem [1]).

Elements. I. Fibre-tracheids. R. 25—45 μ, T. 40—45 μ, sometimes 30—35 μ, rarely still less (these are the upper ends of fibre-tracheids, which have likewise slightly impeded the growth of the neighbouring ones (30—35)), L. 5000—6000 μ, forming 4—6-sided prisms with rounded ribs and pointed outer ends. Lumen more or less cylinder-shaped.

A good radial arrangement generally. Fibre-tracheids apparently septate owing to secretion of resin, numerous. Walls early wood, thick R. 6—9 μ, T. 4—8 μ, late wood,

[1]) Owing to lack of material not examined in the neighbourhood of the primary xylem.

R. 8—15 μ, T. 6—15 μ, so little difference in radial and tangential thickness of wall. Walls lignified, becoming yellow in hydrochloride of aniline, middle-lamella colouring more intensely and therefore more distinctly to be observed, rather thin, about ½—1 μ (double), secondary thickening layers of a very strong, development, not becoming blue in potassium iodide iodine and sulphuric acid 75 %. Tangential walls thicker at a medullary ray (fig. 27), radial wall slightly bent inward there (slightly in consequence of narrow med. rays).

Pits. *Between the fibre-tracheids mutually,* bordered pits, especially on the radial walls or on those nearly radial, seldom on tangential walls.

On radial walls pits in 1 or 2 long rows, generally touching, sometimes at the same time flattening one another, sometimes hardly or not touching at all and then border practically circular in shape. Pore mostly slit-like and than sinistrorse, often nearly vertical, seldom pore circular. Difference of pits in early and late wood slight; in late wood mostly one row, in early wood generally two seldom three; in both, pits chiefly at the outer ends of the fibre-tracheids; consequently parts nearly without pits and parts with nothing but pits.

The structure of the pits for the rest the same as described in the beginning of this work (see p. 489).

Dimensions: border L. 12—15 μ, R. 14—18 μ, pore length mostly about 7 μ, seldom longer up to 12 μ, width much varying, 1—6 μ.

On tangential walls pits, if present, likewise contiguous and not separate. Dimensions border L. and T. 15—18 μ. Pore slit-like, sinistrorse length about 10 μ, width 2—3 μ.

No rims of Sanio observed.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, always in groups on the rhomboid bordering-

plane (2—5), usually opposed, sometimes horizontally alternate, seldom vertically alternate. Border often indistinct, pore slit-like, not more so than in the fibre-tracheids mutually. Dimensions border L. and R. 6—12 μ pore length 6—10 μ width 1—4 μ.

Contents of the fibre-tracheids comparatively slight, near the medullary rays generally large quantities of resin. Here and there trabeculae observed.

Intercellular spaces occasionally at the corners, but

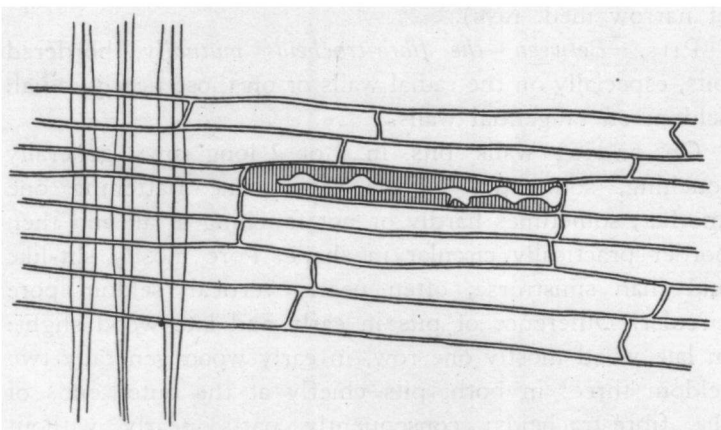

Fig. 27. Araucaria angustifolia. Radial section of stem, showing a medullary ray with a thick-walled ray cell. × 165.

more numerous between the tangential walls, due to diverging of those walls, both kinds especially near the medullary rays.

II. Medullary ray cells.

1. Procumbent cells.

a. Thin-walled ones, R. 160—250 μ, T. 15—18 μ, L. 20—30 μ, in the middle of a cell often more high than at the tangential separating walls, generally forming round cylinders with radially directed axis. Walls thin, 1—2 μ, slightly lignified, slightly colouring yellow in hydrochloride

of aniline, cellulose-content slight, remaining unstained in potassium iodide iodine and sulphuric acid 75 %, especially pectin-substances, becoming intensely red in ruthenium red, having no pits, neither mutually, nor on the side of the fibre-tracheids (see further the fibre-tracheid).

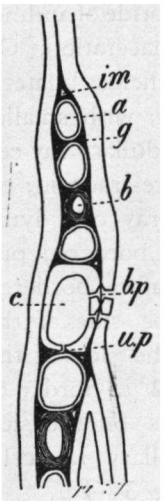

Fig. 28. Araucaria angustifolia. Medullary ray in tangential section; *a*, thin-walled ray cell; *b*, thick-walled ray cell; *c*, tracheidal ray cell; *i. m.*, intercellular space; *g*, gusset; *b.p.*, bilateral bordered pit; *u.p.*, unilateral bordered pit. × 195.

Contents: large quantities of resin, also a few group of starch-grains.

b. Thick-walled ones, occurring fairly profusely scattered among the thin-walled ones and adjoining them entirely regularly, (fig. 27, fig. 28) R. 140—240 μ, T. 18—22 μ, L. 25—35 μ. Walls mostly irregularly thickened 5—12 μ, lignified, less so than the fibre-tracheids, with simple pits both on the side of fibre-tracheids, and on the side of the adjoining medullary ray cells. The former about 2—5 μ in diameter, the latter 12—15 μ (fig. 29) [1]).

Contents of these cells the same as those of the thin-walled ones, or often nihil.

Intercellular spaces between medullary ray cells and fibre-tracheids rare, and if present, small (fig. 30); on those spots mostly large gussets remaining intact as appendices in case of careful maceration (fig. 31).

2. Upright cells absent in adult wood. Material from the neighbourhood of the primary xylem wanting.

3. Tracheidal medullary ray cells, only near leaf-traces

[1]) Owing to these simple pits, these thick-walled medullary ray cells distinguish themselves from the tracheidal medullary ray cells in having genuine bordered pits (see sub. 3).

between the thin-walled procumbent cells, R. 70—300 μ, T. 20—38 μ, L. 25—35 μ, forming circular to oval cylinders with a radially directed axis. Walls thick, lignified 6—8 μ, becoming yellow in hydrochloride of aniline, remaining intact during maceration. On the side of the fibre-tracheids bilateral bordered pits (fig. 28 *b.p.*), with smaller pore on the side of the medullary ray cell than on the side of the fibre-tracheid; on the side of the medullary ray cells lying above and below unilateral bordered pits (fig. 28). Border of the bilateral bordered pit 12—14 μ, pore on the side of the fibre-tracheid 4—5 μ, on the side of the medullary ray tracheid 1—2 μ. Border of the unilateral bordered pits on the side of the neighbouring medullary ray cells about 10 μ, pore fairly large 3—4 μ.

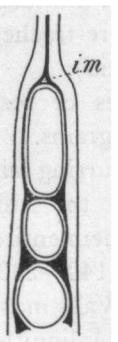

Fig. 30. Araucaria angustifolia. Medullary ray in tangential section with large gussets. *i.m.*, small intercellular space. × 315.

Contents slight, sometimes a little resin. Intercellular spaces like those near the thin-walled procumbent cells.

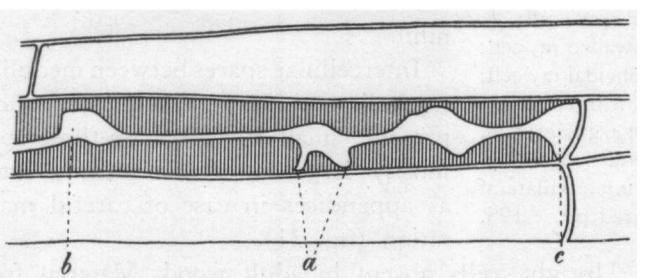

Fig. 29. Araucaria angustifolia. Thick-walled ray cell in radial section; *a*, simple pit; *b*, simple pit obliquely cut off; *c*, simple pit in a tangential separating wall. × 420.

Primary xylem not described, no material of it being present.

5. Araucaria Cunninghamii Sweet.

Material. 1. A disk of a side-branch, about 8 years old, about 6 c.m. in diamater without bark, from the Governmental Botanical Garden of Buitenzorg.

2. A thin branch, bearing leaves.

Material preserved in alcohol.

Description Secondary Xylem.

Topography. Growth rings indistinct, if within the redwood, in other places fairly clearly to be seen, at least macroscopically, owing to the fact that resin is often found in a mass at the end of the periods. Microscopically a few rows of thick-walled fibre-tracheids are seen to alternate with thin-walled ones, gradually passing into one another without clearly marked boundaries. Redwood very strongly developed and very dark in shade, in tangential direction gradually passing into the ordinary wood, in outward radial direction with strongly marked boundaries.

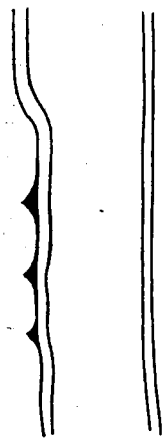

Fig. 31. Araucaria angustifolia. Fibre-tracheid after maceration, with adherent gussets. × 315.

Fibre-tracheids forming the bulk of the wood. No woodparenchyma fibres. Medullary rays moderate, 40—60 per sq. mm., all of them uniseriate, 1—6 cells deep, separated by a number of fibre-tracheids strongly varying (one-many). No tracheidal medullary ray cells [1]). Upright cells only in the neighbourhood of and within the primary xylem, consequently medullary rays irregularly bounded below and above there, for the rest upper and lower boundaries of the medullary rays straight.

[1] It may be a result of the little developed leaf-traces, which are in their turn a consequence of the small needle-shaped leaves.

Elements. I. Fibre-tracheids R. 20—25 μ, T. 15—40 μ, generally 25—30 μ, L. 2200—6400 μ, mostly forming circular to elliptical cylinders tapering towards the outer ends, especially the lumen cylinder-shaped. A fairly good radial arrangement generally (fig. 32). Walls thick R. 4—6 μ, T. 4—6 μ. Radial and tangential walls practically equally thick, lignified, colouring yellow in hydrochloride of aniline, middle-lamella colouring more intensely and therefore clearly to be observed, especially the gussets very well developed, often not entirely solid, gussets large in connection with the circular shape of the fibre-tracheids fig. 32. Secondary thickening layers likewise well developed, especially in the redwood, not becoming blue in potassium iodide iodine and sulphuric acid 75 %. Tangential walls of the fibres much thicker at the medullary ray (7—8 μ), radial walls bent inward there medullary ray, therefore entirely closed round.

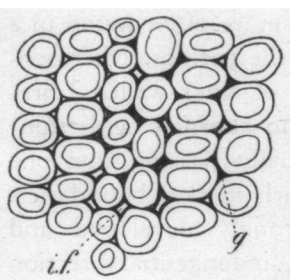

Fig. 32. Araucaria Cunninghamii. Transverse section of stem; *g*, gussets; *i.f.*, intercellular spaces. × 260.

Pits. *Between the fibre-tracheids mutually* bordered pits, especially on radial walls, or those nearly radial, seldom on tangential walls.

On radial walls pits in long contiguous rows, sometimes one row sometimes two, generally touching and at the same time decidedly flattening each other. In the case of two rows mostly alternate and then more or less hexagonal in shape, seldom opposed and then tetragonal in shape (fig. 33) or horizontally alternate (fig. 34). Pore nearly circular or elliptical and then sinistrorse. Pits chiefly in a mass at the outer ends of the fibre-tracheids, in the middle part often scattered in small groups. Structure of the pits entirely as described before p. 489. Dimensions:

border L. 8—11 μ, seldom 14—15 μ (namely a few circular pits, occurring rarely), R. 12—15 μ. Pore circular about 2 μ or elliptical length 4—5 μ, width 1—3 μ, seldom very long and narrow, length 8—12 μ, width 2—3 μ, namely in a few thick-walled rows of fibres or in the redwood. Here sometimes separate pits, circular in shape, border 9—10 μ, pore slit-like length 8—12 μ, width 2—3 μ.

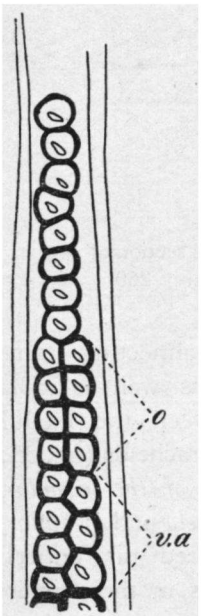

Fig. 33. Araucaria Cunninghamii. Radial wall of a fibre-tracheid, seen from without, showing *o*, bordered pits opposed; *v.a.*, vertically alternate. × 390.

On tangential walls pits rarely observed; if present, sometimes somewhat obliquely cut off and then the pits in contiguous rows, therefore of the radial type and the pits probably standing on walls of a radial origin. Dimensions: border R.—T. about 10 μ. Pore practically circular or strongly slit-like. Dimensions the same as above.

Fig. 34. Araucaria Cunninghamii. Radial wall of a fibre-tracheid, seen from within, showing bordered pits, horizontally alternate. × 390.

No rims of Sanio observed.

Between *fibre-tracheids* and *medullary ray cell* unilateral bordered pits always in groups together on the rhomboid bordering plane, mostly in 2 or 3 rows, less often 1 row (late wood), sometimes somewhat irregular. If in 2 or 3 rows, opposed or horizontally alternate, less often vertically alternate. Border circular or somewhat oval (longitudinal axis horizontal), pore practically circular or elliptical and nearly upright, seldom long and oval (late wood). Dimensions border R.—L.

6—9 μ, pore length about 4 μ, width about 1 μ; in the case of a strongly slit-like pore length difficult to state, width 1 μ or less. The group of pits on a bordering plane

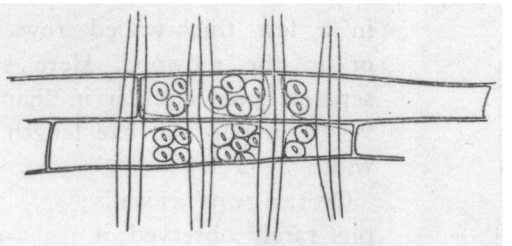

Fig. 35. Araucaria Cunninghamii. Radial section of stem. Dotted line, connecting frames. × 260.

often enclosed by a clearly developed connecting frame, due to the presence of longitudinal as well as radial intercellular spaces between the medullary ray cells and fibre-tracheids (fig. 35).

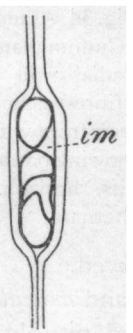

Fig. 36. Araucaria Cunninghamii. Medullary ray in tangential section; *im.*, intercellular spaces. × 260.

In the *first few fibres of the secondary xylem* between *fibre-tracheid* and *medullary ray cell* unilateral bordered pits entirely of the same structure as in the primary xylem (see p. 536).

Contents of the fibretracheids small, here and there a little starch, sometimes a slight quantity of resin.

Intercellular spaces numerous chiefly at the corners (fig. 13), but also between the tangential walls, due to divergence of those walls; both especially in the vicinity of the medullary rays.

II. Medullary ray cells.

1. Procumbent cells. R. 85—130 μ, T. 15—20 μ, L. 15—40 μ, forming circular to elliptical cylinders, with radially directed axis, sometimes fairly

irregular in shape (fig. 36). Walls thin 1—2 μ, lignified becoming yellow in hydrochloride of aniline, cellulose-content slight, not colouring blue in potassium iodide iodine and sulphuric acid 75 %, rich in pectin substances (colouring red in ruthenium red), having no pits neither on the side of the fibretracheids, nor mutually (see the fibre).

Contents: Cells rich in protoplasm and much starch also a little resin here and there.

Intercellular spaces between medullary ray cells and fibretracheids numerous, both in radial and in vertical directions, likewise between the medullary ray cells mutually (fig. 36), in radial sections often the cause of connecting frames on the walls of the medullary ray cells (fig. 35).

2. Upright cells, in the vicinity of and within the primary xylem, not strongly developed, rather irregular in shape. L. 40—100 μ, R. 35—40 μ. Wall and contents the same as those of the procumbent cells. Here no pits either (see further the tracheid of the primary xylem, p. 536).

3. No tracheidal medullary ray cells observed.

Primary xylem. Made after preparations of a one-year-old branch.

Topography. Primary xylem in a tube nearly entirely surrounding the medulla, with little protruding poles. In between the medullary commissures, soon passing into uniseriate medullary rays. Whole range of primary xylem very limited 40—50 μ at most. Medulla fairly large about 1 mm., entire branch about 3 mm.

From the centre going outward: a slight number of crushed elements, a few tracheids, very narrow, with irregularly stetched spiral sculpturing; tracheids with spiral sculpturing of which the spirals very closely together; finally 1 or 2 reticulate tracheids.

Elements. Protoxylem: spiral tracheids R.—T. 7—10 μ L. difficult to measure, generally forming circular, elliptical cylinders, wall-sculpturing 1—2 irregulary stretched

spirals. Spirals 1—2 μ thick, interspaces irregular 4—6 μ, wall of them thin.

Metaxylem: tracheids R.—T. about 10 μ, L. difficult to measure, generally forming circular-elliptical cylinders. Wall-sculpturing of the first few tracheids: spirals, very closely together, frequently with a few reticulate ramifications; number of spirals 2—4, not always regularly continued, spirals thick 1—1,5, mostly circular, with narrowed foot, sometimes angularly circular in section, in the last few tracheids a real reticulate wall-sculpturing.

In both *between the tracheids mutually* numerous bordered pits, generally in long, non-contiguous rows, consequently, border circular, smaller than in the secondary wood. Border about 6 μ, pore circular, about 1 μ.

Between *tracheids* and *medullary ray cells* many unilateral bordered pits, in one long row or in two and then somewhat alternate. Border somewhat horizontally elliptical, pit-canal little narrowed, therefore pore large, also horizontally elliptical.

Medullary ray cells. Upright cells exclusively, of the same structure as those in the beginning of the secondary xylem and already described there (see p. 535).

6. Araucaria excelsa R. Br.

Material. I. A disk of a side-branch, without bark about 2.7 cm. in diameter. 2. a thin branch bearing leaves.

Both from the Governmental Botanical Garden of Buitenzorg and preserved in alcohol.

Description Secondary Xylem.

Topography. Growth rings numerous, very close together, macroscopically not clearly to be seen, microscopically not any better either, formed by a few rows of radial narrow fibre-tracheids, for instance, from within outward as follows: 25—25—25—25—20—*12*—*12*—*30*—25—25; 25—25—*20*—*12*—*25*—20—25—25; 25—25—*20*—*20*—*15*—*30*—25—25.

The bulk of the wood consisting of fibre-tracheids. No woodparenchyma fibres. Medullary rays not numerous 20—25 per sq. mm, all of them uniseriate, 1—6 cells deep, separated by a few rows of fibre-tracheids strongly varying in number, no tracheidal ray cells, upper and lower boundaries straight, at least in adult wood; in the neighbourhood of and within the primary xylem irregular, owing to the presence of irregularly formed upright cells.

Elements. I. Fibre-tracheids R. 25—35 μ, rarely less at the end of a period, down to 12 μ (see above), T. 20—30 μ, L. 1200—3900 μ, usually 2400—3200 μ, forming tetra- to hexagonal prisms with rounded ribs, sometimes more or less elliptical cylinders, especially the lumen cylindrical. Radial arrangement fairly good (see fig. 37). Walls fairly thick, R-T 5—10 μ, practically the same in early and late wood, the radial walls in late wood even less thick than elsewhere; lignified becoming yellow in hydrochloride of aniline middle-lamella colouring more intensely therefore clearly observable, strongly developed 2—4 μ (double), gussets not large. Secondary thickening layers large (4—9 μ), not colouring in potassium iodide iodine and sulphuric acid 75 %, tertiary layers too, clearly observable, about 1 μ, becoming deeply yellow like the middle-lamella. Tangential walls perceptibly thicker at a medullary ray, radial walls bent inward there, owing to which the medullary ray entirely enclosed.

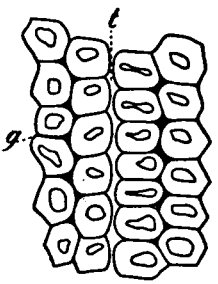

Fig. 37. Araucaria excelsa. Transverse section of stem; *g*, gussets; *t*, top of a medullary ray. × 195.

Pits. Between the *fibre-tracheids mutually*, bordered pits, especially on the radial walls or those nearly radial, seldom on the tangential walls.

On the radial walls, pits in long contiguous rows,

mostly one, often two, usually touching and at the same time flattening each other, seldom separate (transition of two periods). If two rows, often alternate and then more or less hexagonal, less often, but rather frequently, opposed and then tetragonal in shape, or horizontally alternate. Pore slit-like and sinistrorse or practically circular in shape. Pits more numerous at the outer ends, but yet not exclusively in a mass here. The structure of the pits entirely as described before p. 489. Dimensions: Border: L. 8—10 μ, R. 8—10 μ, less often 12—15 μ (in some single rows). Pore circular 2—3 μ, or elliptical, length 4 μ, width 2 μ, at the boundary of two periods border smaller L-R. 6—8 μ, pore very much slit-like length 4—6 μ.

On the tangential walls, pits rarely observed; if present often cut off obliquely and then of the radial type. Dimensions border L. about 10 μ T. about 10 μ, pore elliptical sinistrorse, length about 4 μ, width about 2 μ.

No rims of Sanio.

Between *fibre-tracheid* and *medullary ray cell* unilateral bordered pits, always in groups together on the rhomboid bordering plane between medullary ray cell and fibre-tracheid, mostly in two rows, seldom three, opposed or horizontally alternate, rarely vertically alternate, mostly touching, sometimes a little flattening each other. Border practically circular or oval, in case of flattening sometimes tetra- to hexagonal in outline, pore generally very much slit-like, sometimes having a vertical position. Dimensions border L. 6—8 μ, R. 6—10 μ. Pore length about 5 μ, width 1—1½ μ.

In the *first few fibre-tracheids of the secondary xylem* between *fibre tracheid* and *medullary ray cell*, unilateral bordered pits of the same structure as on the same spot in the primary xylem (see p. 540).

Contents of the fibre-tracheids not observed.

Intercellular spaces at the corners slight, between the tangential walls, owing to divergence of those walls, also slight; if present, both in the vicinity of the medullary rays.

II. Medullary ray cells.

1. Procumbent cells.

Practically straight and everywhere equally long, forming circular to elliptical cylinders, with radially directed axis and with flattened lower and upper side on the places of mutual contact. Walls thin 1—2 μ, somewhat lignified, becoming yellow in hydrochloride of aniline, less so than the surrounding fibre-tracheids, cellulose-content slight, remaining unstained in potassium iodide iodine and sulphuric acid 75 %, rich in pectin substances, becoming red in rutheniumred; no pits, neither on the side of the fibre-tracheids, nor mutually (see also the fibre).

Contents. The cells rich in protoplasm and a good deal of starch, no resin.

Intercellular spaces between medullary ray cells and fibre-tracheids well developed, both in radial and vertical direction; in radial sections often the cause of connecting frames on the radial walls of the medullary ray cells.

2. Upright cells only near and within the primary xylem, not strongly developed, rather irregular in shape. Wall and contents like those in the procumbent cells. Here no pits either (see further: the tracheids of the primary xylem).

3. Tracheidal medullary ray cells not observed.

Primary xylem after preparations of a one-year-old branch.

Topography. Primary xylem in a tube enclosing the medulla with rather strongly protruding poles. In between the medullary commissures, gradually passing into uniseriate medullary rays.

Whole range of primary xylem very limited, 40—50 μ at most; medulla small about 400 μ, entire branch about 4 mm.

From the centre outward; 2—3 tracheids, very narrow, with irregulary stretched spiral-sculpturing, a few tracheids with spiral-sculpturing, very closely together; an occasional one with reticulate sculpturing on wall.

Elements. Protoxylem: spiral tracheids R.-T. 6—8 μ, L. difficult to measure about 700—720 μ, forming circular, elliptical cylinders, sculpturing on wall 1—2, irregularly stretched spirals about 2 μ thick. Interspaces irregular, large, wall in these spaces thin.

Metaxylem Tracheids R.-T. 10—12 μ, L. difficult to measure 700—720 μ, forming circular cylinders. Wall-sculpturing of the first few tracheids a slight number of spirals, very close together, very soon with a noccasional reticulate ramification; spirals about 1 μ thick mostly circular with narrowed foot, sometimes entirely circular in section; interspaces small, about nearly 1 μ, with thin wall. In the last few tracheids, genuine reticulate sculpturing on wall.

Pits: In the last few spiral-tracheids and reticulate tracheids bordered pits between *the tracheids mutually*, mostly in one non touching row, hence border circular, mostly smaller than in the secondary xylem. Border about 6 μ, pore circular 1—1½ μ.

Between *tracheids* and *medullary ray cells*, many unilateral bordered pits in one or more long rows, sometimes somewhat irregular. Border horizontally elliptical, pit-canal little narrowed, hence pore large, nearly coinciding with the likewise horizontally elliptical border.

Medullary ray cells. Exclusively upright cells, entirely of the same structure as in the beginning of the secondary xylem and already described there (see p. 539).

7. Araucaria Cookii R. Br.

Material: 1. A disk of a side-branch, without bark about 5 cm in diameter.

2. A young branch bearing leaves.

Both from the Governmental Botanical Garden of Buitenzorg and preserved in alcohol.

Description secondary xylem.

Topography. Growth rings generally, both macroscopically and under the microscope, not observable, seldom well developed. Often locally much redwood, darker in shade, in tangential and inward radial direction gradually passing into ordinary wood, in outward radial direction with clearly marked boundaries. The bulk of the wood formed by fibre-tracheids. Woodparenchyma absent medullary rays, 60—80 per sq. mm. seldom fewer, usually uniseriate, but sometimes locally biseriate and the two cells then not much wider than a cell lying over or under it (fig. 38), 1—8 cells deep, often 1—3, separated by a strongly varying number of rows of fibre-tracheids (4—18); tracheidal medullary ray cells absent; boundaries above and below straight, except in the neighbourhood of and within the primary xylem, owing to the presence of upright cells, forming commissures between medullary rays lying above one another (Here very clear fig. 42).

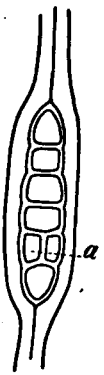

Fig. 38. Araucaria Cookii. Medullary ray in tangential section, locally two cells broad, at *a*. × 260.

Elements. I. Fibre-tracheids R. 25—35 μ, rarely larger up to 40 μ, T. 20—50 μ, mostly 25—40 μ, L. 2100—3200 μ, forming tetra- to hexagonal prisms with rounded ribs and pointed outer ends, unless touching upon a medullary ray or other fibre-tracheid, in that case the end flattened; lumen generally forming round cylinders. Radial arrangement fairly good. Walls of the fibre-tracheids R.-T. 5—6 μ, seldom thicker up to 7—8 μ; at a medullary ray tangential walls thicker 6—7 μ; in the same way in the redwood, both radially and tangentially. Wall lignified, becoming yellow in

hydrochloride of aniline, middle-lamella colouring more intensely, therefore clear discernible, strongly developed 2—3 μ (double), especially the gussets, generally solid. Secondary thickening layers well developed, 4—5 μ, remaining unstained in potassium iodide iodine. Tertiary thickening layers little developed, colouring a little more intensely, like the middle-lamella. Tangential walls thicker at a medullary ray, radial walls strongly bent inward there (inflated medullary rays).

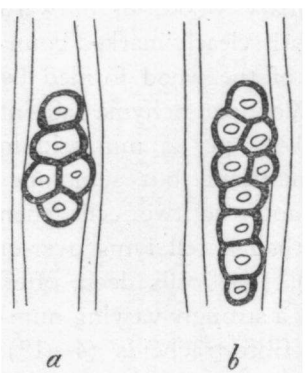

Fig. 39. Araucaria Cookii. Radial walls of fibre-tracheids. *a*. with opposed bordered pits. × 420. *b*. with bordered pits, vertically alternate. × 420.

Pits. Between the *fibre-tracheids mutually* bilateral bordered pits, especially on the radial or nearly radial walls, seldom on the tangential walls.

On the radial walls pits, mostly in one, rarely in two long contiguous rows, usually touching but little flattening one another. Rather often locally two pits in an otherwise single row and these pits alternate or opposed (fig. 39 *a* and *b*). Within the ordinary wood pore circular or elliptical and then sinistrorse or nearly horizontal; within the redwood very much slit-like and sinistrorse, sometimes much protruding outside the border (fig. 40), even here and there two alternate pits with a common slit-like pore (fig. 41). Pits in a mass at the outer ends of the fibre-tracheids, with large parts in between nearly unpitted. The structure of the pits entirely as described at the beginning of this thesis. Dimensions. Ordinary wood: border L. 9—10 μ R. 9—10 μ, sometimes slight ly flattened R. 12—13 μ, pore elliptical, lenth 5—6 μ, width 2—4 μ, sometimes nearly circular about 2—3 μ; in the redwood: border

L. 9—10 μ, R. 9—12 μ, pore length up to 15 μ or more (difficult to state exactly), width about 2 μ.

On the tangential walls, pits seldom observed, if present, often cut obliquely and of the radial type (these pits probably on walls of radial origin). Dimensions border L.-T. 8—9 μ, pore slit-like length 8 μ, width about 2 μ.

Fig. 40. Araucaria Cookii. Radial wall of a fibre-tracheid, seen from without, showing bordered pits with strongly slit-like pore. × 420.

No rims of Sanio.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, always in groups on the rhomboid bordering plane, mostly in two or three rows, seldom in one, as a rule opposed, sometimes horizontally or vertically alternate, mostly touching, sometimes a little flattened too. Dimensions, ordinary wood, border L.-R. 8—10 μ, pore circular about 2—3 μ, or oval length 3—4 μ, width 1—2 μ; in the redwood, border likewise L.-R. 8—10 μ. (difficult to measure because the border is not very distinct), pore very much slit-like, though less so than in the fibres mutually, length 5—9 μ, width ½—1 μ, sometimes here too two neighbouring pits with a common slit-like pore.

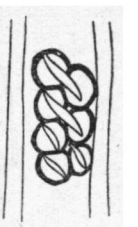

Fig. 41. Araucaria Cookii. Radial wall of a fibre-tracheid, seen from within, showing two bordered pits with a common slit-like pore. × 420.

Between the *first* few *fibre-tracheids* of the *secondary xylem* and *medullary ray cells* unilateral bordered pits entirely of the same structure as in the same place within the primary xylem see there p. 546).

Contents of the fibre-tracheids nihil.

Intercellular spaces at the corners slight, numerous between the tangential walls due to divergence and then especially near the medullary rays.

II. Medullary ray cells.

1. Procumbent cells R. 70—120 μ, T. 10—20 μ, usually

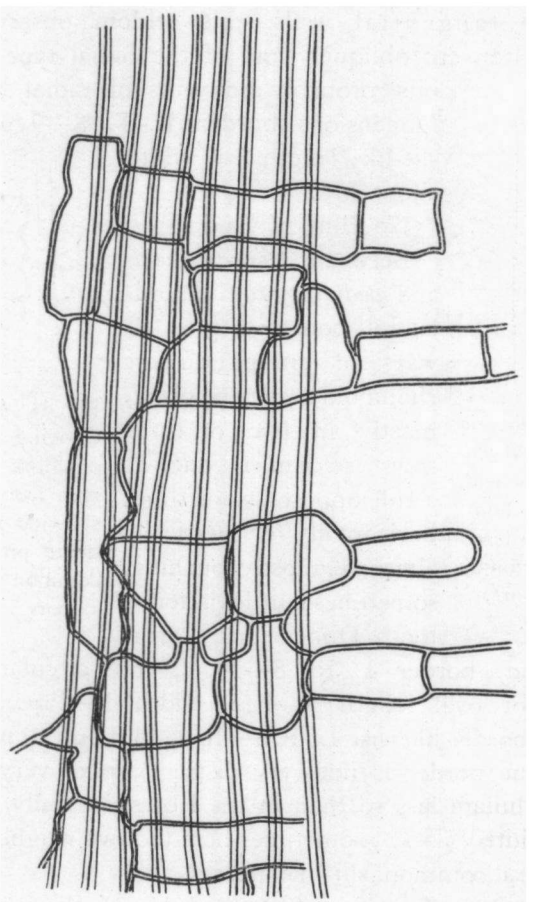

Fig. 42. Araucaria Cookii. Radial section of stem, showing upright medullary ray cells near and within the primary xylem. Primary xylem to the left. Secondary xylem to the right. Pits left out. × 260.

about 15 μ, L. 20—30 μ, sometimes the cells, of medullary rays one cell in depth, up to 50 μ, in the redwood usually

somewhat shorter 15—25 μ, cells nearly straight and everywhere equally long, forming somewhat circular cylinders, more or less flattened below and above, with radially directed axis Walls thin, somewhat lignified, most in the redwood, becoming yellow in hydrochloride of aniline, less intensely than the surrounding fibre-tracheids, cellulose-content slight, not colouring blue in potassium iodide iodine and sulphuric acid 75 %, many pectin substances, no pits, neither mutually, nor on the side of the fibre-tracheids. (see p. 543).

Contents: the cells rich in protoplasm with large, distinct nuclei, also a fair amount of starch, no resin observed. Intercellular spaces between medullary ray cells and adjoining fibre-tracheids little developed owing to the flattened condition of the cells below and above.

2. Upright cells only near and within the primary xylem, well developed, irregular in shape. (fig. 42). Walls and contents like those in the procumbent cells; here no pits either (see further: the tracheid of the primary xylem p. 546).

3. Tracheidal medullary ray cells not observed.

Primary xylem after preparations of a one-year old branch. Primary xylem in a tube enclosing the medulla, with somewhat protruding poles. Between them the medullary commissures, in outward direction passing into uniseriate medullary rays. The entire range of primary xylem rather limited about 60—70 μ (number of elements 6—8). Medulla rather small 500—600 μ, entire branch about 2 mm.

From within outward at the poles: a slight number of flattened elements, strongly crushed; a few tracheids with irregularly stretched spiral-sculpturing on wall; a few elements with spirals standing very closely together; an occasional tracheid with reticulate sculpturing on wall.

Elements. Spiral-tracheids protoxylem R.-T. 6—8 μ, L. difficult to measure, forming circular to ellip-

tical cylinders. Sculpturing on wall 1—2 spirals, stretched irregularly, 1—2 μ in diameter, interspaces irregular, in the last few smaller than in the innermost ones, walls in them thin.

Tracheids metaxylem R.-T. 10—12 μ, L. not measured, forming round cylinders. Sculpturing on wall in the first few, chiefly spirals with a few reticulate ramifications, spirals close together and slight in number 2 or 3, thin, about 1 μ, generally long and narrow in section (fig. 43), interspaces likewise small about 1 μ, wall of the latter thin, in the last few tracheids real reticulate sculpturing on wall.

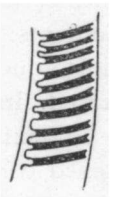

Fig. 43. Araucaria Cookii. Spirals of a spiraltracheid in section. × 630.

Pits. In both, the last few spiral-tracheids and the reticulate tracheids between the *tracheids mutually*, bordered pits mostly in one none touching row, hence border circular, mostly smaller than within the secondary xylem. Dimensions border 5—6 μ, pore fairly large about 2 μ, circular in shape.

Between *tracheids* and *medullary ray cells* many unilateral bordered pits, rather irregular in position. Border circular to horizontal elliptical, pit-canal here more narrowed than in other species, consequently border and pore clearly separated. Pore rather strongly slit-like and horizontal. Dimensions border about 5 μ, pore length 4μ, width 1μ.

II. Medullary ray cells. Exclusively upright cells, very numerous and irregular in shape, for the rest like those in the secondary xylem (see there p. 545, fig. 42).

8. Araucaria Rulei F. Muell.

Material. 1. A disk of a side-branch about 3½ cm in diameter without bark.

2. A young branch bearing leaves.

Both from the Governmental Botanical Garden of Buitenzorg; material preserved in alcohol.

Description Secondary xylem.

Topography. Growth rings, macroscopically discernible, although rather faintly, very close together ½—1 mm; under the microscope in the redwood very indistinct; in the ordinary wood slightly clearer, formed by a few rows of thick-walled fibre-tracheids radially somewhat narrower too than the others, passing into the other layers without strongly marked boundaries. Redwood in the same way as in the other species.

Fibre-tracheids the bulk of the wood. Woodparenchyma absent. Medullary rays not numerous 30—50 per sq. mm, rarely 20, exclusively uniseriate, 1—5 cells deep, separated by a varying number of rows of tracheids (3—13), often about 5. Tracheidal medullary ray cells only very occasionally, namely in the immediate neighbourhood of a penetrating leaf-trace. Upper and lower boundaries straight, except near and within the primary xylem.

Elements. I. Fibre-tracheids R. 20—25 μ, seldom up to 30 μ, at the transition of two periods sometimes smaller 8—20 μ, T. 20—30 μ, L. 1250—2850 μ, forming tetra- to hexagonal prisms, more or less circular or elliptical cylinders within the redwood. Lumen likewise cylindrical in shape. Radial arrangement often a little disturbed. Walls thick R.-T. 4—6 μ, difference in early and late wood slight, lignified (colouring yellow in hydrochloride of aniline, more intensely in the late wood). Middle-lamella colouring more deeply, therefore clearly discernible, strongly developed, especially in the redwood, 3—4 μ (double), gussets also large and usually solid. Secondary thickening layers little developed in proportion to the middle-lamella (3—4 μ), remaining unstained in potassium iodide iodine and sulphuric acid 75 %. Tertiary thickening layers generally little developed. Tangential walls sometimes thicker at a

medullary ray (up to 6—7 μ), radial walls strongly bent inward there and hence the medullary ray entirely enclosed.

Pits. Between the *fibre-tracheids mutually* bordered pits, especially on the radial or nearly radial walls, but likewise very numerous on purely tangential walls (fig. 44) and therefore not cut off obliquely in tangential sections.

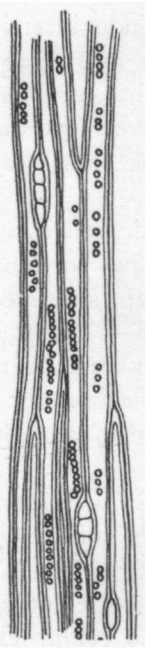

Fig. 44. Araucaria Rulei. Tangential section of stem, showing many pits on the tangential walls. (pits on the radial walls left out) × 100.

On the radial walls pits mostly in one long contiguous row, rarely over short distances two and then alternate, oftener here and there two pits opposed in an otherwise single row. Pits mostly touching, and also slightly flattening. Pore invariably elliptical in the ordinary wood, more slit-like in the redwood, both sinistrorse. Pits in a mass at the outer ends of the fibre-tracheids. The structure of the pits the same as described at the beginning of this work (see p. 489). Dimensions border L. 8—10 μ, rarely 12—14 μ, R. 13—14 μ, in the redwood about 10 μ; pore, ordinary wood length 5—6 μ, width about 2 μ, redwood length 10 μ or more, width 1—2 μ.

On the tangential walls pits likewise in one or two, long rows but always slightly irregular and hardly touching or not at all, and even if touching very rarely flattening each other, sometimes separate and hence border invariably nearly circular. Pore slit-like and sinistrorse. Pits not so much crowded together, but more equably distributed over the fibre-tracheid than on the radial walls (fig. 44, 45). Dimensions border L. 8—10 μ, T. 7—8 μ (less broad than deep, compare the radial wall). Pore elliptical, length about 4 μ, width about 2 μ.

No rims of Sanio.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, in groups together on the rhomboid bordering plane, generally in two rows, seldom one or three, mostly opposed, sometimes alternate and then horizontally, rarely vertically alternate, usually touching, but little flattening one another. Dimensions: border L.-R. 6—8 μ, pore slit-like length 5—6 μ, width 1—2 μ; in the redwood slightly more slit-like.

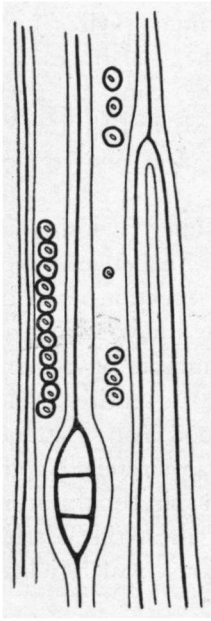

Fig. 45. Araucaria Rulei. A part of fig. 44, more magnified. × 260.

Contents of the fibre-tracheid slight, at most a single grain of starch, no resin.

Intercellular spaces at the corners rather numerous, likewise between the tangential walls due to divergence of those walls, both especially near the medullary rays.

II. Medullary ray cells.

1. Procumbent cells R. 70—140 μ, T. 10—30 μ usually about 20 μ, L. 17—25 μ, those of medullary rays, one cell in depth, mostly higher, up to 30—40 μ. Cells practically straight and everywhere equally long, forming round cylinders with flattened upper and lower planes to tetragonal prisms, in both cases with radially directed axis. Wall thin 1—2 μ (double), somewhat lignified (colouring red in hydrochloride of aniline), less so than the surrounding fibres, not becoming blue in potassium iodide iodine and sulphuric acid 75 %, rich in pectin substances (colouring red in ruthenium red), having no pits, neither mutually, nor on the side of the fibre-tracheids (see there p. 549).

Contents: the cells rich in protoplasm with distinct

nuclei, also much starch and here and there a drop of resin.

Intercellular spaces between fibre-tracheids and medullary ray cells little developed owing to the shape of the cells.

2. Upright cells, comparatively little developed, only within the primary xylem and in the very first beginning of the secondary xylem, rather irregular in shape R. 30—50 μ, L. 70—150 μ, T. not measured. Wall and contents the same as those of the procumbent cells, here no pits either (see for the rest the tracheid of the primary xylem.)

3. Tracheidal cells. Only near the leaf-traces and even then, very rare. The structure the same as in the other species. Dimensions: R. not measured, T. 12 μ, L. 15 μ.

Primary xylem after preparations of a one-year-old branch.

Topography. Primary xylem in a tube, enclosing the medulla, with strongly protruding poles. In between them the medullary commissures in outward direction changing into uniseriate medullary rays. The whole range of primary xylem moderately developed 80—90 μ (number of elements 5—10), medulla rather large 1500—1600 μ, entire branch about 3 mm. From within outward: a good many flattened elements; a few tracheids with irregular stretched spiral sculpturing on wall; some elements with spiral sculpturing, the spirals very close to one another, at most the last few tracheids with some reticulate ramifications; real reticulate tracheids absent.

Elements. Spiraltracheids protoxylem R.-T. about 10 μ, L. difficult to measure, forming circular elliptical cylinders, sculpturing on wall 2—3 irregularly stretched spirals, 1—2 μ in diameter. Interspaces irregular, those in the outermost tracheids smaller than in the innermost ones, wall in the interspaces thin.

Tracheids metaxylem. R.-T. 10—12 μ, L. difficult to measure, forming polygonal prisms with rounded ribs. Sculpturing on wall in the first few exclusively spirals

3—4, sometimes up to 6, very close together, in section circular with narrowed foot, about 1 μ thick or a little more; interspaces small about 1 μ, wall here thin; in the last few tracheids, spirals with occasional reticulate ramifications.

Pits. In the latter elements, also in those exclusively with spiral sculpturing, *between the tracheids mutually*, bordered pits, mostly in long non touching rows, hence border circular about 7 μ, pore likewise nearly circular about 2 μ.

Between *tracheids* and *medullary ray cells* unilateral bordered pits, invariably in large groups together on the bordering planes. Border not being horizontally oblong as in other species, but circular or angular in shape and the position of the pits as in the mature wood namely, often opposed, but occasionally alternate, horizontally or vertically; the latter case especially in very high cells; pits also often touching and flattening one another (hence the angular shape of the border). Pore generally circular and large, sometimes slit-like and sinistrorse as in the adult wood. Dimensions border R.-.L 6—8 μ, pore 3—5 μ.

Medullary ray cells. Exclusively upright cells, not numerous, rather irregular in shape, for the rest entirely as described in the secondary xylem (see p. 550).

9. Araucaria species.

Buitenzorg, numbered 10576.

Material collected during an expedition through New Guinea, made by Prof. Docters van Leeuwen. According to the latter it was collected in a wood at a height of about 1000 m., with Araucaria's up to 40 m. high. The material contained:

1. A part of the stem of a very old tree.
2. A disk of a side-branch.
3. A thin branch with a female cone.

Description Secondary xylem, made after preparations, both of the part of the stem and of the side-branch.

Topography. Growth rings macroscopically distinct, microscopically no marked boundary-line, formed by several thick-walled layers gradually passing into thin-walled ones. In the older stem the thick-walled range consisting of no more than 2—3 rows. In the disk of the side-branch a strong growth of redwood, darker in shade than the ordinary wood, in tangential and radial inward direction gradually passing into ordinary wood, in radial outward direction with well marked boundaries.

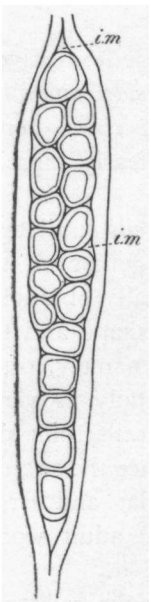

Fig. 46. Araucaria species. Tangential section of a medullary ray, for the greater part two cells broad; *i.m.*, intercellular spaces. × 260.

Fibre-tracheids the bulk of the wood, woodparenchyma absent, a very good radial arrangement generally. Medullary rays not numerous 10—40 per sq. mm., mostly uniseriate, sometimes locally biseriate, and than both cells together practically of the same breadth as the cell above and below, rarely the medullary ray biseriate over a greater distance and the cells not opposed as in the former case (fig. 46), generally rather deep 1—18, seldom more, up to 38 cells. [1])

No tracheidal ray cells normally, only in the neighbourhood of a penetrating leaf-trace, there rather numerous and up to a distance of 3 mm (fig. 11—12).

Upper and lower boundaries only irregular within the primary xylem, due to the presence of upright cells.

[1]) Various transitions lying in between were observed, for instance; 23—29—32—35 etc.

Elements. I. Fibre-tracheids R. 35—65 μ, at the transition of two periods mostly about 35 μ, T. 35—50 μ, seldom narrower down to 25 μ, L. strongly varying, from

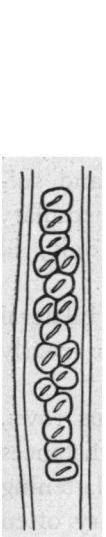

Fig. 47.

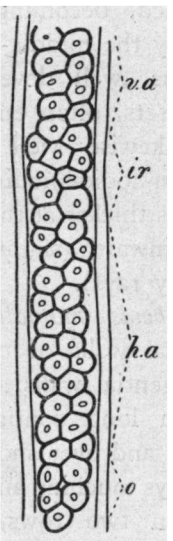

Fig. 48.

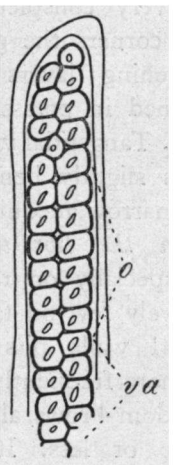

Fig. 49.

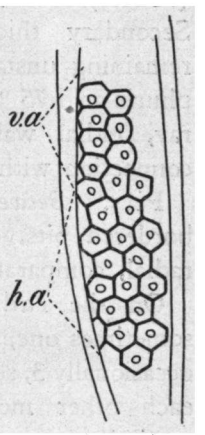

Fig. 50.

Fig. 47. Araucaria species. Radial wall of a fibre-tracheid, seen from without, showing bordered pits, horizontally alternate. × 260.

Fig. 48. Araucaria species. Radial wall of a fibre-tracheid, showing bordered pits; *o*, opposed; *h.a.*, horizontally alternate; *ir.* irregular; *v.a.*, vertically alternate. × 260.

Fig. 49. Araucaria species. Radial wall of a fibre-tracheid, seen from without, showing bordered pits; *o*, opposed; *v.a.*, vertically alternate. × 260.

Fig. 50. Araucaria species. Radial wall of a fibre-tracheid, seen from within, showing bordered pits; *v.a.*, vertically alternate; *h.a*, horizontally alternate. × 260.

very long to very short, 13000 μ—1500 μ, [1]) generally forming tetra- to hexagonal prisms, with a lumen of some-

[1]) Here too various transitions in between for instance: 11650, 10500, 8600, 7300, 5850, 4000, 3050, 2180, 1500.

what cylindrical shape. Walls R. 7—10 μ, in the thick-walled range up to about 12 μ, especially at the corners, the latter even up to about 15 μ, T. 7—10 μ in the above-mentioned parts as well, lignified, becoming yellow in hydrochloride of aniline, especially the middle-lamella, the latter therefore very conspicuous ,well developed, 2 μ (double), at the corners the gussets, often entirely solid. Secondary thickening layers likewise well developed, remaining unstained in potassium iodide iodine and sulphuric acid 75 %. Tangential walls thicker at the medullary ray, radial walls slightly bent inward (slightly only, in connection with narrow medullary rays).

Pits. *Between the fibre-tracheids mutually* bilateral bordered pits, especially on radial walls or those nearly radial, comparatively few on tangential walls.

On the radial walls pits in long contiguous rows, sometimes one, more frequently 2 and over short distances occasionally 3, seldom 4 rows, always touching and flattening each other more or less. If in two rows, very often vertically alternate (normal position) fig. 48. Deviation from this numerous, namely: *a.* horizontally alternate and then often in the following order 1—2 — 1—2 etc. (fig. 47), but sometimes zigzag two above each other (fig. 48).

b. entirely or nearly opposed (fig. 49).

In the first mentioned cases the pits somewhat hexagonal, in the last-mentioned case more or less tetragonal in shape. If in three rows, mostly vertically alternate, but the same deviation as described for 2 rows present (fig. 50) [1]) Pore often nearly circular, sometimes slit-like and then sinistrorse, this especially in the thick-walled layers and still more so in the redwood.

Distribution of pits: Pits chiefly in a mass at the outer

[1]) A case, where all 3 rows are opposed was not observed, cases of two opposed rows and the third alternate fairly frequent.

ends of the fibre-tracheids, therefore the middle part with considerable vacant pieces. Likewise pits scarce in the thick-walled layers, often separate pits here. Sometimes

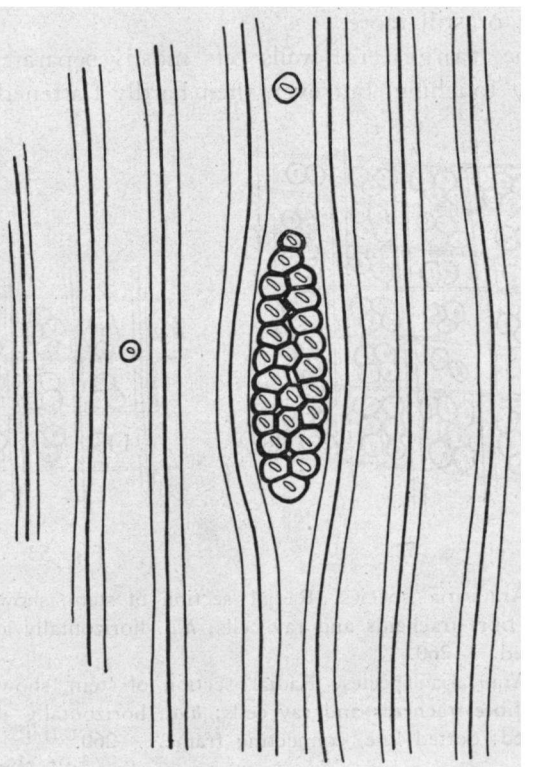

Fig. 51. Araucaria species. Radial section of stem, showing a cluster of pits, and two separate pits. Pits seen from the inside of the fibre-tracheid.

in a part, nearly without pits, widened pieces in the fibre-tracheids, crowded with pits (fig. 51).

Structure of the pits entirely the same as described at the beginning of this work p. 489. Dimensions: Border R. mostly 11—17 μ, L. 12—16 μ, seldom still more flattened,

R. up to 20 μ, L. about 10 μ, in the thick-walled part pits smaller, R.-T. about 10 μ. Pore generally normal slit-like, length 6—7 μ, width 3—4 μ, less often practically circular, about 4 μ, or strongly slit-like width about 1 μ, length 12—14 μ or still more.

On the tangential walls pits mostly separate, sometimes just touching, but even then hardly flattened or not

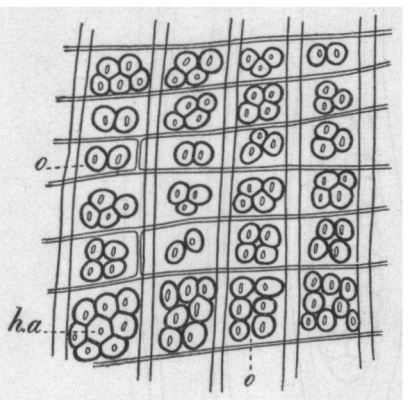

Fig. 52.

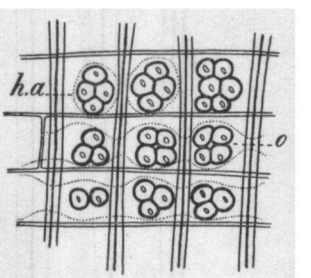

Fig 53.

Fig. 52. Araucaria species. Radial section of stem, showing pits between fibre-tracheids and ray cells; *h.a.* horizontally alternate; *o*, opposed. × 260.

Fig. 53. Araucaria species. Radial section of stem, showing pits between fibre-tracheids and ray cells; *h.a.*, horizontally alternate; *o*, opposed; dotted line, connecting frame. × 260.

at all. Border circular L.-T. 10—14 μ. Pore small circular to oval length 3—4 μ, width 1—2 μ.

Rims of Sanio absent.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, always in groups together on the rhomboid bordering plane. Often in 2 or 3 rows sometimes more, seldom 1, mostly touching and somewhat flattening each other; the rows opposed or horizontally alternate (fig. 52

and 53), rarely entirely irregular and not touching each other. Border nearly circular L.-R. 8—10 μ, pore slit-like, sinistrorse, often nearly vertical, length about 6 μ, width 1—2 μ.

Contents of fibres slight, no starch or resin observed.

Intercellular spaces not numerous, neither at the corners, nor between the tangential walls, due to divergence. If present at all, both in the vicinity of the medullary rays.

II. Medullary ray cells.

1. Procumbent cells R. 90—120 μ, T. 16—28 μ, at the tangential separating walls often shorter than in the middle of a cell for instance: 10—30—10 etc., forming practically circular cylinders, with radially directed axis. Walls rather thin about 2 μ (double), but fairly firm, distinctly lignified (becoming yellow in hydrochloride of aniline), cellulose-content slight (remaining unstained in potassium iodide iodine and sulphuric acid 75 %), pectin-substances very profuse (colouring red in ruthenium red), having no pits, neither mutually, nor on the side of the fibres (see further the fibres p. 556).

Contents: sometimes a fair amount of starch, seldom a little resin.

Intercellular spaces between medullary ray cells and fibre-tracheids well developed, both in radial and in longitudinal direction, due to this often distinct connecting-frames on the radial walls of the ray cells.

2. Upright cells, little developed, only in the primary xylem, sometimes just reaching into the secondary xylem, R. 40—60 μ, T. not measured, L. 40—60 μ, rather regular in shape, mostly four-sided prisms, of which L. and R. practically alike. Walls, contents and pits like those of the procumbent cells, (see further the primary xylem p. 560).

3. Tracheidal medullary ray cells. Scattered among the procumbent cells and usually adjoining them in a normal way (fig. 54). R. 70—180 μ, T. 15—30 μ, L. 9—25 μ,

generally forming circular cylinders with radially directed axis, sometimes irregular in shape. Wall thick 4—8 μ,

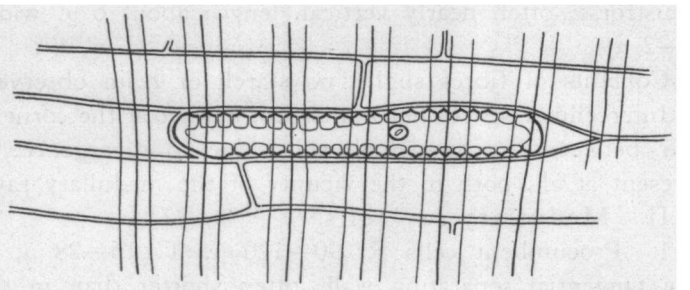

Fig. 54. Araucaria species. Radial section of a medullary ray, with a tracheidal ray cell. × 260.

strongly lignified with numerous unilateral bordered pits on the side of the other medullary ray cells, border about

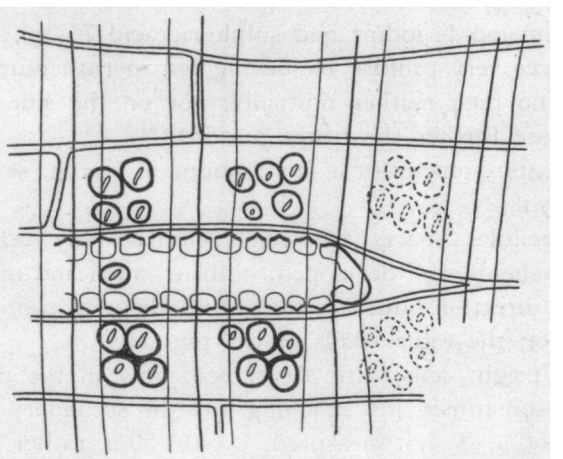

Fig. 55. Araucaria species. Showing a part of fig. 54 more magnified. × 420.

7 μ, pore about 1 μ, and few bilateral bordered pits on the side of the fibre-tracheids, border 6—7 μ, pore length about 7 μ, width about 1 μ. (fig. 55).

Primary xylem, description after preparations of the branch bearing the female cone (see p. 551).

Topography. Primary xylem in a practically closed tube round the medulla, with wide, little protruding poles. Between them medullary commissures and these, near the beginning of the secondary xylem only, passing into uniseriate medullary rays. The whole range of primary xylem rather extensive 100—120 μ. Number of elements 8—12. Medulla rather large 1000—1400 μ, entire branch about 4 mm. From the centre outward: some flattened elements (comparatively few); 3—4 tracheids with irregularly stretched spiral sculpturing, in the last few tracheids less so than in the first few; some tracheids with spiral sculpturing, the spirals very closely together, in the last few with occasional reticulate ramifications.

Elements. Protoxylem; spiral-tracheids R.-T. 7—10 μ, L. difficult to measure, forming circular elliptical cylinders. Sculpturing on wall 2—3 spirals, irregularly stretched and not entirely uninterrupted. Spirals 1 to 2 μ thick, generally angularly circular in section. Interstices irregularly large, walls in them thin.

Metaxylem: tracheids R.-T. 10—16 μ, getting wider from the centre outward, L. difficult to measure, mostly forming polygonal prisms with rounded ribs. Sculpturing on wall in the first few exclusively 2—6 spirals, regularly continued. Spirals 1—2 μ thick, in section circular with narrowed foot. Interspaces small about 1 μ, wall in these spaces thin. In the last few tracheids, the spirals with occasional reticulate ramifications.

Pits. In the *last spiral-* and *reticulate tracheids* between the tracheids mutually *bordered pits,* generally in 1—2, sometimes 3 long rows, not touching each other, consequently border practically circular. If in 2 or 3 rows, pits alternate or opposed. Border large 5—7 μ, largest in the outermost tracheids of the primary xylem. Pore circular 1—2 μ, also largest in the outermost tracheids.

Between *tracheids* and *medullary ray cells* unilateral bordered pits, not numerous (in connection with a slight number of medullary ray cells) mostly in 2 rows, often opposed. Border somewhat horizontally elliptical, pit-canal in proportion to other species rather narrowed, consequently pore fairly distinct, likewise horizontally elliptical.

Medullary ray cells. Exclusively upright cells, fairly regular in shape, of the same dimension as already described for the secondary xylem (see p. 557).

10. Taxonomic result of the anatomy of the wood of the Araucaria genus.

The structure of the various species is very similar. They might be divided into two groups according to the medullary rays. These groups are largely but not entirely the same as those of the two sections which have been made in the ground of morphological features:

Group I.	Group II
Araucaria angustifolia	Araucaria araucana
„ Cunninghamii	„ Bidwillii
„ excelsa	„ Cookii
„ Rulei	„ species

Group II is distinguished from group I by the often locally biseriate medullary rays. In group I they are exclusively uniseriate. The following table might be drawn up:

1. Medullary rays one cell broad, but sometimes locally two cells in breadth 2
   Medullary rays exclusively one cell broad 3
2. Medullary rays very numerous
   (juvenile wood 80—140 per sq. mm., adult wood 30—80 usually 60—70 per sq. mm).
   Araucaria araucana
   Medullary rays less numerous
   (juvenile wood 50—80 per sq. mm., adult wood 10—60 usually 30—40 per sq. mm.).

Araucaria Bidwillii
„ Cookii

For the distinction between these two species see the detailed descriptions.

3. Walls fairly thick 5—15 μ, shape of the fibre-tracheid prismatic 4
Walls thinner 4—6 μ, fibre-tracheid more or less cylindershaped.
Araucaria Cunninghamii
„ Rulei

4. A dusky-coloured resin throughout the wood [1]), often scattered thick-walled medullary ray cells.
Araucaria angustifolia.
No resin, no thick-walled medullary ray cells.
Araucaria excelsa.

CHAPTER III.

DESCRIPTIONS OF THE WOOD OF THE DAMMARA GENUS.

1. Introductory remarks.

A description of the Dammara genus as a whole has not been given, owing to lack of material. With the exception of Dammara alba, of which species I had ample material to work on, I only had a three-to four year-old branch of Dammara (Agathis) australis at my disposal. If the number of species for a comparison was already slight, a still greater difficulty was in the way here, owing to the nature of the material. While investigating the wood of the various species, it appeared again and again that the best material

[1]) The presence of resin may generally not be alleged as a characteristic, because in one and the same tree, it is locally very abudant in other parts entirely absent. An exception might perhaps be made for Araucaria angustifolia, the entire wood of which contains a dusky coloured resin.

for investigation was provided by the strongly developed stems.

If therefore, in a possible comparison of the two species of Dammara alba and Dammara australis, I should have struck on minor differences, as for instance a smaller number of rows of pits or better developed growth rings, the latter would sooner have been due to a difference between wood of a juvenile branch and that of an older stem.

This might of course have been avoided, if juvenile material of Dammara alba had likewise been examined and used for purposes of comparison. As, however, in this description it was my intention to give a picture of the Dammara genus, it would little answer its purpose, based, as it was, upon juvenile material only. For this reason, it seemed better to me not to insert them here as such. The description of Dammara alba can better be used for this purpose, since it was drawn up on the basis of material of various kinds.

2. **Dammara alba** Lam. 1786.
(Agathis alba (Lam.) Foxworthy).

Material. Several disks, both of the stem and the root of a large tree grown in the garden of the Palace at Buitenzorg. Total length of the stem 40 m., in circumference at the foot 6 m. The material consists of:

1 a disk of the stem 5 m. above the ground about 80 cm in diameter;
2 „ „ „ „ „ 15.10 „ „ „ „ „ 50 „ „ „ ;
3 „ „ „ „ „ 1.30 „ below the top „ 3.7 „ „ „ ;
4 „ „ „ „ root 1.18 „ from the stem grown excentrically about 30 cm. in diameter;
5 „ „ „ „ „ 2.95 „ „ „ „ developed normally;
6 „ „ „ „ „ 4.25 „ „ „ „ about 6 cm. in diameter;
7 „ „ „ „ „ 5.25 „ „ „ „ ;
8 a disk of a thin side-root, about 1 cm. in diameter;
9 a branch bearing leaves.

There was some additional material under the name of

Agathis alba likewise from Buitenzorg; namely some disks of stems of a young tree together with a few disks of roots of the same tree.

A. Stem.

The following descriptions were made after preparations of the first series, with which those of the latter were compared. As no differences could be noticed, these were not described separately.

Description secondary xylem. Chiefly made after preparations of the disk of the stem at 15.10 m. above the ground, with which the first and the third were compared.

Topography. Growth rings macroscopically clear, rather irregular, now closer together, now wider apart, from 1½—2½ mm., sometimes to 7 mm. from one another. Microscopically likewise with clearly marked boundaries, formed by 2 or 3 rows of narrow fibre-tracheids with much thickened walls (8—10 μ), for instance the succeeding fibres in radial direction from within outward: 45—*35*—*25*—*50*—47 or 45—*37*—*25*—*55*—45 in diameter.

Fibre-tracheids the bulk of the wood. Woodparenchyma scattered through the wood, comparatively rare, if present, sometimes separate, but often 2 elements in succession in radial direction. Woodparenchyma comparatively rare in the disk of 15.10 m. above the ground; more frequent in the older stem and then especially at the transition of two periods, but in other places as well.

Medullary rays numerous 10—50 per sq. mm., generally one cell broad, sometimes locally two cells broad and those cells together of the same breadth as one above-lying cell, seldom somewhat irregular, 4—20 cells deep, rarely less, separated by 1—7 rows of tracheids. Tracheidal ray cells absent. Upper and lower boundaries generally straight, except of those, being one or two cells in depth (fig. 56 and 57), just like those in the neighbourhood of

and within the primary xylem; the latter case due to the increasing depth of the medullary rays.

Elements. I. Fibre-tracheids R. 25—55 μ, at the transition of 2 periods narrower 15—30 μ (see also topo-

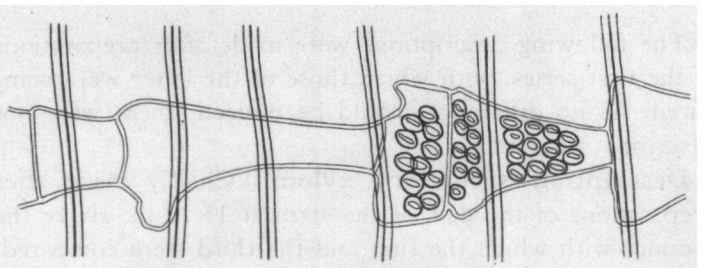

Fig. 56. Dammara alba. Radial section of a medullary ray, one cell in depth, bounded irregularly above and below. × 195.

graphy), T. 25—65 μ, L. 4400—4800; forming tetra-to hexagonal prisms, sometimes rather circular to elliptical cylinders, especially the lumen cylinder-shaped. Outer ends pointed, unless touching upon a medullary ray or other fibre-tracheid, in that case more or less straight. Radial arrangement often disturbed, especially in the beginning

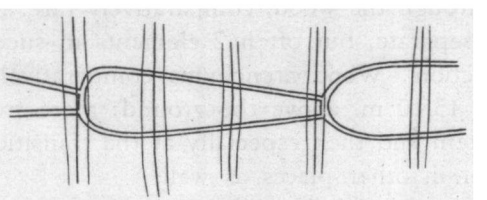

Fig. 57. Dammara alba. Radial section of a medullary ray, one cell in depth, bounded irregularly. × 195.

of a new period. Walls of the fibre-tracheids radially 2—5 μ, tangentially 2—7 μ, especially at the corners often thicker. Tangential walls perceptibly thicker at a medullary ray, namely 6—10 μ, again the corners especially. Wall of the

2 or 3 rows of fibre-tracheids at the boundary of 2 periods thicker, R. 5—10 μ, T. generally about 5 μ, sometimes up to 8 μ (the radial walls especially increase in thickness).

Wall lignified, colouring yellow in hydrochloride of aniline, middle-lamella colouring more intensely and therefore clearly visible, moderately developed 1—2 μ (double). The gussets not large and not always solid. Secondary thickening layers little developed, often becoming somewhat blue in potassium iodide iodine and sulphuric acid 75 %. Tertiary layers discernible, sometimes clearly, owing to their greater clarity and their more intensely colouring in hydrochloride of aniline just like the middle-lamella. At a medullary ray the radial walls slightly bent inward, therefore the medullary ray nearly enclosed, except above and below, consequently the entire aspect less striking than in Araucaria (fig. 58) [1])

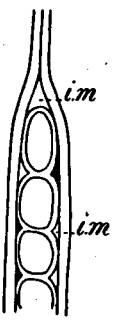

Fig. 58. Dammara alba. Medullary ray in tangential section; *i.m.*, intercellular spaces. × 260.

Pits. Between the *fibre-tracheids mutually* bordered pits especially on the radial walls in very large quantities, but also on the tangential walls in great masses.

On the radial walls pits in long contiguous rows, one, two, three or sometimes still more. If in one row, being rare, pits touching and flattening each other more or less, therefore in the former case the border oval, in the latter case nearly circular. If in two rows, pits mostly vertically alternate, therefore border somewhat hexagonal in shape. Deviations fairly often, for instance, pits horizontally alternate or sometimes opposed. In the latter case border more

[1]) In Araucaria medullary rays usually inflated and adjoining fibre-tracheids below and above directly closed.

or less tetragonal in shape. If in three rows, then too, three vertical alternate rows frequently, although here too seldom entirely regular for any long distance. For instance: often two rows opposed, the third alternating with them; in other respects too frequent irregularities, for instance where three rows temporarily pass into two or the reverse case.

The pits more numerous at the outer ends of the fibre-tracheids, but also on other places in great numbers. The structure of the pits in principle as described for the "araucarioid pitting" at the beginning of this work (see p. 489).

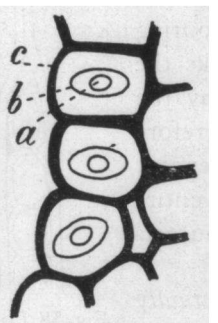

Fig. 59.

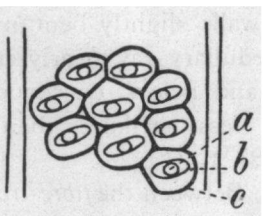

Fig. 60.

Fig. 59. Dammara alba. Pits on a radial wall of fibre-tracheid; *a*, outer aperture; *b*, inner aperture; *c*, pectic annulus. × 630.
Fig. 60. Dammara alba. Pits on a radial wall of fibre-tracheid; *a*, outer aperture; *b*, inner aperture; *c*, pectic annulus. × 390.

Inner and outer aperture of the pit-canal, however, in a characteristie way, generally of unequal sizes. Hence from without inward in front-view on the pits (see fig. 59—60):

1. The pectic annulus, bounding the border (59 *c*).
2. Within the pectic annulus a fainter contour, often oval in shape (59 *b*), the inner aperture of the pit-canal.
3. A clear, very striking spot, mostly circular, sometimes oval or slit-like (59 *a*), the outer aperture of the pit-canal,

consequently smaller than the inner aperture and often more circular in shape besides.

In transverse sections of the pits too the corresponding places easily to be observed (fig. 61 *a, b, c*).

In tangential sections inner- and outer aperture often of equal dimensions (fig. 62 *a, b, c*), entirely agreeing with the fact that the inner aperture is much oftener oval in shape in front-view than the outer aperture [1]) (compare fig. 59). Dimensions border in diameter L. 10—14 μ,

[1]) In order to bring out still more clearly that the places, to be observed in transverse sections of the pits, correspond with those in front-view, some measurements were taken, both in transverse and radial sections (showing pits in front-view), which are represented by the following tables:

Transverse sections			Radial and measured in radial direction		
Border	Inner aperture	Outer aperture	Border	Inner aperture	Outer aperture
15	10	4	14	10	5
15	10	3	16	10	5
11	7	2	17	7	5
13	5	3	12	6	3
12	7	3	10	7	3
10	7	2	12	8	4
11	7	2	13	8	4
10	4	2	13	6	3
10	5	2	12	6	3
12	6	3	14	8	5
11.9	6.8	2.6	13.3	7.6	4.0

If these tables are compared, the average dimensions of border inner and outer aperture correspond fairly well. The dimensions in transverse sections are of course smaller, as it will be an exception if border and pore are cut along the diameter and a measure will generally be obtained smaller than the largest section, which is measured in radial sections. Besides it is evident that this deviation will be considerably greater for the smaller outer aperture than for the border and inner aperture. We find that the deviation for the former (outer aperture) is about 25 % and for the two latter (inner aperture and border) is about 10 % each.

R. 10—14 μ, seldom a little broader, up to 17 μ, for instance the outermost pits of a group. Pore generally circular about 4 μ, or sometimes slit-like and then sinistrorse (at the boundaries of 2 periods), length 6—8 μ, width 1—3 μ.

In most cases a torus hardly to be observed, the closing membrane being generally equably thickened, clearly discernible in tangential sections after treatment with ruthenium red.

Fig. 61. Dammara alba. Pits in transverse section; *a*, outer aperture; *b*, inner aperture; *c*, pectic annulus. × 630.

On the tangential walls too, the pits often in one or two long rows, frequently forming crooked lines, the pits often hardly touching or not at all and therefore retaining their circular shape, seldom flattening each other, and then consequently of a more radial type. Sometimes the pits in smaller groups or even entirely separate. Inner and outer aperture of the pit-canal nearly the same dimensions here. Dimensions: border in diameter L. 9—12 μ, T. 8—10 μ (so often more long than broad). Pore small, mostly circular about 2 μ, or slightly slit-like and then sinistrorse length 2—4 μ, width about 1.5 μ

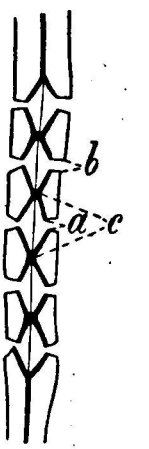

Fig. 62. Dammara alba. Pits in tangential section; *a*, outer aperture; *b*, inner aperture; *c*, pectic annulus. × 630.

Rims of Sanio absent.

Between *medullary ray cells* and *fibre-tracheids* unilateral bordered pits, generally in groups togehter on the rhomboid bordering plane between medullary ray cells and fibre-tracheids, generally in 2 or 3 vertical rows, seldom

1 or 4, mostly opposed, sometimes more or less alternate or fairly irregular (fig. 63). Within the more adult wood, often on each bordering plane only 1 horizontal row of 1—3 or more pits (fig.64), or sometimes entirely wanting on an occasional bordering plane. Border in diameter 8—10 μ, pore often slit-like and sinistrorse, length 5—6 μ width 2—3 μ. In the late wood more slit-like, length 7—10 μ, width about 1 μ. In the first fibre-tracheids of a new period (1—3 rows of fibre-

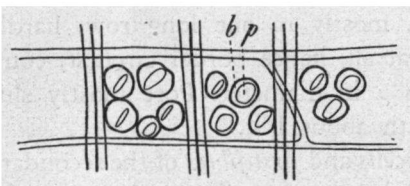

Fig. 63. Dammara alba. Radial section of stem, showing unilateral bordered pits between fibre-tracheids and ray cells; *b*, border; *p*, pore. × 260.

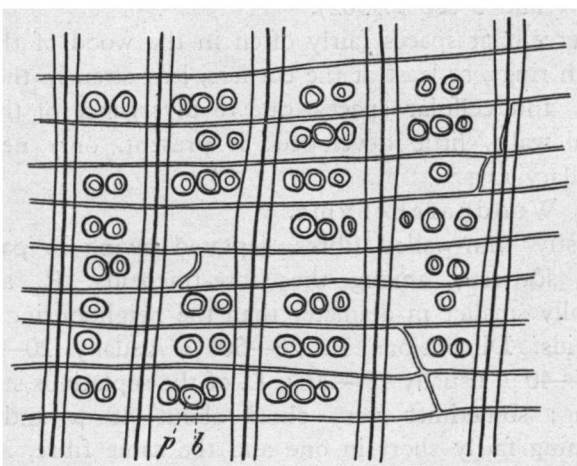

Fig. 64. Dammara alba. Radial section of stem, showing unilateral bordered pits between fibre-tracheids and ray cells; *b*, border; *p*, pore. × 260.

tracheids, sometimes more), the pit-canal little narrowed, therefore pore very wide, sometimes even nearly taking up

the entire border and in some places coinciding with it (see fig. 62 *b, p* and 63 *b, p*).

Between *fibre-tracheids* and *woodparenchyma* likewise unilateral bordered pits, mostly in one long row, hardly touching or usually not at all, hence border circular, comparatively small about 8 μ in diameter. Pore mostly slit-like, length 7—8 μ, width about 1 μ.

Between *medullary ray cells* and *first fibres* of the secondary xylem unilateral bordered pits, entirely of the same structure as in the same place within the primary xylem and described there (see p. 576 and fig. 69).

Contents of the fibre-tracheids only in the wood of 15.10 m. above the ground a great deal of resin, especially in the neighbourhood of the medullary rays. Both in the juvenile and in the more mature wood no contents observed (no's 1 and 3 see p. 562).

Intercellular spaces fairly often in the wood of the first growth rings, at least at the corners, less often in the adult wood. Intercellular spaces, due to divergence of the tangential walls, little developed; if present, only near the medullary rays.

II. Woodparenchyma.

Mostly thin-walled fibres, septated owing to partition walls, scattered among the fibre-tracheids. R. and T. generally smaller in diameter than the neighbouring fibre-tracheids. Dimensions R. 20—50 μ, usually 20—25 μ, T. 15—40 μ, usually 15—20 μ, L. of the septations strongly varying; sometimes very short about 40 μ and then remaining fairly short in one and the same fibre, namely 30—80 μ; sometimes much longer, namely up to 310 μ. Walls thin about 1—2 μ, little lignified, containing many pectin substances (becoming red in ruthenium red), having no pits, neither between the septations mutually nor on the side of the fibre-tracheids (see further above). Sometimes thyloses-like formations observed, always at

the transitions between two periods, probably originating from the medullary rays [1]). Cells of these formations irregular in shape R. 40—100 μ, T. 40—50 μ, L. 25 μ—100 μ, walls mostly thin, about 4 μ (double), little lignified and pits entirely wanting then, sometimes thick 5—28 μ, often stratified, and more lignified, becoming yellow in hydrochloride of aniline and then with numerous simple pits, both on the mutual walls and on the side of the fibre-tracheids. These pits of peculiar structure, namely pit-canals outwardly ending infundibularly, therefore apparently giving the impression of bordered pits [2]); at the same time pit-canal often ramified from within outward. Between two thick-walled septations the pits mostly corresponding; between the woodparenchyma-fibre and adjacent fibre-tracheid no-co-operation, neither on the side of the woodparenchyma, nor on the side of the fibre-tracheid (fig. 65*a* and 65*b*); sometimes the pits of the woodparenchyma corresponding with intercellular spaces.

III. Medullary ray cells.

1. Procumbent cells R. 120—200 μ, in the juvenile wood occasionally smaller 60—200 μ, T. 12—25 μ, L. 25—40 μ, especially the marginal cells of a medullary ray

[1]) They gave the impressions of abnormal formations, perhaps in consequence of injury, although irregularities in the radial arrangement were for the rest not observed.

[2]) Also when viewed from above the double contour of these pits are reminiscent of bordered pits. It appears from the following, however, that they are not bordered pits.

1. All sorts of transitions to the ordinary shape are met with.

2. The middle-lamella runs on uninterruptedly, especially clear where two pits are corresponding in succeeding septations, so there is no closing-membrane.

3. The apparently formed border is not covered by the primary border membrane, as in the real bordered pits.

The bordered pit-like shape is therefore of a later date, probably because the secondary thickening layers of younger origin invariably left an opening getting narrower and narrower.

higher (30—40 μ). Walls thin 1 to 2 μ (double), somewhat lignified, becoming yellow in hydrochloride of aniline, although less intensely than the surrounding fibres; in potassium iodide iodine and sulphuric acid 75 % colouring slightly blue here and there, but yet a small cellulose-

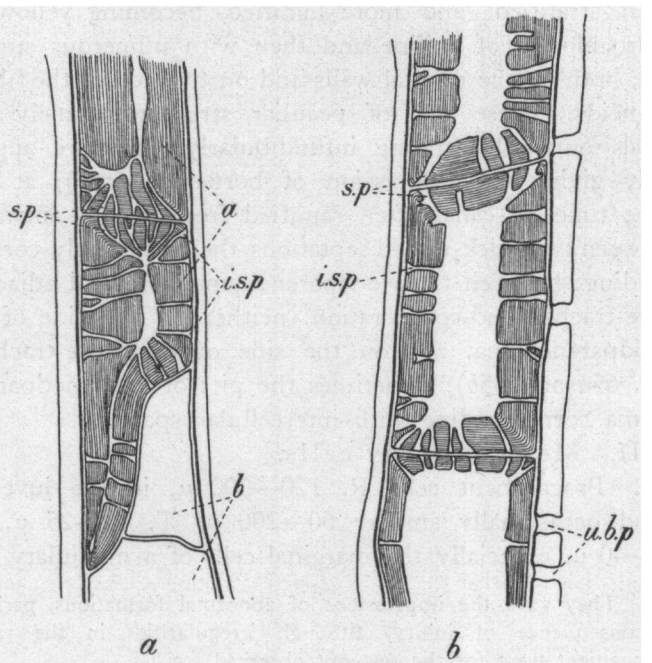

Fig. 65. Dammara alba. Woodparenchyma fibres; *a*, thick-walled septation; *b*, thin-walled septation; *i.s.p.*, infundibularly simple pits; *s.p.* ramified simple pits between the septation mutually; *u.b.p.*, unilateral bordered pits in the adjacent fibre-tracheid. × 260.

content; rich in pectin substances, colouring deeply red in ruthenium red, no pits, neither on the side of the fibre-tracheids, nor mutually (see further the fibre p. 568).

Contents. The cells rich in protoplasm with distinct nuclei (the latter especially conspicuous after being treated

with ruthenium red); in the juvenile wood (No. 1 see p. 562) likewise some starch here and there, sometimes a little resin as well, but both sporadically; in the wood of 15.10 m. above the ground resin exclusively, in great masses, in the still older stem (5 m. above the ground) starch only, likewise in large quantities [1]).

Intercellular spaces between medullary ray cells and fibre-tracheids generally fairly well developed, especially below and above a medullary ray, (fig. 56), sometimes intercellular spaces between the cells mutually.

2. Upright cells. Only in the neighbourhood of and within the primary xylem, mostly irregular in shape R 15—40 μ, L 40—120 μ (fig. 69). Wall and contents the same as in the procumbent cells, just like these, without pits (see for this: the tracheid of the primary xylem, p. 575).

Primary xylem after preparations of a one-year-old branch likewise from Buitenzorg.

Topography. Primary xylem in a tube round the medulla with protruding poles, between them the medullary commissures from within outward merging into uniseriate medullary rays. The entire range of primary xylem not large, 90—100 μ (about 7—8 elements). Medulla fairly large 1000—1100 μ. Entire branch about 2.5 mm.

From within outward: crushed elements, not numerous; a few elements with very strongly stretched spirals; tracheids with spiral sculpturing, the spirals of which very close together and presently with a few reticulate ramifications; finally distinct reticulate tracheids adjoining the secondary xylem.

[1]) Something of the kind was observed in Ar. Bidwillii p. 518, where in different places, different substances were observed, namely, resin and starch (resin in the older stem 8 m. above the ground and starch in the wood of 16 m. above the ground).

Elements. Protoxylem spiraltracheids R. 10—14 μ, T 10—14 μ, but both dimensions sometimes irregularly, owing to the shape of the elements, forming irregularly round cylinders, L. difficult to measure. Sculpturing on wall two, more or less stretched spirals. In the case of the innermost ones very irregular, sometimes even entirely

Fig. 66.

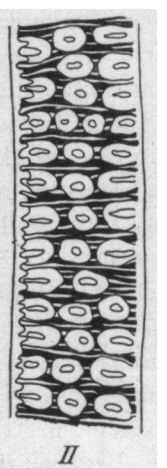

Fig. 67.

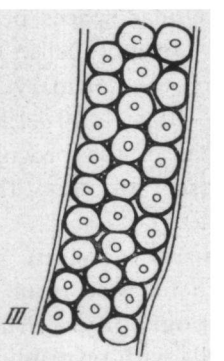

Fig. 68.

Fig. 66. Dammara alba. The last tracheid but one of the primary xylem, sculpturing on wall chiefly spirals with bordered pits; interspaces blank. × 500.

Fig. 67. Dammara alba. Last tracheid of the primary xylem, sculpturing on wall chiefly spirals with bordered pits; interspaces blank. × 500.

Fig. 68. Dammara alba. First tracheid of the secondary xylem. × 500.

broken off. Spirals very thick 3—4 μ. Interspaces large, walls in them very thin.

Metaxylem. Tracheids R.—T. 12—34 μ, from within outward strongly increasing in breadth, for instance: 12—15—20—27—34 μ or 12—15—15—22 μ, 12—22—22—30 μ etc., length diffcult to measure, forming practically

circular cylinders, sometimes slightly irregular. Sculpturing on wall in the innermost ones for the greater part spirals with only few reticulate ramifications. Number of spirals difficult to state, probably only one. Spirals sometimes thin 0.5—1 μ, especially in the outermost, sometimes

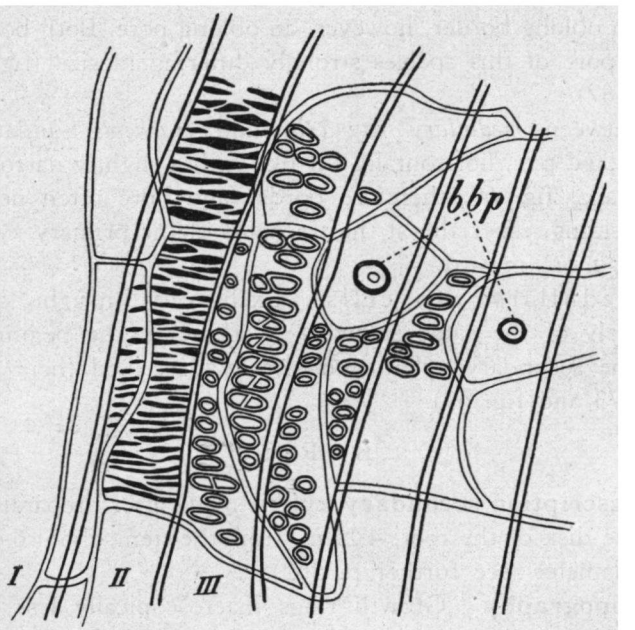

Fig. 69. Dammara alba. The same tracheids as in fig. 66, 67 and 68, adjoining a medullary ray; *b b p.*, bilateral bordered pits, between two adjacent fibre-tracheids mutually; all the others unilateral bordered pits between fibre-tracheids and medullary ray cells; interspaces dark. × 420.

much thicker up to about 4 μ. Interspaces very small about ½ μ, section of the spirals generally with narrowed foot.

Pits. Between the *tracheids mutually* real bordered pits especially in the reticulate tracheids, sometimes standing

in one row, but often in 2 or 3, in the two latter cases as a rule opposed or horizontally alternate, less often vertically alternate fig. 66, 67, 68. Border usually circular about 6—8 μ in diameter, sometimes border much larger and then horizontally oblong in shape.

Pore likewise mostly circular, about 2 μ in diameter, in an oblong border, however, an oblong pore. Both border and pore of this species strongly differing in size (fig. 66 and 67).

Between *medullary ray cells* and *tracheids*, unilateral bordered pits, horizontally slit-like with a slightly narrowed pit-canal fig. 69, therefore border and pore often nearly coinciding, especially at the tracheids of the primary xylem lying more inward.

Medullary ray cells. Exclusively upright cells, entirely of the same structure as those in the beginning of the secondary xylem and already described there (see p. 573 and fig. 69).

B. Root.

Description secondary xylem made after preparations of the disk of the root, 4.25 m. from the stem, about 6 c.m. in diameter (see further p. 562).

Topography. Growth rings macroscopically less distinct than in the stem, in so far as observable rather irregular and fairly close together. Microscopically formed by 1—3 rows of less broad fibre-tracheids, difference in thickness of wall slight, therefore the boundaries also microscopically less clear than in the stem.

The bulk of the wood fibre-tracheids, woodparenchyma fibres fairly frequent scattered among the fibre-tracheids. Medullary rays fairly numerous 20—50 per square m., seldom 10, usually one cell broad, rarely locally 2, 1—13 cells deep, often 1—4, usually separated by 1—8 rows of tracheids. Tracheidal ray cells entirely wanting;

upper and lower boundaries often practically straight or somewhat waved owing to the peculiarly shaped walls of the medullary ray cells (fig. 72*a* and *b*), sometimes entirely irregular in consequence of the presence of upright cells (fig. 76).

Elements. I. Fibre-tracheids. R. usually 60—100 μ, less often narrower 40—50 μ, at the end of a period still narrower 20—40 μ. T. mostly smaller R. 20—50 μ, usually 35—45 μ, L. 3000—8900 μ, forming tetra- to hexagonal prisms, sometimes more or less circular to elliptical cylinders. Walls rather thin 2—3 μ, seldom up to 5 μ. R. and T. practically the same, at most thicker at the corners. At the transition between two periods likewise somewhat thicker 3—4 μ, generally the corners larger. Wall lignified, becoming yellow in hydrochloride of aniline. Middle-lamella colouring slightly more intensely than the rest and therefore less clearly marked against the secondary thickening layers, not strongly developed, about 1 μ (double). Gussets little developed, if present often not solid. Secondary thickening layers not much developed either, becoming slightly blue in potassium iodide iodine and sulphuric acid 75 %. Tertiary thickening layers mostly little developed or not at all. At a medullary ray the tangential walls usually hardly any thicker. Radial wall at a medullary ray only slightly bent inward (narrow medullary ray and tracheids below and above not directly closed).

Intercellular spaces fairly numerous both at the corners and between the tangential walls owing to diverging of those walls, both kinds especially near the medullary rays.

Pits. Between the *fibre-tracheids mutually* bordered pits especially on the radial walls but also on the tangential ones in great numbers.

On the radial walls, pits very crowded and chiefly at the outer ends, therefore the middle part with considerable vacant pieces. In the former parts pits in long contiguous

rows, seldom 1 or 2, usually 3 or more (4—5). If in one row, the pits touching and flattening each other more or less, if in two rows, generally alternating, therefore pits hexagonal in shape, sometimes two rows opposed and then pits more or less tetragonal in outline. Sometimes pits hardly touching and consequently more or less retaining a circular shape. If in 3, 4 or 5 rows the pits often alternating, but with many irregularities; for instance 2 or 3 rows alternating, the 2 outermost rows opposed; or an additional row or a disappearing one and in this place the regularity totally disturbed; sometimes irregularities over a large extent without any direct cause (fig. 70). The structure of the pits in principle as described at the beginning of this thesis (see p. 489). For the rest as already described for the stem (see p. 566).

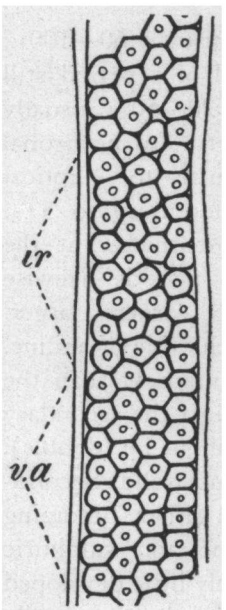

Fig. 70. Dammara alba. Radial wall of a fibre-tracheid, covered with pits all over; *v.a.*, vertically alternate; *ir.*, irregular. × 195.

Especially the inner aperture very clear, generally horizontally ellipitcal. Outer aperture circular or oval, seldom slit-like and then sinistrorse, namely at the transition of 2 periods.

Dimensions: border in diameter L. 12—16 μ, R. 14—18 μ, at the transition between 2 periods somewhat smaller and more or less circular in shape, pore generally circular about 4—6 μ.

On the tangential walls pits more regularly distributed, more numerous at the end of a period, often in one or two long rows, less often three, generally hardly touching or not at all and consequently not flattening

each other, therefore nearly circular in shape. The rows as a rule alternating. Sometimes the pits in smaller groups or entirely separate. Rarely so crowded as on the radial walls. Pore mostly elliptical, seldom very long and narrow and than sinistrorse. Inner and outer aperture often equally large. Sometimes the former larger and then horizontally slit-like. Dimensions: border in diameter L. 12—15 μ, often 13 μ, T. 12—15 μ, often 13 μ (circular pits). Pore circular about 4 μ, elliptical length 5—8 μ, width 3—5 μ, seldom very slit-like, length up to 10 μ, width about 2 μ.

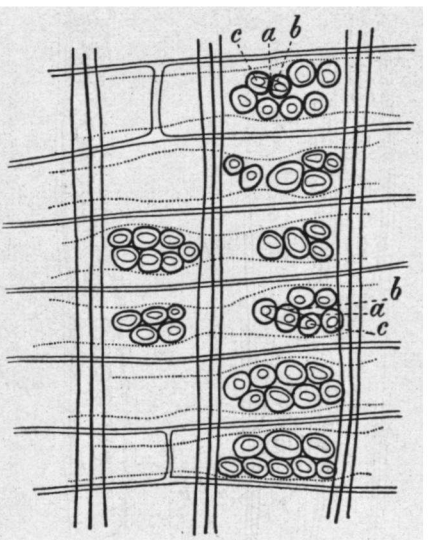

Fig. 71. Dammara alba. Radial section of root. Dotted line shows connecting frames; *a*, pectic annulus; *b*, inner aperture; *c*, outer aperture. × 260.

No rims of Sanio, neither on the radial walls nor on the tangential walls.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits, always in groups on the rhomboid bordering plane, seldom in one vertical row, (on narrow fibre-tracheids at the transition between two periods), generally horizontally alternate, sometimes rather irregular (fig. 71), often entirely separate or just touching, very rarely flattening each other. Border fairly different in shape and size, L—R. 10—15 μ. Pore large, irregular in shape, sometimes taking up the whole border, or two or three pits with a common pore (fig. 71). Especially the outer apertures

often united and the inner apertures of the various pits separate fig. 71*a*, b, *c*, (very clearly to be seen in preparations heated in glycerin). Therefore difficult to state the measures. In the few narrow fibre-tracheids at the transition of 2 periods pits small, border circular about 8μ, pore much slit-like, length about 8 μ, width about 1 μ.

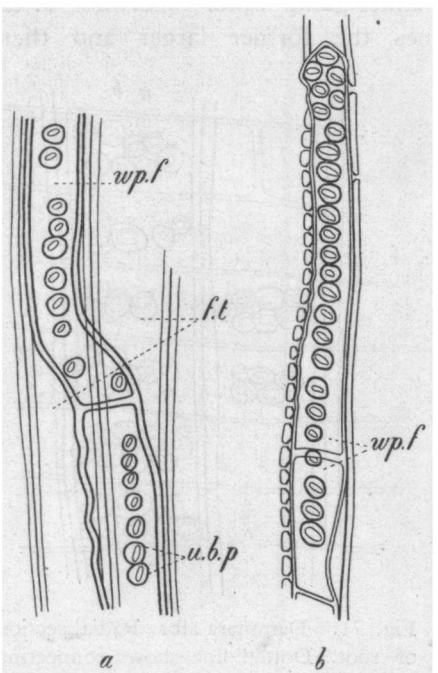

Fig. 72. Dammara alba. Radial section of root. a. *f.t.*, fibre-tracheids; *wp.f.*, woodparenchyma fibre; *u.b.p.*, unilateral bordered pits. × 195. b. Tangential wall of fibre-tracheids shows many unilateral bordered pits.

Between *fibre-tracheids* and *woodparenchyma* unilateral bordered pits, usually in long simple rows, rarely two for long distances, not touching and consequently circular in shape. Border in diamater 14—15 μ. Pore elliptical, fairly large, length 10-12 μ, width about 6 μ, sometimes much smaller length 5—6 μ, width about 3 μ (fig. 72 *a* and *b*).

Contents of the fibre-tracheids slight, here and there an occasional grain of starch, but very few, a small quantity of resin in various places besides.

II. Woodparenchyma-fibres, scattered among the

fibre-tracheids very numerous [1]), mostly thin-walled fibres, septate owing to walls of partition, R. and T. mostly smaller than the neighbouring fibre-tracheids R. 30—40 μ, T. 20—35 μ, L. of the septation strongly varying 100—490 μ Total

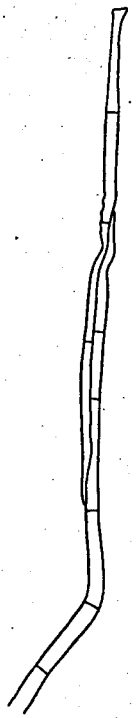

Fig. 73. Dammara alba. Some septations of two wood parenchyma fibres after maceration in chromic acid 10 %. × 30.

[1]) Since this woodparenchyma is abundant here, a trial was made to isolate the woodparenchyma fibres. As they are, however, exceptionally thin-walled, they, like the medullary rays, entirely vanish during maceration with Schulze's macerating mixture. Even when setting to work in the way described by O. Vodrázka (1926), no satisfactory result was obtained. Other methods had, therefore, to be applied. As such were used: 1. Van Wisselingh's method; splinters of wood in closed tubes, filled with glycerin, were heated to 300° (a temperature of about 280° was in most cases sufficient). After the treatment the pectin substances had dissolved, in consequence of which the particles could be disentangled with needles. If the heating process is not continued too long, the medullary ray cells and the wood parenchyma partly remain intact in groups of 2—4 cells together. A second method to obtain this result was the putting of splinters of wood in chromic acid of 10 % for about 24 hours (fig. 73).

The first method is in so far preferable because the structure of the walls remains uninpaired. This is also true for the fibre-tracheids, the pits for instance are much more distinct in this way than after maceration with Schulze's or chromic acid. As a result of this it proved to be a fact, on examing the walls of the medullary ray cells that the radial walls showed pits indeed, corresponding with the unilateral bordered pits of the adjoining fibre-tracheids, a feature which is not discernible in ordinary sections, so that in literature it is generally stated that they are entirely wanting. Whether on the tangential separating walls similar pits were present, could not be ascertained.

length difficult to measure [1]). Walls generally thin 1—2 μ (fig. 72 *a* and *b*), little lignified, with many pectin substances, colouring red in ruthenium red, without pits neither between the septations mutually, nor on the side of the fibre-tracheids (see further p. 580), very rarely thicker 8—10 μ and then with simple pits of a more or less infundibular shape, at least on the side of the fibre-tracheids [2]).

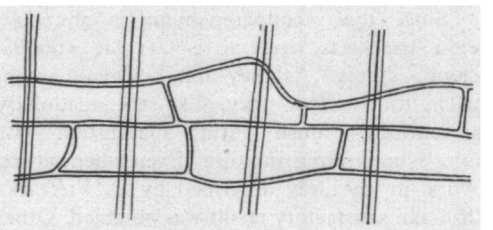

Fig. 74. Dammara alba. Radial section of root, showing a medullary ray, bounded irregularly. × 195.

Contents sometimes none, often some starch, resin less frequent.

III. Medullary ray cells.

1. Procumbent cells R. 70—190 μ, T. 10—30 μ, usually 15—25 μ, often irregular in shape, consequently one cell in different places very unequal in length, often highest at the tangential walls of 2 adjacent fibre-tracheids, lowest at the tangential walls of the ray-cells (fig. 74). Especially the marginal cells of a medullary ray of this shape. Walls thin 1 to 2 μ, somewhat lignified, colouring yellow in hydrochloride of aniline, less intensely than the surrounding fibre-tracheids, colouring slightly blue in

[1]) With the above-mentioned methods even, the absolute length of the woodparenchyma fibres cannot be measured entirely, since they are apt to break at the septations. In thin radial sections coloured in ruthenium red, in which these elements are very striking, they may often been followed for long distances, 3000—3600 μ for instance.

[2]) These thick-walled ones are probably septations between the thin-walled ones and then also with simple pits on the sides, but these elements are only observed in transverse sections.

potassium iodide iodine and sulphuric acid 75 %, hence a slight cellulose-content, mostly pectin substances (colouring red in ruthenium red), without pits, neither mutually nor on the side of the fibre-tracheids (see further p. 579).

Contents: rich in protoplasm, somewhat less than in the stem, on the other hand large quantities of starch, and here and there some resin.

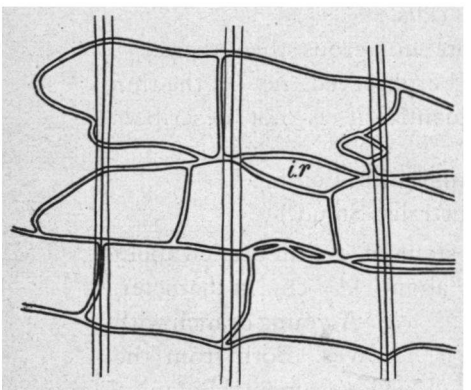

Fig. 75. Dammara alba. Radial section of root showing a medullary ray; *i.r.*, intercellular spaces between the ray cells mutually. × 195.

Intercellular spaces between medullary ray cells and fibre-tracheids numerous, especially below and above, but also on the sides, due to this, often distinct connecting-frames on the radial walls of the ray cells fig. 71; likewise large intercellular spaces between the ray cells mutually (fig. 75).

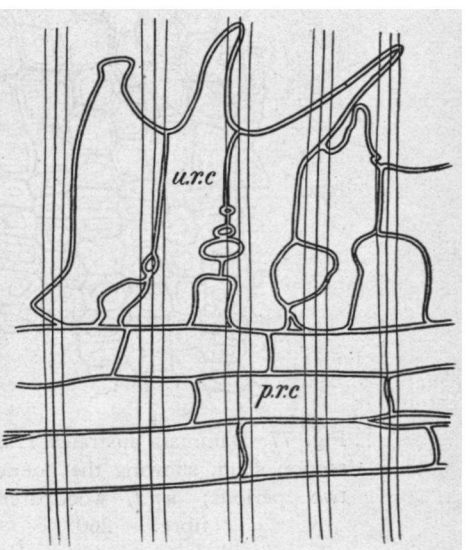

Fig. 76. Dammara alba. Radial section of root showing a medullarly ray; *u.r.c.*, upright ray cells; *p.r.c.*, procumbent ray cells. × 195.

2. Upright cells, in various places in the root, irregular in shape and with L. > R., for instance R. 50—60 μ, L. 150—190 μ, for the rest dimensions difficult to state owing to the peculiar shape (fig. 76). Sometimes these

cells forming parenchymatic commissures between two medullary rays lying above one another. Wall and contents like those in the procumbent cells.

Intercellular spaces still more numerous than there.

No **primary xylem** could be observed, not in the thin side-roots either, and consequently it is not described.

3. Dammara australis Lamb.
(Syn. Agathis australis Steud.)

Material. 1. Disk of the stem of a thin branch about three years old, without bark about 1½ cm. in diameter. 2. A young branch with leaves. Both from the Governmental Botanical Garden of Buitenzorg.

The material was preserved in alcohol.

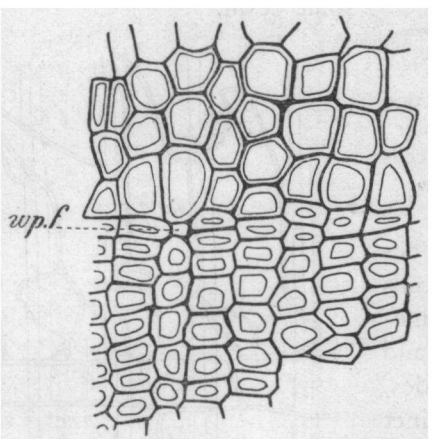

Fig. 77. Dammara australis. Transverse section stem, showing the boundary of two periods; *wp.f*, woodparenchyma fibre. × 260.

Description Secondary Xylem.

Topography. Growth rings macroscopically well marked, fairly regular 0.5—1 mm., microscopically likewise very distinct, the two periods with a keen transition line (fig. 77), formed by a considerable difference in thickness of wall, and by the elements getting narrower at the end of a period.

Fibre-tracheids the bulk of the wood. Woodparenchyma comparatively little, as woodparenchyma fibres scattered through the wood, especially at the beginning of a new periods (fig. 78). Medullary rays numerous 80—140 per

square mm., usually uniseriate, very rarely locally biseriate, 1—4 cells deep, usually separated by 2—18 rows of tracheids, but much varying, no tracheidal ray-cells, bounded straight above and below; sometimes the walls of the marginal cells slightly bent; near the primary xylem medullary rays connected, owing to the presence of fairly regular upright cells.

Elements. I. Fibre-tracheids R. 11—30 μ, broadest at the beginning of a new period 28—30 μ, narrowest at the end of it 11—15 μ (fig. 73, 74), T. usually 20—30 μ, sometimes narrower 12—15 μ, L. 1000—2000 μ, generally forming tetra- to hexagonal prisms, sometimes a little cylinder-shaped, sometimes with pointed, but often with flattened outer ends in consequence of the frequently touching of the fibre-tracheids upon each other or upon a medullary ray (see fig. 79). Walls of the fibre-tracheids R.—T. early wood 3—4 μ, late wood 4—5 μ, perhaps the corners a little thicker, also tangential walls perceptibly thicker at a medullary ray, up to about 6 μ, lignified, becoming yellow in hydrochloride of aniline, the middle-lamella colouring more intensely, therefore very distinct, fairly well developed 2—3 μ (double), large gussets, often not solid. Secondary thickening layers properly developed, becoming a little blue in potassium iodide iodine and sulphuric acid 75 %, tertiary layers likewise fairly well developed. Radial walls strongly bent inwards at a medullary ray (inflated medullary rays)

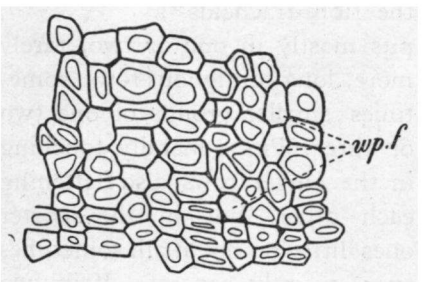

Fig. 78. Dammara australis. Transverse section of stem. Boundary less sharply demarcated as in fig. 77. Woodparenchyma fibres (*wp.f*) fairly frequent in early wood. × 260.

Contents of the fibres generally none.

Intercellular spaces between the tangential walls, due to divergence of those walls, little developed, likewise at the corners; if present, both in the vicinity of the medullary rays.

Pits. Between the *fibre-tracheids mutually* bordered pits, especially on the radial walls, very rarely on the tangential walls, if present, at the end of a period or on walls bordering on woodparenchyma fibres. Often pits at the flattened outer ends of the fibre-tracheids [1]).

On the radial walls pits mostly in one or two, rarely more, long contiguous rows, sometimes smaller groups of one two or three. Pits generally touching in the longer rows, also flattening each other, but in the shorter ones little or not at all, sometimes even entirely separate. If in two rows usually alternate, sometimes opposed. Pore circular to elliptical and then sinistrorse; in a few places strongly protruding from the border. Inner and outer apertures mostly of the same size, sometimes the former much larger (fig. 80). Dimensions border, comparatively small L. 8—10 μ, R. 7—10 μ, seldom up to 12 μ, practically circular, often even L. > R., at the end of a period smaller

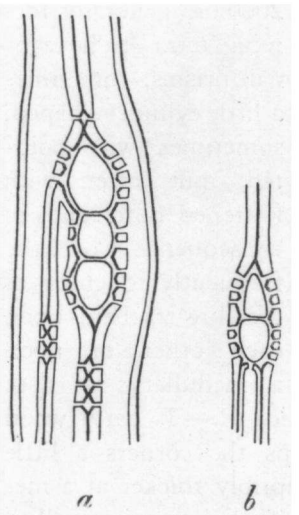

Fig. 79. Dammara australis. Medullary rays in tangential section. × 260.

[1] It is a peculiar thing that at the medullary ray, the fibres end very frequently, or are just continued for a little while, this is very striking in tangential sections, fig. 79 *a*, *b*. It was not observed that these out r ends were parenchymatic in contrast with E. Conrad (1910).

5—6 μ. Pore elliptical length 4 μ, width 3 μ; or strongly slit-like length 8 μ, width 1—2 μ.

On the tangential walls pits usually having the same position as on the radial walls, less often separate and then very small. Dimensions L.—T. 6—8 μ, pore mostly small, slit-like, length 4 μ, width 1 μ, in the smaller ones length 2 μ, width 0.5 μ, sometimes two neighbouring pits with a common pore.

Rims of Sanio absent.

Between *fibre-tracheids* and *medullary ray cells* unilateral bordered pits always in groups on the rhomboid bordering plane, mostly in 2 rows, sometimes in one, rarely in three, alternate, both horizontally or vertically, or opposed, generally touching and flattening each other. Dimensions border R.—L. 6—8 μ, often not clearly marked; pore usually slit-like and then sinistrorse, length 4 μ, width 1 μ or more, up to length 7 μ, width 1 μ, seldom wider (at the beginning of a new period).

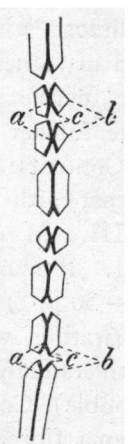

Fig. 80. Dammara australis. Tangential walls of fibre-tracheid, showing bordered pits in section; *a*, pectic annulus; *b* inner aperture; *c*, outer aperture. × 420.

Between *medullary ray cells* and *first fibre-tracheids* of the *secondary xylem* unilateral bordered pits, entirely of the same structure as in the same place in the primary xylem (see p. 590).

Between *fibre-tracheids* and *woodparenchyma* unilateral bordered pits, generally in one long contiguous row, sometimes touching, but frequently more or less separate. Border nearly circular about 7—8 μ in diameter. Pore mostly elliptical, length 4—5 μ, width 2—3 μ.

Contents of the fibres slight, here and there an occasional grain of starch, no resin.

Intercellular spaces numerous at the corners, but few between the tangential walls due to divergence; if present, both especially near the medullary rays.

II. Woodparenchyma-fibres, mostly thin-walled fibres, septate, due to walls of partition, R. 10—27 μ, rarely up to 30 or 40 μ, T. 10—20 μ, L. of the septation 75—175 μ, total length difficult to measure. Walls thin about 2 μ, very slightly lignified, colouring little in hydrochloride of aniline, becoming distinctly blue in potassium iodide iodine and sulphuric acid 75 % with the exception of the middle layer (middle-lamella), hence a fair amount of cellulose [1]), likewise many pectin substances, colouring red in ruthenium red (especially the middle part), without pits, neither mutually, nor on the side of the fibre-tracheids (see further the fibre).

Contents: rich in protoplasm with distinct nuclei, together with quantities of starch.

III. Medullary ray cells.

1. Procumbent cells R. 50—100 μ, T. 12—25 μ, L. 15—30 μ, often longer in the middle than at the tangential separating walls, forming round to elliptical cylinders, with radially directed axis. Walls fairly thick [1]) 2—4 μ (double). Constitution the same as that of the woodparenchyma fibre. No pits, neither mutually, nor on the side of the fibres (see further there p. 587).

Contents: rich in protoplasm with distinct nuclei, masses of starch, here and there a few drops of resin.

Intercellular spaces in radial direction moderately developed, especially below and above, sometimes wanting (if fibre-tracheids happen to touch upon the medullary ray, which is frequently met with here see p. 586).

2. Upright cells rather regular in shape, forming practically round cylinders with vertically directed axis,

[1]) At least in proportion to Dammara alba or the Araucaria species.

R. 15—30 μ, from within outward getting wider, L. 70—170 μ. Wall and contents like those in the procumbent cells, in the same way the pits (see further for this the tracheid of the primary xylem).

Primary xylem described after preparations made from a one year old branch.

Topography. In a tube more or less enclosing the medulla with little protruding poles, between them the medullary commissures passing into uniseriate medullary rays, the whole range small 70—80 μ, number of elements 5—7; medulla small 500—700 μ between the xylem poles, entire branch about 3 mm. From within outward: very few crushed elements; some tracheids with irregularly stretched spiral sculpturing, at least in the first two or three, in the last few the spirals more and more regular, interspaces small, finally spirals very thin and very close together; usually one (rarely more) reticulate tracheid, adjoining the secondary xylem.

Elements. Protoxylem, spiraltracheids R. 6—8 μ, T. 10—14 μ, length difficult to measure; sculpturing on wall one to two spirals, irregularly stretched in the innermost, fairly regular in the outer tracheids. Spirals 2—3 μ thick, interspaces irregular, in the outermost tracheids smaller than in the innermost ones. Wall in these interspaces thin. Section of the spirals angularly circular to oval (the greatest dimensions // wall of tracheids).

Metaxylem, tracheids R.—T. 14—16 μ, sometimes up to 20 μ, namely from within outward getting wider, usually forming nearly round cylinders. Sculpturing on wall in the first few, chiefly spirals 2—4, about 2 μ thick, interspaces about 1 μ. Section of the spirals oval (greatest dimension // wall), with narrowed foot; in the last few, more or less reticulate sculpturing.

Pits. Between the *tracheids mutually* bordered pits, that is to say in the reticulate tracheids and last few spiral

tracheids only. Pits usually in one non touching row. In the last few spiral-tracheids border mostly horizontally oblong, L. 6—8 μ, R. about 10 μ, pore length 1—2 μ, width 4—5 μ; in the reticulate tracheids, border better developed, mostly circular in shape L.—R. 6—7 μ, pore circular about 1—2 μ in diameter.

Between *reticulate tracheids* and *medullary ray cells* unilateral bordered pits in long rows. Border often indistinct, circular to oval, L. 6—8 μ, R. about 8 μ. Pore large, horizontally slit-like, length about 3 μ, width 6—8 μ.

Medullary ray cells, well developed entirely of the same structure as in the beginning of the secondary xylem (see there p. 588).

CHAPTER IV.

SUMMARIZING DESCRIPTION OF THE WOOD OF THE ARAUCARIACEAE.

If, after having fully described the available materials of wood of the two genera of Araucaria and Dammara (Agathis), we compare them mutually, it will be evident that they strongly resemble each other in many respects, both in stem- and in root-wood.

Secondary xylem.

Topography. Topographically, only slight differences occur. With the exception of a few special cases (Araucaria araucana, Araucaria angustifolia), the tendency to the formation of growth rings is small, often represented by two or three rows of fibre-tracheids, which are radially somewhat narrower than the rest and at the same time slightly thicker of wall. In the case of Dammara, however, they are more regular and better developed than in Araucaria.

Especially in the case of Araucaria, redwood (Rotholz) frequently occurs.

In both cases the bulk of the wood consists of fibre-

tracheids, the radial arrangement of which is generally fairly good. Woodparenchyma fibres may occur in both, mostly within the root, but in Dammara they are more numerous than in Araucaria. If present they lie scattered through the wood, generally in groups of two or three together, sometimes they are separate.

The medullary rays, occurring in great numbers in both, are generally uniseriate and few cells deep, mostly amounting to about twenty. If they are locally biseriate, these two cells together are in most cases practically of the same breadth as one cell lying above or below. For the rest the medullary rays are as a rule of a simple structure and consist of thin-walled procumbent cells. Upright cells are invariably to be found in the neighbourhood of and within the primary xylem and form here commissures between medullary rays, lying above one another. In special cases thick-walled and tracheidal medullary ray cells were observed, only however, in the case of Araucaria (see p. 498 and 499), whereas upright cells, except in the already mentioned places, occur regularly distributed within the root of Dammara alba (see p. 583).

Elements. I. Fibre-tracheids; they generally form tetra- to hexagonal prisms, rarely more or less circular to elliptical cylinders; often they have a more or less cylinder-shape lumen, especially in the case of Dammara. They are radially and especially tangentially in Dammara wider than in Araucaria. In the same way the walls in the former are thinner (3—5 μ) than in the latter (4—15 μ), in both they are lignified with a well developed middle-lamella and gussets. The secondary thickening layers colour slightly blue in potassium iodide iodine and sulphuric acid 75 % in Dammara only. The tangential walls are generally thicker at the medullary rays, and the radial walls are slightly bent inward there, so that the medullary ray is entirely enclosed (this is most evident with inflated medullary rays).

Intercellular spaces at the corners and between the tangential walls, due to divergence, occur fairly frequently in both genera, especially in the neighbourhood of the medullary rays.

Pits. Between the fibre-tracheids mutually, bordered pits are found, in both genera as a rule practically of the same structure (see p. 489). They occur especially on the radial walls, are more numerous towards the outer ends of the fibres and stand in long contiguous rows; in the case of Araucaria in one or two, very rarely in three; in Dammara in two to five, rarely in one. For the rest the pits touch and they often flatten one another and consequently they are somewhat polygonal in shape. Frequently they are not entirely contiguous and hence the borders are more or less circular in outline, especially if there are one and two rows [1]).

They usually stand vertically alternate, but deviations from this normal case are numerous (opposed, horizontally alternate). In Araucaria the pore is generally slit-like and then sinistrorse, less frequently circular, inner and outer aperture are practically the same size; in Dammara the inner aperture is as a rule considerably larger than the outer aperture. The former is mostly wide, elliptical, horizontal; the latter is generally circular, seldom slit-like and then sinistrorse.

In neither of the genera any rims of Sanio were observed. On the tangential walls the pits are far less numerous; in so far as they occur, they are met with at the end of a period and then equably distributed all over the fibre-tracheid. These pits are generally smaller than those on the radial walls; they hardly touch or not at all and are there-

[1]) The idea which is easily formed from the literature, that the pits are hexagonal in shape and placed in three rows at least, is certainly not correct, especially not in the case of Araucaria. Dammara may in some places answer to this idea.

fore circular in shape. The pore is rather small, circular to slit-like.

Between the fibre-tracheids and medullary ray-cells occur unilateral bordered pits, mostly in one to three vertical rows, touching one another and sometimes flattening; they are opposed or horizontally alternate, less often vertically alternate; sometimes the position is fairly irregular and the pits are separate. This is more frequent in Dammara than in Araucaria. The pore is in most cases more slit-like than in the fibres mutually, at least in Araucaria. In Dammara the pore is sometimes very large and takes up almost the entire border.

Between fibre-tracheids and woodparenchyma fibre occur unilateral bordered pits, in both genera, in long rows, touching hardly or not at all.

Between the first fibres of the secondary xylem and the medullary ray cells occur unilateral bordered pits of the same structure as in the primary xylem (see p. 597).

The contents of the fibres are slight. In both genera resin may occur and then chiefly in the vicinity of the medullary rays. Often the resin forms resin-plates, owing to which the fibre-tracheids are sometimes apparently septate.

II. Woodparenchyma fibres. They are generally thin-walled fibres divided by walls of partition, sometimes with thick-walled septations between the thin-walled ones. In the former case the walls are little lignified and rich in pectin substances, without pits; in the thick-walled septations, the wall is more lignified and has peculiarly-shaped, branched, simple pits, both on the side of the fibre-tracheids and mutually.

III. Medullary ray cells. In both genera procumbent cells chiefly occur. They mostly form round cylinders, the axis of which are directed radially. The walls are thin and without pits. They are little lignified and have a slight

cellulose-content, they contain, however, many pectin substances.

Contents. The cells are rich in protoplasm with distinct nuclei, they often contain much starch, less frequently resin (resin is probably met with in the very old stem).

Intercellular spaces between the fibre-tracheids and medullary ray cells are varying in number. In Dammara they are more strongly developed than in Araucaria. Sometimes they are the cause of distinct connecting-frames on the radial walls of the ray cells. In Dammara large intercellular spaces are also often found between the cells mutually.

The upright cells, locally occurring, are irregular in shape and have the same wall and contents as the procumbent cells, described above.

As a final conclusion it might be said that the secondary xylem of Dammara is looser and of a lighter structure than that of Araucaria (wider fibres, thinner walls, less strongly lignified, more intercellular spaces especially near the medullary rays, more woodparenchyma).

Primary Xylem.

The primary xylem of either genus is in principal of the same structure. It consists of a tube, practically enclosing the medulla, with more or less protuding poles. Between these poles the medullary commissures occur, outwardly merging into uniseriate medullary rays. The entire range of the primary xylem is fairly limited and contains 8—12 elements, from within outward, consisting of a few crushed elements; a few tracheids with spiral sculpturing, the spirals of which are strongly stretched; a few tracheids with spiral sculpturing of which the spirals stand very close together, the last few with some reticulate ramifications; sometimes an occasional reticulate tracheid. No sharp demarcations between proto- and metaxylem are to be found anywhere; the elements gradually merge

into one another. The spirals of the first few tracheids are mostly angularly circular in section, in the last few generally with narrowed foot.

In the last few spiral tracheids and possible succeeding reticulate tracheids occur bordered pits. These bordered pits are generally smaller in size than those in the secondary xylem, for the rest they are entirely of the same structure. Here they are likewise surrounded by the pectic annulus, while the border too is covered with the primary border-membrane.

They generally stand in one row, but sometimes in two, or even in three rows, especially in Dammara. In contrast with the secondary xylem, the pits never touch in a vertical direction in these rows. If two or more rows occur, the pits may be opposed. There is no question of alternation proper, since there is no contact between pits lying above one another. If two pits stand side by side, so opposed, lateral contact may occur, with which the pectic annuli coalesce (fig. 81 *a*). If we consider the conduct of the pits and the spiral bands, with or without reticulate ramifications, we shall see that two things may happen: *a*. The spiral bands may be bent a little, so that they do

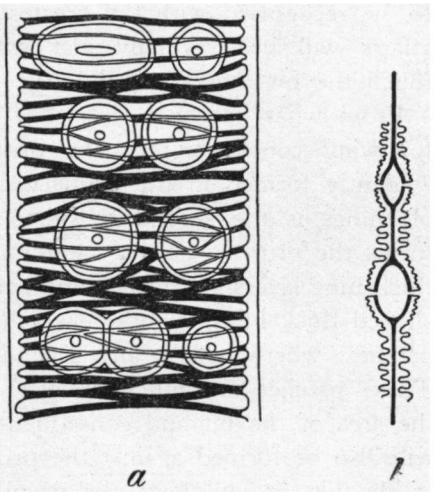

Fig. 81. Schematic figure to show the course of the spiral-thickenings in respect to the bordered pits. *a*, tracheid in front-view; *b*, walls of two adjoining tracheids in longitudinal section.

not cross the pit. This will be especially met with, if the place, where the pit is touched, is situated in such a way that in case of little swerving the spiralband stands clear from the pit. Sometimes the entire course of the spiral bands is modified near the pits. We may see for instance in fig. 66 that the same spiralthickening, near two pits side by side, has such a course that the upper rim of the one pit and the lower rim of the other is touched. *b*. The second way in which the spiralbands may pass the pits is crossing the pit. In this case they greatly decrease in strength and form hardly protruding rims, which are only to be recognised with the greatest effort [1]). This state of affairs will be especially met with, if the spiral bands touch the pit more centrally (fig. 81 *a*).

From what has been described above we come to the following conclusion. In the primary xylem the pit is evidently formed in the primary cell-wall, as is the state of things is the secondary xylem and this cell-wall also forms the primary border-membrane. Then the secondary thickening layers are formed and here they consist of spiral-shaped thickenings, between which thickenings lie thinner patches, where hardly any secondary layers are formed. These patches are much smaller in size, however, than the area of the pit and consequently the secondary layers will also be formed against the primary border membrane of the pit. It will have the usual shape here, this is in spirals, possibly with reticulate ramifications. It may easily be understood, however, that the spirals will be influenced by the pit already present .This influence will be stronger, as the tracheids are nearer to the secondary xylem, whereas the spirals stand out more clearly in the tracheids situated at the inner sides of the metaxylem. In agreement with

[1]) The course of the spiral bands with respect to the bordered pit may again be best observed by a treatment with ruthenium red.

this is the more or less horizontal slit-like pore, the greater visibility of the spiral bands along the pits in these tracheids in the beginning of the metaxylem.

In agreement with the explanation given above, is the colouring with ruthenium red. In tracheids in radial section we may observe: *a.* a strong red colour of the spaces between the spiralbands in consequence of the transparence of the primary cell-wall; *b.* a red colour of the pectic annuli; *c.* the pit standing out nearly white against the remaining part of the tracheids, owing to the far less strong development of the primary cell-wall i. e. as a primary border membrane, besides the interspaces are far less deep (compare fig. 81 b). In tracheids in tangential section we may observe: *a.* a red colour of the primary cell-wall (middle-lamella); *b.* a red colour of the primary border-membrane.

Between the tracheids and the medullary ray-cells are found unilateral bordered pits, profuse in number in connection with the increased height of the medullary rays. They stand in 1—3 long rows and do not touch. The border is horizontal, slit-like, likewise the pore; the pit-canal is little narrowed, and therefore the border and pore almost coincide.

Medullary ray cells; the ray cells are upright cells exclusively. They are irregular in shape and entirely of the same structure as those in the beginning of the secondary xylem (see p. 594).

CHAPTER V.

GENERAL VIEWS.

In the preceding descriptions no quotations from the literature will generally have been found. I therefore wish to discuss a few results here in connection with the opinions of previous authors. As principal points I shall subsequently consider:

1. Pits, to be divided into:
   a. Nature of the pits.
   b. Rims or bars of Sanio.
   c. Relation between pits and spiralsculpturing.
   d. Spreading of the pits.
2. Resinous tracheids.
3. Wood parenchyma.
4. Medullary rays.

1. Pits.

a. *Nature of the pits.* Beginning with the pits, I shall in the first place discuss the nature of the pits in the Araucariaceae. For the way of pitting in this family has always played a leading part in the literature. In the literature existing the pitting is known as „araucarioid pitting", and is generally stated as the chief characteristic of the wood of the Araucariaceae. Of this „araucarioid pitting" we find the following statement by Potonié-Gothan (1921 p. 246). „Die Hoftüpfel stehen dicht gedrängt, über- und alternierend nebeneinander, sich gegenseitig abplattend und daher hexagonale Form bei mehreren Reihen annehmend". Seward too, in Vol. IV p. 133, mentions the same characteristics of the above mentioned pitting. My investigations have led me to attach less importance to the arrangement and form of the pits, but to think the way, in which the touching of the pits is brought about, the essential feature of the „araucarioid pitting". For, this touching always happens in such a way that the pectic annuli of two adjoining pits coalesce on the place of contact, owing to which the two pits are only divided by the straight common part of the pectic annuli (fig. 1, 4, 5, 9) (see p. 489 for a more detailed description). This touching — generally, but not invariably accompanied with flattening — is, therefore, in my opinion of more diagnostical value than the alternation frequently met with, which alternation

may often be replaced here and there, especially in more adult wood, by opposition. The presence of several rows should certainly not be too much emphasized as a characteristic. In the Araucaria genus especially one row, two at most, is the rule, which has already been stated in Schacht (1862), Winkler (1872), Gothan (1905). R. Pilger 1926, on the other hand, emphasizes again too strongly the occurrence of 3—5 rows of polygonal bordered pits, even though he adds that 1—2 rows may occur. From the investigations made by me, it has appeared besides that the chance of the occurrence of several rows of pits is greater in adult wood than in juvenile wood, which has also been observed by Gothan (1905 p. 13). I want to state, however, that Gothan's explanation for this phenomenon, that in the generally wider fibre-tracheid of the older wood, there is more room for pits, does not hold. For the very old stem of Araucaria angustifolia has wider fibre-tracheids than the majority of the other species, whereas in this species one row of pits is the rule, while the pits themselves have on an average larger dimensions (see p. 527).

b. *Rims or bars of Sanio.* Besides the nature of the pits, in the last years, the rims of Sanio have played an important part in the views on the structure of the secondary xylem of the Coniferae, because the lack of „rims" has been made the criterion, to recognize the Araucariceae, by Jeffrey and his pupils (Gerry (1910); Holden (1913); Sifton (1913)). For this reason the rims of Sanio are often treated separately from the pit. Since their origin is closely related to that of the pits, I shall discuss the rims in connection with the pits.

What is meant by these rims cannot always sufficiently be made out in the literature. It is usually taken to mean the upper and lower boundaries of the original „Primordialtüpfel" described by Sanio or properly „Umriss" (Sanio p. 74 and 86) and I myself shall follow the same course.

The „Querleisten" mentioned by Sanio arise, when two „Primordialtüpfel" stand so closely together that the lower boundary of the one coalesces with the upper boundary of the „Primordialtüpfel" lying under it (Sanio p. 74). For this Querleisten, however, the word „rim" is also used sometimes. [1])

The spreading of the „rims" in the wood of the Coniferae has been especially examined by Gerry 1910, from which investigations it is clear that they are absent in the Araucariaceae. Jeffrey (1917) likewise thinks this to be the general rule, but he adds that they may sometimes occur in the first annual bands of the cone axis. The result of my investigations in so far agree with this that no such rims were anywhere observed, neither in the first annual bands mentioned before.

It is true that such bands, as Jeffrey 1917, p. 324, fig. 233 reproduces in a schematic figure, are to be seen in the last few tracheids of the primary xylem, where many pits already occur between the spirals, which spirals may or may not have reticulate ramifications ,but I take them to be spiralbands, which have remained. In my opinion these rims have, therefore, nothing to do with the rims of Sanio proper.

The lack of „rims" in the Araucariaceae once having been assumed as a fact, several attempts have been made to explain this absence.

Jeffrey and his pupils think it to be a regression, in connection with a descent of the Araucariaceae from the Abietineae, without, however, giving a reason for this regression.

Thomson (1914) thinks that the „rims of Sanio" are present in a rudimentary state as „small dark areas which are so common above and below the pits, especially when

[1]) See also Bailey 1919 p. 450 for a more detailed explanation.

these margins are free from other pits" (p. 22). It is not absolutely clear to me, what Thomson means by this; it probably refers to the horizontal coalesced part of the pectic annuli of two adjoining pits [1]) In case this opinion should be right, I want to point to some drawbacks attached to the hypothesis made by him.

If we have another general look at the bordered pits, we shall find the border surrounded everywhere by the pectic annulus. In the Araucariaceae two pits lying above one another have generally such a close juncta-position, that the pectic annuli coalesce for some distance. The horizontal common part formed by this has the appearance of a rim. But such a rim is formed in all places of contact. Hence not only between two pits lying above one another, but also in case of multiseriate pitting between two pits lying side by side. In the latter case the rim has a vertical position (fig. 33). These vertical rims have been left out of consideration by Thomson, whereas the horizontal rims, formed in the same way, have been compared with rims of Sanio.

Should it be strange already, to judge the different sides of the pits in a different way, still more difficulties present themselves if we compare it with Pinus sylvestris. Within the root-wood of this Pinus species, two rows of pits occur several times and in this case it may happen that two, three, sometimes four pits together are bounded below by a rim of Sanio and above by another one, in other words that these pits together have been formed on one „Primordialtüpfel". Naturally these pits stand fairly close together and it may happen now that two of these pits get into contact, owing to which the pectic annuli coalesce and a similar rim will be formed as is the rule in Araucaria.

[1]) See in connection with this a more detailed description about the formation of the pectic annulus at the beginning of this thesis. p. 489.

We evidently have to do here with a similar formation as in Araucaria, which, in its origin, proves to be entirely independent of the rim of Sanio, also present here.

W. Gothan (1910) p. 32 too, gives his opinion to explain the absence of the rims in Araucaria. Gothan assumes that the pits are so close together that there is no room left. Jeffrey (1912) p. 546, on the other hand rightly assumes, as has been done by Holden (1913) p. 541, that surely this cannot be an objection for the separate pits also being present here.

The only way to solve this question would be, in my opinion, to make a thorough investigation into the development of the pits within the cambium, as was done by Sanio (1873/74) for Pinus sylvestris.

It may be possible that the large groups of pits arise on a single large „Primordialtüpfel", which is less sharply demarcated, or that the „Primordialtüpfel is invariably entirely taken up by the border, which is after Sanio likewise the case in most places in the wood of Pinus.

c. *Relation between pits and spiralsculpturing.* In Potonié-Gothan (1921) we find of the „araucarioid pitting", which only occurs at present in the Araucariaceae, that this pitting should be looked upon as the more primitive one and closely related to reticulate and scalariform sculpturing on the walls.

In so far as I have been able to examine, this opinion is based on the assumption of a phylogenetic origin of bordered pits from a kind of reticulate and scalariform thickening of the wall (cf. Gothan 1907). For this assumption the following facts have been pointed to: 1. the relations in the primary xylem of the recent Coniferae. „Hier sind die ersten Zellen noch mit Ringverdickung versehen, die dann schnell über einige mehr treppenförmig verdickte Zellen in die typisch hofgetüpfelten übergehen" (Gothan 1907, p. 14). These relations are still more conspicuous in the

extinct Cordaites 2. the similarity of the bordered pits to scalariform thickenings in still older forms, such as Protopitys Buchiana.

Concerning the first point of discussion I cannot hold with Gothan. For, if we examine the Araucariaceae, it will be seen, that the sculpturing on the walls chiefly consists of spirals, that sometimes no reticulate tracheids at all are formed (cf. the descriptions of the primary xylem). The last few spiral tracheids have already bordered pits, and they directly adjoin the secondary xylem. Reticulate ramifications, through which bordered pits would be formed certainly do not occur in that case. The spiral bands themselves bend round the place, where the pit will come or they cross the spot as hardly visible rims. Both are formed therefore independently of each other. For other Coniferae too, namely Pinus sylvestris, something to the same extent has been described by L. Kny (1874). The pits in the primary xylem have not sprung from the spiral thickening here, but they are independent formations. In this connection it would not seem probable to me that the pits within the secondary xylem of Araucaria would arise in another way and would be formed through a coalescing of primarily formed spiralbands.

About the second point of discussion the origin of the bordered pits in the course of phylogeny, I can little judge. It is very well possible that in the course of the evolution bordered pits have originated in the way mentioned by Gothan. Even now this seems to be so in the development of the pits in the walls of the vessels of the dicotyledons, where the pits seem indeed to arise from anastomoses of primarily formed spiral bands (cf. Scherer 1904, Alexandrov 1926). Why it must be the araucarioid pitting, which arises in this process and why especially this pitting should be looked upon as more primitive is even then not quite clear to

me. The primitive Protopitys Buchiana, mentioned before, has no such pitting either.

In my opinion we have no positive proof that the araucarioid pitting should be so closely related to reticulate and scalariform sculpturing on wall.

Another attempt to connect bordered pits and spiral-, reticulate thickening of the wall in the case of Coniferae has been made by W. G. Alexandrov (1927), after a similar treatise on the pitting in the vessels of Dicotyledons by the same author had appeared (1926). If in the case of the vessels of the Dicotyledons an inspection of the succeeding wall sculpturing of a single vessel in the course of its development suffices, in the Coniferae the sculpturing of those tracheids, situated within the transition part between primary and secondary xylem, in which part the bordered pits are to be seen first, should be examined. This is done accordingly by Alexandrov, namely with material of Pinus eldarica, which was in his opinion, very well suited for that purpose. After the investigations made by him, Alexandrov comes to the following conclusions:

There are two ways, in which bordered pits may arise. The first way is the one, in which the pits stand in one vertical row. This way of formation happens as follows:

In the tracheid are to be seen peculiar spots, which colour more deeply with colouring matters (safranin). Therefore they are called „chromophile Körperchen". Alexandrov thinks that from these „Körperchen" the torus of the pits will arise, because Dippel (1896) has seen similar spots in the tracheids of the secondary xylem near the cambium and according to the latter's description there the torus arises from them. Alexandrov did not examine the further development of those spots. At any rate these „Körperchen" seem to play a part in the formation of the bordered pits, for the spiralbands, adjoining them, undergo a change,

i. e. they unite under these spots [1]) and in this way a large circular patch is formed, where no spiralbands are to be observed. [2]) Round every „chromophiles Körperchen" a border is subsequently formed and this border closes itself „durch Umrandung" in the way, which has been described in detail by Dippel [3]). Alexandrov does not speak about the part, which the coalesced spirals play in this process.

Besides the formation of the pits, Alexandrov examines in these tracheids the course of the spiralbands. These would gradually disappear, owing to coalition and remain longest on the sides of the tracheids [4]) and round the pits. The latter are compared with „die seinerzeit von Sanio beschriebenen Falten an den Tracheidenwandungen der Kiefer in der Nähe der Hoftüpfel (scheibenförmige Ver-

[1]) Since the „chromophile Körperchen" were to form the torus, so that it is evidently situated in the primary cell-wall, it is not possible that the spiral bands are situated beneath them. The intention will have been therefore „above the spots".

[2]) At least in so far as it is clear from the figures. In the text no mention is made of a final result, but reference is made to the figures mentioned.

[3]) Although it has not been mentioned to which treatise of Dippel's this quotation refers, I think the following essay is meant: Über die Entstehung und den Bau der Tüpfel, Bot. Ztg. 1860. If this supposition is right, I should wish to point to Sanio 1873/74, in which the way of formation as described by Dippel has been refuted.

[4]) Since Alexandrov particularly examines the bordered pits, which are generally found on the radial walls, it is probable, that the radial sides of the pictured tracheids have been drawn. Hence by the sides will be meant the tangential sides. Alexandrov does not account for this unequal development of the spiralbands on the various sides of the tracheids. It does not seem quite impossible to me that this difference does not exist in reality either, but that in the preparations the spirals were only more visible in optic section (that is in the preparation along the side) than in front-view (that is between those sides).

dickungen der Scheidewand) [1]). It is probably the writer's intention to make a comparison with the „Umriszen der Primordialtüpfel", as described by Sanio. This may be gathered from the remarks on the spreading of the „Saniobänder" added to it.

Besides this first way of formation of the pits as described above, there would be a second one, in which the pits stand in two rows. This happens as follows: A „chromophiles Körperchen" does not occur. Between two succeeding spiralbands arises a connecting-band. The parts of the spirals, united by the connecting-band, round themselves off and coalesce, or if this does not happen, a superficial connecting-band is formed. [2]) After this process the bordered pit seems to be ready. The intention is probably, that the remaining open spaces between the spirals have changed into bordered pits.

Besides the two above-described ways, in which bordered pits might arise, Alexandrov distinguishes a third, according to him a link between the two first. In this third way of formation no connecting-bands occur, but in certain places the spiralbands themselves come into contact in order to coalesce. Owing to this direct contact, this third way of formation differs from the second one. In this process two rows of bordered pits will arise. Probably here too the writer means that the bordered pits are formed in those places, where the spirals have no contact.

[1]) In the treatise quoted by Alexandrov, nowhere is spoken of „Falten", by Sanio, no more of „Scheibenförmige Verdickungen der Scheidewand" with reference to the entire pit. On the contrary the latter would be formed, according to Sanio on „rundliche Stellen, die sich durch ihr optisches Verhalten als Verdünnungen der Membran herausstellen (l.c. p. 74). Afterwards p. 78 Sanio speaks of „Scheibenformige Verdickungen" as being local thickenings formed at a later date on the „verdünnten Stellen", mentioned before.

[2]) Whether it lies over the former or that it should be looked upon as an extension of the former, could not be made out from the context.

The description of these forms of development is mixed up with various conclusions, the principal of which is that through the intermediate form the connection would be laid between the formation of bordered pits in one row and in two rows. The way, in which two rows of bordered pits arise in the Coniferae, would agree with the way of formation in Angiosperms on the one side and Pteridosperms and lower Gymnosperms (Cycadales) on the other side. In consequence of this, it would have been proved that there was no essential difference in the bordered pits of the various groups of plants.

The reader may easily form an opinion from what precedes. Is it in itself not strange already that there would be so great a difference in the formation of bordered pits, in possibly adjoining tracheids, or even in one and the same spiraltracheid, only dependent on the formation of pits either in one or in two rows?

In my opinion in this treatise of Alexandrov, the connection between the formation of bordered pits and spiralsculpturing has no more been proved than in Gothan's papers. In the Coniferae they must be looked upon as formations independent of one another.

d. *Spreading of the pits.* After having discussed the nature and relation of the pits, I wish to say a few words about the spreading of pits.

The number of pits on the radial walls is generally great, but it seems to be smaller in the recent species than in the more or less related Palaeozoic ones, even though in various Cordaites the radial walls are not entirely covered with pits either.

W. Gothan (1907) tries to account for this decrease of pits, as follows: The bordered pits have been formed from a reticulate wall sculpturing, so they originally cover the entire wall. This large number of pits will decrease, because in such a way the firmness of the wall may be increased.

This is necessary in connection with the formation of annual bands, which, in their turn, are a result of the refrigeration of the earth. As a matter of fact both phenomena appear at the same time, namely in the Mesozoic. For this decrease of the number of pits it was necessary that the pits became separate and it was only possible to occur separately, if the alternation was abandoned. The Araucariaceae with their badly developed annual bands did not need to abandon their alternation, but their range was limited in this connection to a region with a little variable climate. In consequence of the kept alternation, however, separate pits will never be found in these plants.

It would seem to me that this explanation gives rise to many difficulties:

Araucaria most positively shows separate pits in the secondary xylem. In the primary xylem of these plants the pits even stand always free from each other and not alternating. The cause of this is not far to seek. That the pits alternate, when extremely numerous, is in keeping with the fact that this is the way to place a number as great as possible on a surface as small as possible. It seems to me unnecessary to think in regard to this of a „Zusammengehörigkeit als eine Art Prinzip". That on the other hand the alternating grows less imperative, when the number of pits diminishes and may disappear altogether or in part, will be easily understood.

I should wish to point to the fact that in the case of Dammara the fibres are wider, the wall is thinner and the annual bands are better developed than in Araucaria. In accordance with the theory of Gothan, it might be expected that the number of pits were smaller than in Araucaria and on the other hand the number of pits is much greater.

It does not seem probable to me that the Araucariaceae should have been limited to the climates mentioned before

in connection with the lack of the annual bands, for the trees may very well develop annual bands, as soon as they grow in districts with a strongly variable climate (cf. Araucaria araucana p. 504 Ar. augustifolia p. 526). These annual bands differ in no respect whatever from those of the native trees, while in the pitting there is not a single difference to be found with the related species, grown in the tropics.

Even though the numerosity of the pits on the radial walls of the Araucariaceae has occasionally been exaggerated, it may be said that the quantity is indeed great. In contrast with this, is the state of things with the tangential walls, where a much smaller number of pits is to be found. This is also stated by Gothan (1905), De Bary (1874) p. 509, Conrad (1910), while in Seward (1919 VI) p. 143 we find that they are entirely wanting. This last statement is not quite in accordance with the facts; sometimes the pits on the tangential walls may be fairly numerous, cf. Araucaria Rulei p. 548 and Dammara alba p. 568.

Regarding the pits between medullary ray cell and fibre-tracheids it is generally stated that they belong to the wall of the fibre, and that the walls of the ray cells have no pitting. This does not quite agree with the facts either. Undoubtedly the wall of the ray cell forms the pit-canals in its slightly developed secondary thickening layers, but owing to the slight development of those layers, the pits are hardly to be observed and they can only be shown in a special way see p. 581.

For the rest we generally read in the literature that the pits on the rhomboid bordering plane between medullary ray cells and fibre-tracheids are always found in clusters (Thomson 1914, Gothan 1905). Gothan takes this to be a difference with the extinct species, where 1—2 pits is the rule. For this opinion, I should like to make a certain restriction, since in the mature wood of Dammara a slight number of pits occurs likewise (see p. 569, fig. 64).

2. Resinous tracheids.

Penhallow (1907) assumes systematic value to the presence of resinous tracheids, that is to say, ordinary tracheids in which resin-plates occur, so that the fibre seems to be septated. Record (1918) already rightly denies this, just like Conrad (1910). For, if much resin is formed in the medullary rays, this will naturally be given to the adjoining fibre-tracheids. The fact that resin-plates are often formed along with this, cannot be called a special characteristic of the plant, but should rather be attributed to physical causes. What might be characteristic is the formation of resin in the medullary rays, but, as is clear from my investigations, this may differ even locally in one and the same tree and the resin may have been substituted by starch (cf. p. 518 and p. 573). Kräusel (1924) p. 7 draws attention to the fact that it is not impossible that these resin-plates are sometimes mixed up with trabeculae, which occur among the Aracariaceae as well.

The tracheids themselves slightly remind of a septated woodparenchyma fibre and to this even the fossil Dadoxylon pseudoparenchymatosum Gothan (Gothan 1908) owes its name.

3. Woodparenchyma.

For the rest, it might be asked whether a part of these resin tracheids is not in reality woodparenchyma, for too much stress is laid on the absence of woodparenchyma in the wood of Araucaria, Dammara and Cordaites. As appears from the investigations by the present writer, it occurs more frequently than is generally stated. Recapitulating it is indeed rather rare in Araucaria, and generally limited to the root and first annual bands In the case of Dammara, however, it is generally scattered both through the stem and through the root, even so much that, in my opinion, it might be taken for a characteristic of Dammara,

the more so as it has always a characteristic appearance (see p. 580, fig. 72).

Contrary to these investigations Penhallow (1907) found parenchyma entirely absent, like Gothan (1905) and Burgerstein (1907), where as Pilger (1926) states that it only occurs in the root; Schacht (1862), Conrad (1901) are of the same opinion; Seward (1919, Vol. IV) mentions the absence in the case of Araucaria, but he adds that, after W. Noelle (1910), it occurs fairly often in a certain species of Agathis (Agathis robusta).

According to Jeffrey's investigations (1912), it only occurs in the conservative parts as root and first growth rings and it decreases in number from within outward.

This is in contrary to the facts I met with in Dammara alba, where it occurred more generally in the mature stem than elsewhere.

4. Medullary rays.

In determining fossil species of wood, Gothan often makes use of shape and nature of the medullary rays and their walls, in which he is followed by Kräusel (see Kräusel 1907).

The characteristics to which Gothan (1905) pays attention for Araucaria in doing this are the following:

a. General shape of the medullary rays, examining the depth and the width.

b. The shape of the medullary ray cells.

c. The pits of the medullary rays.

Concerning these three points, I should like to make the following remarks: *a.* After Gothan the medullary rays of the living Araucariaceae are comparatively low, at least lower than those of the extinct related species. According to him the cause of this would be partly due to the fact that the depth of the medullary rays increases with the age of the individual. As the investigations, which are spoken of in existing literature have been made with

wood more juvenile than the examined fossil wood of the gigantic relations of earlier geological times, this will partly explain the observed differences. Nevertheless Gothan assumes that the medullary rays in recent species remain lower too and that those being 30—50 cells in depth do not occur in these species. If we look into the investigations made by me in this connection, it is clear that the depth of the medullary rays indeed increases with the age of the individual. This is most conspicuous in Araucaria species (see p. 552), where the investigation was made with wood of a very old stem and where the medullary rays, to 38 cells deep, were not rare. It appears from this, that the depth of the medullary rays may only be used diagnostically, if the age of the material is known. At the same time, it may be noticed that the medullary rays, 30—50 cells in depth, are not only peculiar to extinct species.

Concerning the width of the medullary rays, Gothan states that the presence of more than one row in the recent Araucariceae is „etwas Auszergewöhnliches". These statements largely agree with the results of my investigations. I should, however, like to add that the number of times, that the medullary rays are two cells broad, is not so slight, but that these two rows are invariably local and that the medullary ray hardly widens in these places. The two rows of cells themselves are always tangentially opposed (see fig. 38). In one case only, the position of the cells was irregular and the medullary ray consisted of two rows over a large distance (Araucaria species p. 552, fig. 46).

b. Gothan represents the shape of the medullary ray cells by means of measures, both in longitudinal and in tangential direction. He goes on to say of these dimensions that diagnostically they are often useful and in connection with this he accordingly gives a table of dimensions in various recent and extinct species, from which it appears that in the former the length (L) is between 20—26 μ.

For the width (T) too, Gothan finds a value varying between 20—25 μ, so that the cells are somewhat iso-diametrical.

I myself observed much larger fluctuations for both dimensions. In Araucaria Cunninghamii the length (L) may even vary between 15—40 μ, while in the root of Dammara alba the limits were still greater, varying between 30 and 70 μ. In the same way the width, (T), varied between 10 and 30 μ, while in most species 15 μ, was a very common measure.

In connection with this, it seems to me a dangerous supposition, on the ground of the dimensions mentioned, or generally on the ground of the shape of the medullary ray cells, to draw conclusions on the origin or relation, at least concerning the Araucariaceae.

c. As a last characteristic Gothan examines the pits between the medullary ray cells and adjoining fibre-tracheids. I shall not go into details here, since this point has already been considered in discussing the pits (see p. 609).

From what precedes it appears that Gothan has paid attention to characteristics, which do not invariably hold.

In my opinion we had better look at the great uniformity of the medullary rays, which chiefly consist of procumbent cells with a thin practically unpitted wall, largely consisting of pectin substances, whereas the ray cells in the fresh wood possess a rich protoplasmatic contents.

It stands to reason that, in spite of the great uniformity deviations from the character described above do occur. These deviations may be ranged into three groups viz: *thin-walled upright ray cells*; *thick-walled procumbent ray cells* with simple pits; *tracheidal ray cells* with bordered pits.

Of these three kinds of cells the following may be said:

One kind of *thin-walled upright ray cells* has already been mentioned by Schacht (1862), as being present in the root of Araucaria brasiliensis (syn. Araucaria angustifolia), where these cells give rise to parenchymatous connections

between two medullary rays lying above one another. In more recent times Pilger (1926) mentions these very connections for the root of Dammara. Like Pilger, I found these cells profuse in number in the root of Dammara. In Araucaria on the other hand, they were not seen.

Another kind of upright cells are mentioned by Thomson (1914), namely, those, which are present in the neighbourhood of the pith of the stem. Of those cells Thomson only says, that they are fairly long, at least more long than broad. It is not mentioned, whether they are irregular in shape and connect medullary rays lying above one another. This kind of upright cells I found both in Araucaria and Dammara. They are usually less irregular as the above mentioned upright cells scattered at random in the root of Dammara. In the neighbourhood of the primary xylem always these cells are found in groups, so that radially fairly wide parenchymatic connections are formed between several medullary rays lying above another (see fig. 22).

This same kind of upright cells are occasionally met with in the first growth ring (fig. 24).

The *thick-walled procumbent ray cells* occur after R. B. Thomson (1914) in Agathis australis, but remains limited to the medullary rays in the region of the exit of a leaf-trace and in these rays up to about half the first annual band. According to his description they are of a sclerenchymatous nature. Their appearance might be accounted for owing to the close relation, which should exist between these first cells of the medullary rays and those of the adjoining pith, where sclerotic nests are generally present.

We may compare this statement of Thomson's in connection with my investigations, in the following order: *a.* the spreading of the cells; *b.* the character of the cells; *c.* an account for their origin.

a. The spreading of these cells is much greater than

Thomson states. I found the cells mentioned not only in the first growth rings but also on a much larger distance from the pith in any case up to the eighteenth growth ring and even still further away; it is true often within those medullary rays, which are found near the leaf-traces. Moreover they were numerous and regularly spread in the wood of Araucaria angustifolia.

b. About the character of the cells mentioned, we may say that especially those, which occur in the neighbourhood of the leaf-traces are of a strongly sclerenchymatous nature, that is to say, they are often stratified and the wall is provided with simple pits, which show an infundibularly widening from within outward. Especially through these apparent bordered pits, these cells are sometimes difficult to distinguish from tracheidal medullary ray cells, which likewise occur in the neighbourhood of leaf-traces (see fig. 28).

The thick-walled medullary ray cells occurring here and there in the wood of Araucaria angustifolia bear the sclerenchymatous character less strongly.

c. From the much larger spreading as stated by Thomson, it is already clear, in my opinion, that it is not very probably that these thick-walled medullary ray cells are closely related to the sclerotic nests in the pith.

We may say that the Araucariaceae are eminently capable to form sclerenchymatous cells in all parenchymatous parts, both outside and inside the secondary xylem. In the secondary wood, parenchyma only occurs as medullary rays and sometimes as septate parenchyma fibres running vertically, and in both, sclerenchymatous cells occur (cf. p. 508; p. 529).

Why this capability is so strongly developed in the Araucariaceae is difficult to make out.

The *third kind* of cells, the *tracheidal ray cells*, are, up till now in contrast with the two former, nowhere described in the literature. The cells distinguish themselves from

the ordinary thick-walled cells, owing to their having bordered pits (see p. 529, and fig. 28; 55 p. 557). These bordered pits may be recognised from the following: They have a closing-membrane, differentiated in a way, as is the rule in bordered pits, that is to say this closing-membrane is much thinner than the middle-lamella of the cells, in the walls of which the bordered pit is situated. (Thickness closing-membrane about $^1/_{10}$ of the middle-lamella). In the funnel-shaped simple pits on the other hand, the middle-lamella runs on uninterruptedly, especially clear, where two pits correspond in adjoining cells. Further on the real border is covered with the primary border membrane, which is not the case with the apparent border of the simple pit.

The tracheidal ray cells were especially met with in the neighbourhood of the leaf-traces (p. 499, fig. 11 and 12). As has already been stated their presence in the medullary rays of Araucaria is nowhere spoken of in the literature. On the contrary, the existence of them is denied by R. Holden (1913 p. 61). Their absence is even alleged there as a proof that the Araucariaceae should have sprung from the Abietineae even before the Cretaceous.

5. Conclusion.

It has been my aim to give a contribution to the knowledge of the structure of the wood of the Araucariaceae in view of the fact that the anatomy of this family is of great importance to the phylogeny of the family itself, as well as that of the Coniferae generally.

In doing this, it has not been my object to draw conclusions concerning this phylogeny itself. In my opinion, a much more thorough knowledge of the wood of the other recent Coniferae, as well as that of the extinct species, now available in the literature, would have been necessary. Being too hasty at drawing conclusions is a but too common

mistake in many authors. In this connection I only wish to point to R. Holden's conclusions based on the absence of tracheidal medullary ray cells, which proved to be present after an accurate and systematic examination.

Therefore, without wishing to point to a certain relation, I want to confine myself to the following remarks:

The anatomy of the secondary xylem of the Araucariaceae strongly resembles that of the Cordaiteae, both as regards the way of pitting on the radial walls of the fibre tracheids, the structure of the medullary rays and medullary ray cells, and the presence of woodparenchyma-fibres scattered through the wood.

The structure of the primary xylem of the Araucariaceae, on the other hand, is much more similar to that of the Abietineae, both owing to the presence of well-developed bordered pits in the spiral and reticulate tracheids and owing to the occurrence of irregularly formed upright medullary ray cells within and near the primary xylem, while also, the pitting between the latter and the adjoining tracheids strongly resembles that of the Abietineae in those places. Likwise the range of primary xylem is comparatively small as it is in the Abietineae.

The resemblance to the primary xylem of the Cordaiteae is only slight, owing to the absence of bordered pits in the primary xylem in the latter, at least as far as I can tell. Likewise the irregularly shaped upright medullary ray cells are wanting. The range of primary xylem is much greater than in the Araucariaceae.

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