

MEDDELELSER OM GRØNLAND

UDGIVNE AF

KOMMISSIONEN FOR VIDENSKABELIGE UNDERSØGELSER I GRØNLAND

Bd. 167 · Nr. 2

DE DANSKE NÛGSSUAQ EKSPEDITIONER 1938 OG 1939

UNDER LEDELSE AF ALFRED ROSENKRANTZ

ON TWO SPECIMENS OF
FOSSIL WOOD WITH ADHERING BARK
FROM THE NÛGSSUAQ PENINSULA

BY

FR. J. MATHIESEN

WITH 20 FIGURES IN THE TEXT AND 15 PLATES

KØBENHAVN

C. A. REITZELS FORLAG

BIANCO LUNOS BOGTRYKKERI A/S

1961

INTRODUCTION

An important part of the paleontological material collected by the "Danish Nûgssuaq Expeditions" under the leadership of A. ROSENKRANTZ consists of very extensive collections of fossil wood. The greater part of the samples brought home are distinguished by a very good, in some case an excellent state of preservation which has made it possible to obtain from them slides of a unique quality. While previous finds of fossil wood from the arctic have been mostly of a casual nature, the samples collected as erratics, the greater part of the material gathered in 1938 and 1939 has been taken either from strata of known geological age or at least found in the screes originating from such strata. This applies also to the more recent collections, carried out by A. ROSENKRANTZ under the auspices of The Geological Survey of Greenland. The geological age of the layers from which the expeditions in question have brought home determinable samples of fossil wood, extends from the Senonian up to and including the Paleocene period.

In the Danian strata on the north side of the Nûgssuaq peninsula, fossil wood is very common. From the locality Saviarqat (see the map Fig. 1, compiled by A. ROSENKRANTZ) is available a collection of 11 samples, which preliminary cuttings have shown to be mainly wood of gymnospermous origin. Fossil wood is also common in the local moraines at higher altitudes above sea-level where 8 samples were collected.

The sample No. 43 (label marked No. 3403) comes from a moraine in the Saviarqat delta (col. I. C. TROELSEN 28/7 1938), this locality is marked A on the map Fig. 1, while sample No. 53 (col. TH. SORGENFREI 28/7 1938, label marked No. 3220) was taken from a concretion found in situ at a height of 280 m in the large ravine Igdlorssuaussap-Kangilia, east of Saviarqat (marked B on the map). These two samples immediately drew my attention, partly because their state of preservation, as seen under the pocket lens, seemed so perfect, but also because the cortex appeared to be preserved, undoubtedly a rather uncommon feature in the case of fossil wood.

In sample No. 53 the cortex was standing out fully intact; in No. 43 however, which has been affected by abrasion, only the inner parts are preserved. These two particularly inviting samples were submitted

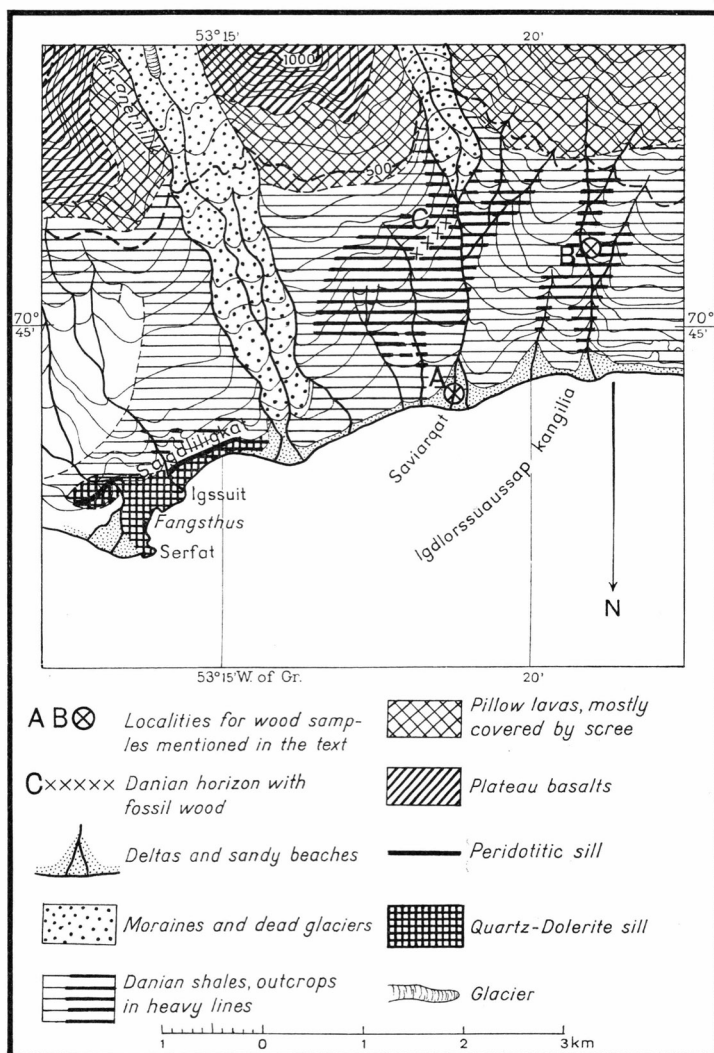


Fig. 1. Geological map of the Serfat-Kangilia area of the Nûgssuaq peninsula, indicating localities of wood samples mentioned in the text.

to a close investigation, the results of which are presented in the following pages.

The rock containing the sample of wood No. 53 is a calcified, arenaceous mudstone, poor in organic constituents. It matches well with the matrix adhering to the surface of the sample of wood marked No. 43 which, probably like No. 53, has originally formed part of a concretion. Such fossiliferous concretions are rather common in the black bituminous shales, so dominant in the marine series of the Nûgssuaq peninsula,

which embrace the period Emscher-Paleocene. In the Saviarqat area it has been possible to determine the age of the concretions in question as Danian.

Acknowledgments. The descriptions of the two pieces of fossil wood dealt with in the following pages, are based on microscope slides which were, for the greater part, cut by myself in the laboratory of the Mineralogical and Geological Museum of the University of Copenhagen. The map Fig. 1, is due to Mr. F. Røhling, Cartographer of the Geological Survey of Greenland; the drawings of anatomical details were executed by means of a Camera lucida; most of the drawings are reduced to two third size for publication, while a few are a half of the original size. The photos reproduced in the Plates No. VI, VII, XI, XII and XIII were taken by Mrs. E. Karlog, Assistant at the Royal School of Pharmacy, Copenhagen, while Mr. Chr. Halkier of the Mineralogical and Geological Museum has with his usual skill and care executed the rest of the photographs reproduced.

Material for comparison was kindly placed at my disposal by the Botanical Museum and the Botanical Garden of the University, and by the Botanical Garden of the Royal Veterinary and Agricultural School, Copenhagen, by the Botanical Museum of the University of Lund (Sweden), by the Yale University's School of Forestry and by l'Inspection des eaux et forêt, Madagascar; The Musée d'Histoire Naturelle, Paris and the Riksmuseum, Stockholm have kindly lent me some relevant papers through the Botanisk Centralbibliotek, Copenhagen.

The Carlsberg Foundation has obliged me with a grant for the execution of a series of paleobotanical papers, which is to a large extent responsible for my concentration on such studies, of which the present is to be considered the first result. The Mineralogical and Geological Museum of the University as well as the Royal School of Pharmacy, Copenhagen have kindly placed working facilities at my disposal, and finally I feel myself indebted to Professor A. Rosenkrantz for the kind interest he has taken in my work.

The two samples of fossil wood (No. 43 and No. 53) and the slides made from them are kept in the collection of type specimens belonging to the Mineralogical and Geological Museum of the University of Copenhagen.

To all individuals and institutions mentioned, I wish to tender my best thanks for all the favours and hospitality which I have received from them.

Mr. WATTERSON, B. Sc., has been kind enough to revise the translation and to read a proof.

***Cedroxylon saviarqatense* n. sp.**

A piece of coniferous wood strongly bored by *Teredo*, ca. 8 cm long, with an elliptical outline, 7×5 cm in size and, as mentioned, with partly preserved cortex. As a rule the growth-rings vary greatly in thickness and as shown in Plate I, Fig. B, series of very narrow rings may alternate with series of rather broad ones. The elliptical shape is due to the fact that most of the younger growth-rings are essentially thicker in the direction of the greater transverse axis of the piece, while the difference in thickness of the individual growth-rings in the central and median parts does not exceed what is sufficient to cause a slight eccentricity; the flattened form of the piece has consequently not arisen by mechanical means (pressure) before fossilization or in the fossil state, but is to be considered as original and determined by growth. Two of the growth-rings in the middle of the transverse section, still almost circular, are outwardly bordered by a layer of whitish spots 0,5 mm broad, which stand out distinctly on the dark greyish background; in the younger and outer of the said two growth-rings, these spots appear as a markedly discontinuous layer, in the older and inner as an almost continuous one. Also the border of many other growth-rings is marked by local groups of such whitish spots each representing an anomalous (traumatic) axial resin canal. Under the pocket lens on the polished surface of the transverse section the rays, in spite of their delicacy, stand out rather distinctly and they can also be traced in the spaces between the resin canals. Where the cortex is preserved the surface of the specimen is uneven, on account of rather regularly distributed low protuberances, in outline irregularly elliptical, 3—5 mm long and 2—3 mm broad; in the transverse section they appear under the lens as shining black spots, tangentially stretched and about 1 mm thick, well differentiated from the bulk of the otherwise dark-greyish, 3—4 mm thick cortex.

As can be seen from the photographs reproduced in Plates I—V, the microstructure of wood as well as of cortex is in most cases well preserved; only in the central part is the tissue ruptured and the elements somewhat disintegrated (Plate I, Fig. A). Difficulties in the photographic reproduction of the slides were caused especially by the dense black content (for the greater part presumably of resinoid origin) of the parenchymatous

elements of the wood; the main part of the secondary lamella of the tracheidal wall is often dissolved and replaced by calcite, but even in such cases the primary lamella as well as the part of the wall bordering the cell cavity may be well preserved. Where the pit membrane and torus have disappeared, the place of the bordered pit on the tracheidal wall is, of course, only discernible by the pit aperture and the outline of the pit chamber.

A small piece of the fossil wood (ca. 5 grammes) was pulverized and then heated in a combustion-tube. During this process whitish vapours with an aromatic odour reminiscent of that of pine tar were given off, and on the inner side of the tube a coating was deposited consisting of yellowish drops and microcrystalline particles, evidently decomposition products of resins and other heat volatile components.

Anatomical description of xylem.

As is evident from the photograph Plate I, Fig. A, the specimen shows no medulla, consequently it must be part of a root. As mentioned above, the centrally located tissue is unfortunately less well preserved, and so it has not been possible to determine with certainty the number of primary xylem strands; a diminutive centrally located resin canal has left a few traces of its epithema. As can be seen from the figures in Plate I, the broader growth-rings may show a rather even transition between the tracheidal layers first formed and those formed later, while especially the narrow and quite narrow growth-rings exhibit features characteristic of root-wood i. e. large thin-walled tracheids in the layers of first formed (spring) wood with a rather abrupt transition to the few layers of small and thick-walled elements of the last formed wood of the season. In the Figs. C and D, Plate I, some bordered pits can be observed in transverse section on the radial walls of the broad tracheids of the spring-wood, one or two on each wall. In Plate I, Fig. D, parts of two tangential series of traumatic axial resin canals are shown; apart from their position in the growth-zone, the irregular and partly dissolved epithema indicates their anomalous character; where a medullary ray is crossing the series of resin canals, the ray cells are in size and structure approaching the adjoining epithema cells, and like these are filled with a dense black resinous material. Plate II, Figs. A and B, show resin canals developed where there is an even transition between the first formed parts of the growth-ring and those formed later, but here too, they appear to originate in the border layers between spring- and summer-wood. In Fig. B a short horizontal resin canal, also anomalous, is seen emerging from one of the axial canals and wedging its way through three rings; the border layer of this canal is at least partly developed as an epithema.

In the first formed part of the growth-rings the tracheids measure up to 100μ in radial transverse section, while the traumatic axial resin canals attain a width of up to 600μ ; their outline may vary — as shown in the figures — from being almost circular to short elliptical.

Radial section. Of considerable interest is the arrangement of the bordered pits on the radial walls of the tracheids. Where the first formed elements of the growth-ring are of the maximum width, the pitting — especially towards the ends of the tracheids — offers a view as shown in Plate II, Fig. C; the bordered pits are here alternating and densely crowded, with polygonal outlines due to mutual pressure. In the last formed narrow tracheids the pits are arranged in a single row and are more or less detached from one another (Plate II, Fig. D). Where the transition between spring- and summer-wood is abrupt, a characteristic of the growth-rings of a root, the last formed tracheids of the spring-wood very often exhibit a pitting of the type shown in Fig. 2, A and B. In Fig. 2, A, the last formed and outermost broad tracheid exhibits markedly opposed bordered pits, with crassulae (rims of Sanio) which sharply separate the pit-pairs; in Fig. 2, B, are shown two tracheids with predominantly opposed bordered pits, but with more densely connected pit-pairs between which the impacted crassulae are seen; the outermost broad tracheid also shows some star-clusters of bordered pits. As can be seen from the figures, crassulae develop immediately where the method of arrangement of the pits changes from, as some authors consider, the “araucarioid” to the “abietoid” type.

Fig. 2, C, shows part of a radial tracheidal wall, with well preserved bordered pits exhibiting torus as a finely dotted disk with a stellate-lacinate outline. In the parts of the radial section shown in Fig. 3, A and B, some rows of the normal xylem parenchyma are discernible; its cells are rather thick-walled with pits distinctly visible in the transverse as well as in the tangential walls; parenchyma seems to be a common feature in the wood described, but it occurs only between the tracheids in the outer part of growth-ring. These figures show tracheids with detached or opposed bordered pits, with the pit-pairs intersected by crassulae; Fig. 3, A, shows also some cells of a ray. The pits in the tangential as well as the horizontal walls of the ray-cells were here, as well as in the parts given in Fig. 2, D, and Fig. 3, C (transverse section), to some extent so distinct that they could be fully drawn up in the figures. The pits in the radial wall appear as oculipores, in all those cases where it has been possible to follow the contour in the wall of the tracheids. Most often this is not the case, partly on account of the dense black material (resin) which so often fills the ray-cells and thus obscures the structure of the radial walls, and partly because, as mentioned above, the radial walls of the

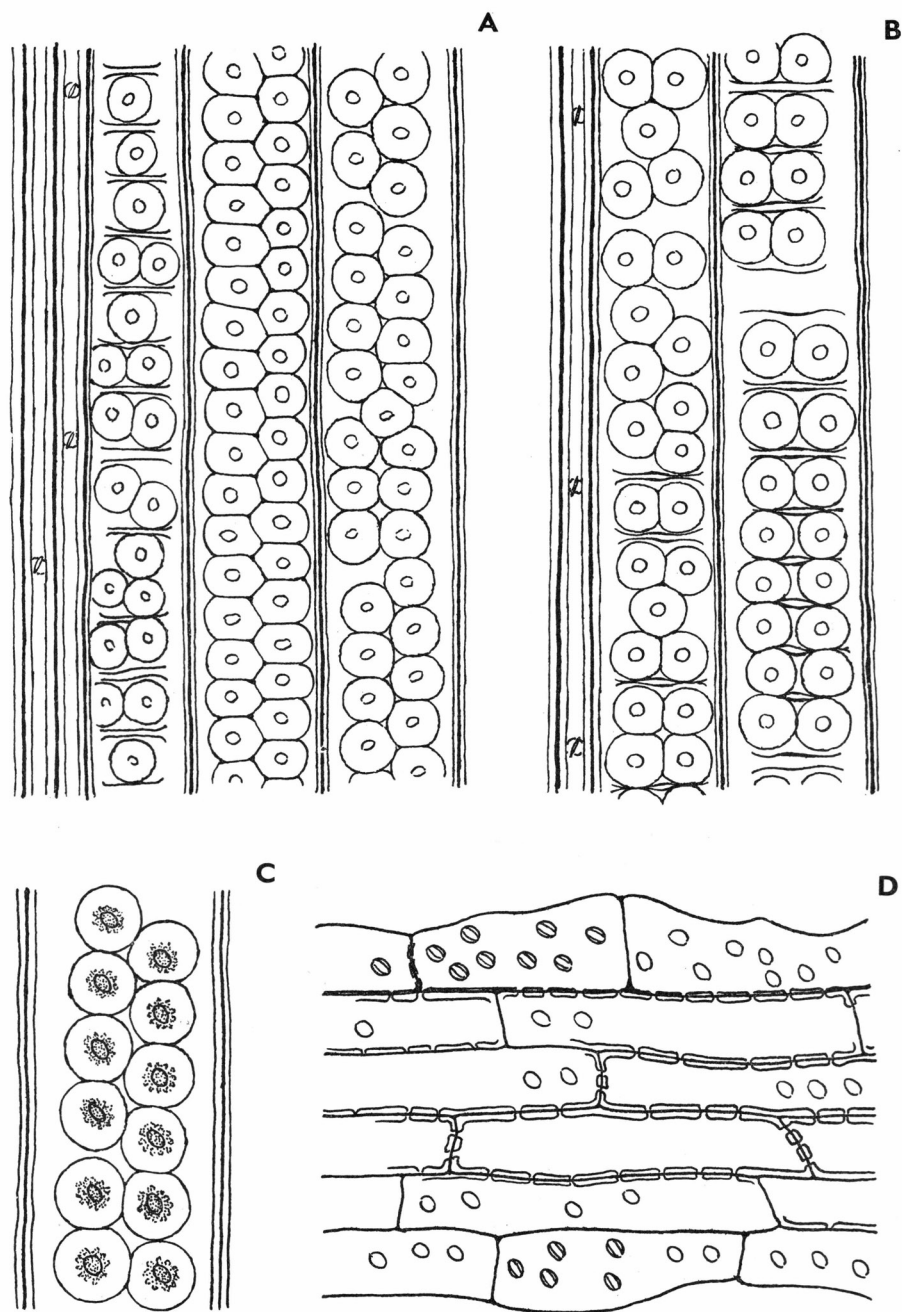


Fig. 2. *Cedroxylon saviarqatense*. Radial longitudinal sections of xylem, A is showing the transition from alternate to opposed pitting with crassulae in the tracheids at the boundary between spring- and summer-wood. B, two tracheids of the boundary with predominantly opposed pits. C, bordered pits of a tracheidal wall with tori of a stellate-lacerate outline. D, ray cells with pitting partly discernible. (A, B and D $\times 280$; C $\times 430$).

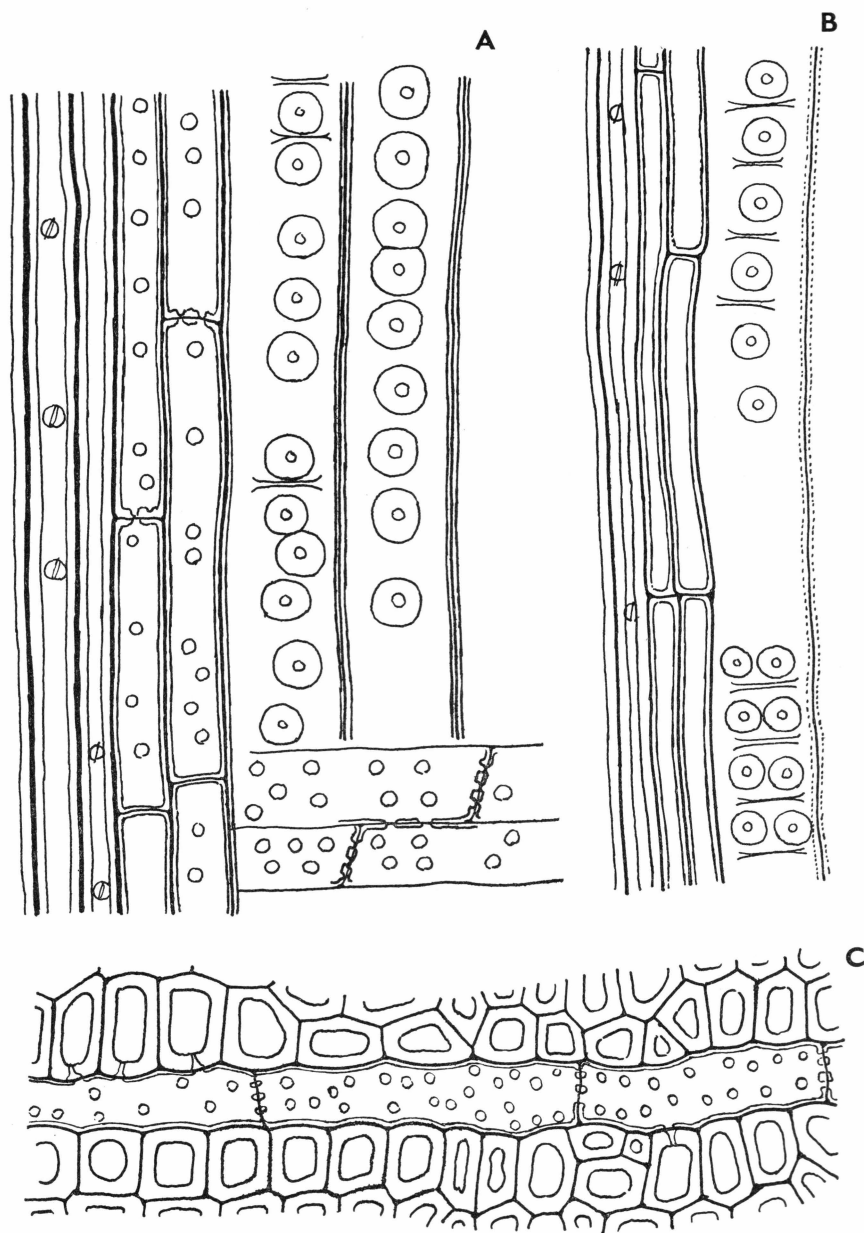


Fig. 3. *Cedroxylon saviarqatense*. A and B, radial longitudinal sections of xylem showing tracheids and xylem parenchyma. C, part of a transverse section of xylem including some ray-cells, exhibiting the Abietinian pitting in the horizontal as well as in the tangential walls, with adjacent tracheids of summer wood. (A, B and C $\times 280$).

adjacent tracheids in most places show the secondary membranes in an advanced state of dissolution. In the latter case the pits in the radial walls occur only in the part belonging to the ray-cell, i. e. without border. The marginal cells which are more thin-walled than the other cells of the ray, have undulating free borders, they line the edges of the rays as a continuous layer. Each ray-cell spans 3—6 tracheids radially.

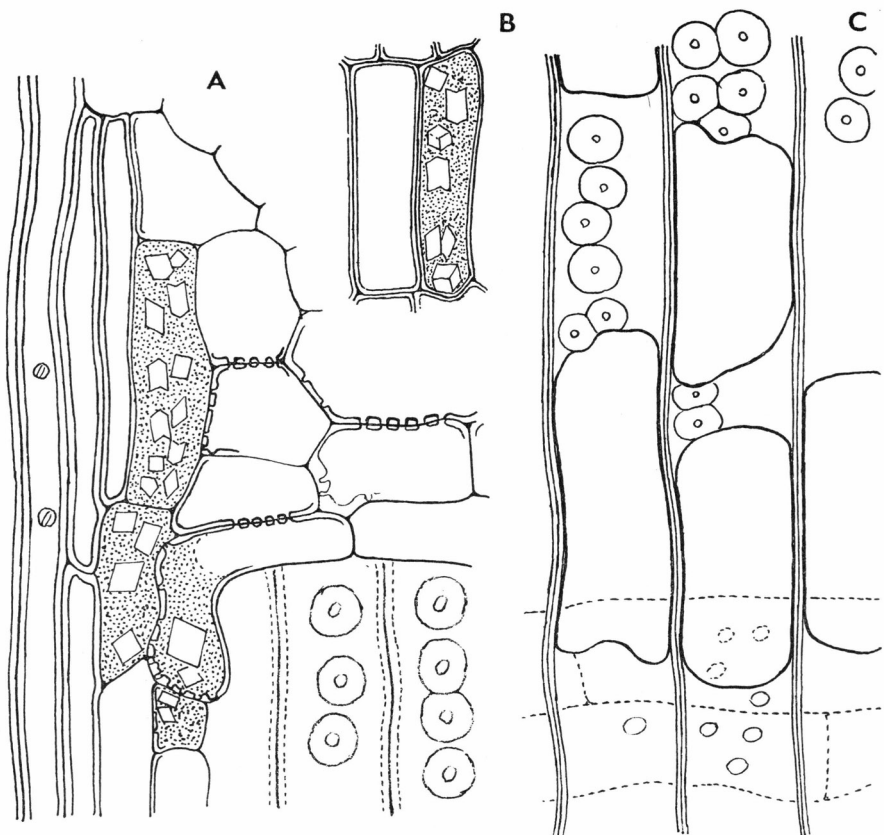


Fig. 4. *Cedroxylon saviarqatense*. A, B, and C, radial longitudinal sections of xylem. A and B, crystal-bearing cells of rays as found in connection with the parenchyma lining the balsam-cysts. C, tylosis in springwood tracheids. (A, B, and C $\times 280$).

In the anomalous cellular tissue occurring where the ray crosses a layer of resin canals, crystals are rather common, whereas they could not be seen in the normally developed parts of the rays. A resin cyst with the surrounding tissue is shown in Plate III, Fig. B, and crystal-bearing parenchyma is also figured in Figs. 4, A and B. The crystals (single or twin crystals) must be considered as pseudomorphs after calcium oxalate crystals, presumably jacketed by a thin lignified layer.

They are conspicuous in the resinous material which fills the rest of these parenchyma cells, the walls of which are thick and strongly pitted. In the broader tracheids tyloses are not uncommon; Fig. 4, C, shows such tracheids blocked up by tylosis. Traumatic resin canals, as they appear in radial section, are figured in Plate III, Figs. C and D. In the part shown in Fig. C the resin canals seem to be developed in the outer part of the growth-ring, whereas in Fig. D they occur on the border between spring-and summer-wood. The canals have the character of an axial row of anastomosing cysts and are, as is seen in the photographs, bordered by thick-walled, pitted parenchyma cells: the cells of that part of the ray running between the resin canals approach the epithema cells of the canals in regard to the thickness of their walls and the style of pitting. In addition they may, as mentioned previously, become crystal-bearing.

Plate IV, Figs. A—D, show parts of tangential sections. Some rays, especially those attaining maximum height (20—25 cell rows), are locally 2 cell-rows broad, but rays with a width of 1 cell-row are most common. Plate IV, Fig. B, shows the pitting in the tangential walls of the latest formed tracheids of the growth-rings, i. e. in the thick-walled small tracheidal elements. The bordered pits, as is typical in conifers, are here distinctly smaller than the pits in the radial walls. In the tangential walls of the ray-cells the simple pits are recognizable in some places. (Plate IV, Fig. B).

Plate IV, Fig. C, shows the features of a tangential section through a series of resin canals. The traversing ray-cells are seen on each side flanked by one or two layers of the thick-walled epithema, and thus they appear as conspicuous formations, 3 or 4 cell-rows broad. The resin cysts anastomose laterally, thus forming a network of considerable resin-bearing capacity. The vesicular, gritty content filling the cavities presumably represents the balsam secreted in the cysts — though certainly in a transformed condition. Plate IV, Fig. D, shows radial resin canals which in tangential view of course present themselves in transverse section. It is apparent from the figure that they are developed as what can be considered as a very high and broad ray; in the tangential view the cells of the epithema are more prominent than in transverse section (cf. Plate II, Fig. B).

Anatomical description of the cortex.

The cork and outer parts of the cortex have been worn away by abrasion so that only the inner layers remain; with its well preserved anatomical details this tissue presents, however, some facts of no little interest. A characteristic feature is the enormous groups of sclereids (Plate V, Fig. A) forming clusters up to ca. 5 mm long, 2—3 mm broad,

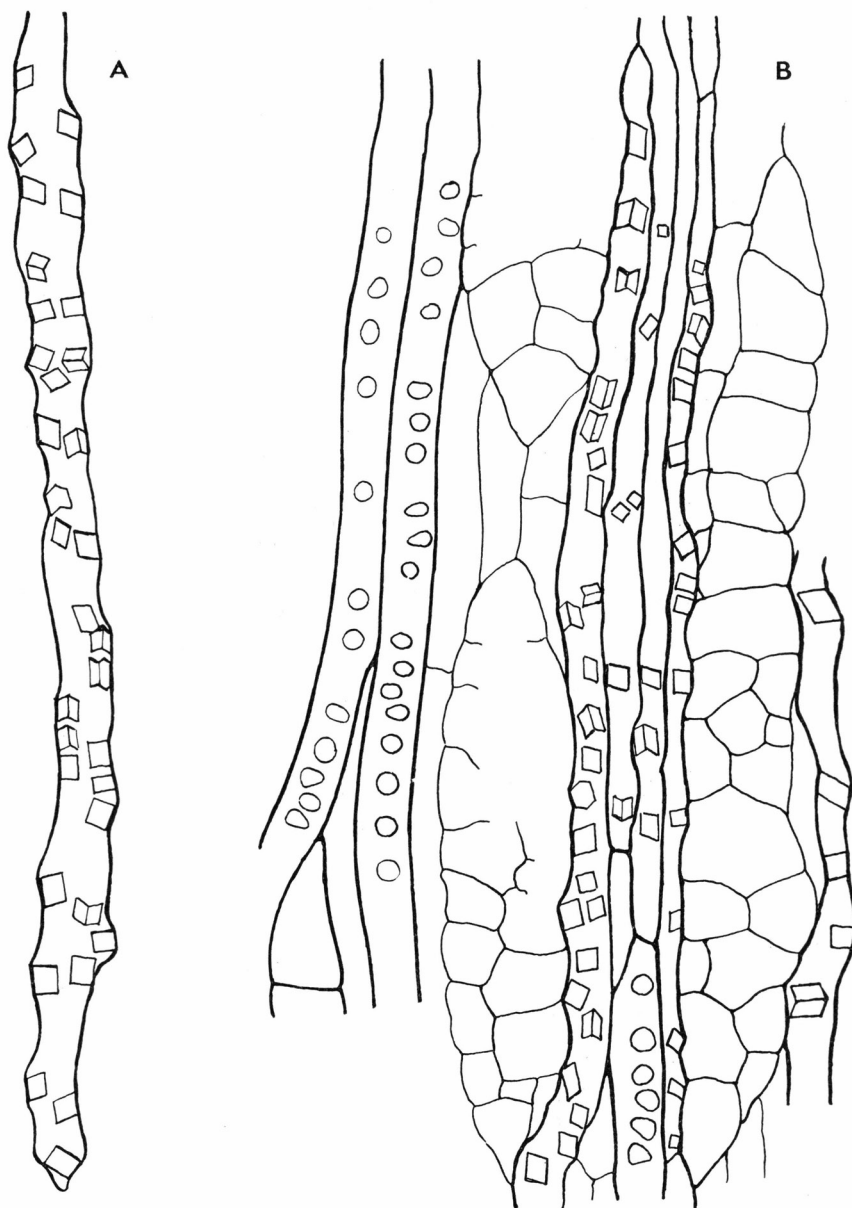


Fig. 5. *Cedroxylon saviarqatense*. Tangential longitudinal sections of cortex. A, fusiform cell enclosing numerous pseudomorphs after calcium oxalate crystals. B, fusiform crystal-bearing cells, rays and a few sieve-tubes. (A, B $\times 280$).

and ca. 1 mm thick. As they are more resistant to the influence of abrasion than the interjacent tissue consisting of thin-walled elements, they form the low protuberances on the surface of the cortex which were mentioned above. The sclereids of which they are composed are very thick-walled, and have laminated and finely pitted walls; in Plate V, Fig. A, their contours in the section can easily be followed under the reading glass: they may be described as short ramifying astrosclereids. In Plate V, Figs. B and C, such sclereids are seen more highly magnified, B also shows parts of cortical ray-cells and vertical rows of crystals, and in C the cambial layer is visible. In the last developed cambial tissue, consisting of thin-walled elements, a series of axial traumatic resin canals is still under formation. Between the parenchyma rays of the cortex the radial rows of sieve tubes are discernible.

In Fig. 5, A and B, some more details of the anatomy of the cortex are shown. An axially stretched fusiform element containing abundant crystals, both single crystals and twins, is figured in A. The rows of crystals shown in Plate V, Fig. B, are also enclosed in such cells, and crystals here, like those in the xylem, are of course pseudomorphs presumably after calcium oxalate; each single crystal has been jacketed by a thin probably cutinised coat. This may also have been the case with the wall of the surrounding fusiform cell, by analogy with what is found in recent *Abies* and *Cedrus* species. In the tangential section of the cortex given in Fig. 5, B, some ray-cells are seen, as well as several crystal-bearing elements of the type in question. To the left of the figure, some sieve tubes are also figured; as the sieve plates are dissolved, the sieve pores could not be observed. The circular figures within the longitudinal walls of the sieve tubes, indicate the sites of the plates.

Summary.

Root-wood of a conifer with adhering patches of well preserved cortex. Growth-rings of varying thickness, in some series rather narrow with thin but sharply defined "summer-wood". The tracheids of the "spring-wood" measuring up to 100 μ in radial extent. A minute resin canal is found in the centre of the primary xylem; tangential bands of axial traumatic secretory ducts frequent, always formed in the border layers between summer- and spring-wood and in some cases forming a continuous layer encircling the growth-ring; radially orientated ducts, emerging from the axial ducts and traversing several growth-rings, may be observed; the axial as well as the radial ducts are coated with short, thick-walled cells with finely pitted walls. Tracheids of the spring-wood pitted on the radial walls with two, only towards the ends of the tracheids with three, rows of generally alternating bordered pits, angular in

outline by mutual pressure with elimination of crassulae, 10—15 μ in diameter; in the tracheids at the transition between spring- and summer-wood the pits often become opposite and the pits-pairs separated by crassulae; one row of separate bordered pits is the common feature in radial walls of the tracheids of the summer-wood. Where torus is preserved, it shows a lacerate outline with small radiating lobes in the circumference. On the tangential walls of the summer-wood bordered pits are numerous, they measure 4—6 μ in diameter and are arranged in a regular row. Lumen of the spring-wood tracheids is often occluded by tyloses. The rays are devoid of marginal tracheids, but have distinctly differentiated thin-walled marginal cells, somewhat higher than central ray-cells, with undulating free borders, the tops of the undulations corresponding to the walls of the tracheids. The ray-cells exhibit Abietinian pitting fairly distinctly, and in the cross-field between tracheid and ray-cell are found 1—2 rows of oculipores. Normally developed wood parenchyma is common in the summer-wood; the parenchyma cells as well as the ray-cells, are most commonly filled with a black resinous material, as is also the parenchyma bordering the ducts. Crystals are present, predominantly developed in ray-cells adjacent to the resin ducts. Rays attain a height of up to 25 cells, most commonly 1, but locally 2 cells broad; the radial resin ducts are formed in abnormally widened rays.

In the secondary cortex the sieve tubes are discernible, and between them are found cells with the form of a slender spool, containing numerous pseudomorphs of single or twin crystals; the crystals are coated with a thin special membrane. The wall of the crystal-bearing spool and the coating of the crystals are resistant to the action of hydrochloric acid. Enormous clusters of short ramifying astrosclereids are a very striking feature of the bark.

Affinities.

The type of fossil coniferous wood designated as Cedroxylon includes, according to the definition given by W. GOTHAN (1905), those form-species the xylem structure of which falls within the range of types represented by the recent genera: Keteleeria, Pseudolarix, Cedrus, Tsuga, and Abies.

Cedroxylon (KRAUS 1872) is redefined by R. KRÄUSEL (1949 page 158) as follows "Kreuzungsfeld: Tüpfel klein, zu mehreren auf dem Felde; Quertracheiden, wenn vorhanden, glattwandig; waagerechte und tangentielle Wände der Markstrahl-Zellen \pm stark getüpfelt. (Abietinéen-Tüpfelung); Holzparenchym (meist spärlich) vorhanden oder fehlend. Harzgänge nur im Wundholz".

In the Cedroxylon group the same author has also included fossil form-species, such as *C. Nordenskjöldi* and *C. (Cedrus) Penhallowii*, which clearly show the transitional form of pitting-style, characterized as a "Mischtypus" of the "araucarioid" and the "abietoid" pitting. Consequently they should be expected to fall within the range of types 14–23 in the key given on page 150 (l.c.). However, as the same features occur in the recent *Cedrus* sp. and are rather frequent at least in the secondary xylem in the root of these trees, as pointed out by F. BAILEY (1933) and thoroughly discussed by R. KRÄUSEL (1949 pp. 98 — 102) — it must be permissible to expand the definition in this respect and consequently to incorporate the two fossil species referred to, as well as the species here described, in the form-genus Cedroxylon. Thus use of the key in question demands some foresight; but the existence of the typical "abietoid" pitting-style: opposed bordered pits with crassulae intersected between the pit-pairs — or rows — in at least some of the tracheids, will probably be in most cases a safe guide. The type of pitting-style found in the Auracarians living and extinct does otherwise not quite match with the type found in most of the form-genera described as exhibiting the "Mischtypus".

As can be seen from our figures and description, the fossil in question has, besides the series of annual-rings characteristic of rootwood, other growth-rings which cannot be distinguished from those of stem — or branch-wood. However, as the centre of the piece is without medulla, it must be derived from a root. The difficulty in determining from the structure of the growth-rings whether a certain piece of wood of which the central part is not available, derives from a root or a stem (branch) is thoroughly discussed by W. GOTHAN (1905).

On the whole, the xylem of our fossil corresponds very closely to the secondary xylem of the recent *Cedrus* species. The structure of the rays, the development of the xylem-parenchyma, the configuration of torus and the structure of the traumatic axial resin canals all point to this; the presence of short radial resin ducts emerging from the axial canals is a feature which according to E. W. Jeffrey (1904) occurs only in *Cedrus*. In R. KRÄUSEL'S key (1949, p. 158), *C. Shimakurae*, *C. Nordenskjöldi*, *C. Schenkii*, and *C. affine* are stated to be devoid of a normal wood parenchyma. As to *C. Penhallowii*, an error has slipped into the key indicating "Rand-Tracheiden vorhanden", but this particular species is not provided with marginal tracheids ("no ray tracheids are present in the miocene wood" (E. S. BARGHOORN and J. W. BAILEY. 1938, p. 645) — these authors assign *C. Penhallowii* to be of Miocene age. *C. Orvini* O. ARBO-HØEG possesses marginal tracheids and lacks horizontal resin ducts, while *C. greenlandicum* WALTON (1927) has no marginal tracheids but differs from our fossil in lacking ducts of the

said type. The latter two Cedroxyla as well as *C. Nordenskjöldi* are presumably of about the same geological age as our fossil (Danian-Paleocene). *C. Nordenskjöldi* also has marginal tracheids, a feature of obviously earlier origin than supposed by E. S. BARGHOORN and J. W. BAILEY (l. c.), who consider them a rather modern acquirement in *Cedrus*. Among the other Cedroxyla admitted to the key, *C. Yezoense* is distinguished by having only 1—2 rather large pores in the crossing field between ray-cell and tracheid; *C. Salisburiodes* (GOEPPERT) KRÄUSEL seems of a rather doubtful systematic position, it is showing Abietinian pitting of the ray-cells and anomalous axial resin canals. *C. Yendoii* STOPES and FUJII (1911, including *C. Yendoii* SHIMAKURA (1937)), are described as having one row of bordered pits on the tracheidal radial walls, axial as well as radial ducts, and several small half bordered pits in the crossing field — it may be a species related to the fossil described in this paper. The age is given as Cretaceous.

Of the Cedroxyla known, *C. Penhallowii* is no doubt that which is most closely related to our fossil; furthermore the excellent description and figures given by E. W. JEFFREY (*Sequoia Penhallowii*) (1904) and E. C. BARGHOORN and I. W. BAILEY (*Cedrus Penhallowii*) (1938) allow a more detailed comparison than is the case with most of the other fossil woods referred to as Cedroxylon. Our diagnosis corresponds very closely to the one given by E. C. JEFFREY l. c. p. 328; and the description given by the last named authors contains details complementary to Jeffrey's diagnosis and found again in our fossil. The layers designated as "Auriferous gravels", in which *C. Penhallowii* is said to be found, seem to embrace series of different ages ranging from Cretaceous to Miocene or even Pleistocene. The authors in question refer them, as previously mentioned, to the Miocene; in the *Lexicon of Geologic Names of the United States* (1938 Part I p. 92) it is stated "*Auriferous gravels*. A descriptive term that has had considerable usage in northern California for gravels of Cretaceous, Eocene, and Pleistocene Age (see under Weaverville Formation)"; under this item is noted (Part II, p. 2292): Weaverville Formation-Eocene. North-California (Klamath Mountains) 1. Series, Cretaceous; 2. Series, Lignitic shales and lignites. The fossil plants present toward the base of the series at various localities are of Eocene age, but whether all the beds belong to a single sequence has not been determined. By F. H. KNOWLTON, like the Fossil Floras of Sierra Nevada auriferous gravels, considered to be Miocene. According to N. MACGINITIE (personal communication), who worked on this flora under the direction of R. W. CHANEY, the fossil plants are Eocene, and probably to be correlated with the floras of auriferous gravels of the Sierra Nevada.

In 1935 (Geol. Soc. Am. Proceed. 1934) HINDS assigned their age to Eocene or Miocene. The geological age of *Cedroxylon Penhallowii* is consequently somewhat doubtful; in a accumulation of fluvial sediments fossils such as lignites may easily be moved from older to younger strata. Our fossil undoubtedly originated from Danian layers, and if the Californian wood may be referred to Eocene, the two fossils also approach each other with regard to geological age; however, the *Cedroxylon* type can be traced from Cretaceous to the present time.

E. S. BARGHOORN and I. W. BAILEY term their fossil wood *Cedrus* (*Cedrus Penhallowii* JEFFREY n. comb.) and not *Cedroxylon*, arguing that "if *Cedroxylon* is to cover the range of structural variability of such genera as *Abies*, *Tsuga*, *Cedrus*, *Pseudolarix*, and *Keteleeria*, as has frequently been assumed, it must be obviously redefined in such a manner as to obviate the necessity for several of the form-genera which are listed in the preceding paragraph" (*Protocedroxylon* GOTHAN, *Metacedroxylon* HOLDEN, *Planoxylon* STOPES, *Thylloxyylon* GOTHAN and *Protopiceoxylon* GOTHAN). The last named are all wood types with Abietinian pitting of the ray cells but with a more or less marked "araucarioid" pitting of the tracheids, i. e. (exhibiting the "Mischtüpus" of R. KRÄUSEL).

In these cases it is mainly a question of geologically older types (Triassic, Jurassic and Cretaceous) which could very well be excluded from the real *Cedroxyla* (R. KRÄUSEL 1949, pp. 99—100); the presence or absence of crassulae, a feature most often admirably preserved in the fossil state, will probably serve in most cases as a valuable criterion for distinguishing the geologically older from the younger types. Anatomically the characters of the secondary wood of *Cedrus* are very much like those of *Abies*, and it can hardly be anticipated that it will be always possible to keep these genera separated in fossils of poor condition. Following W. GOTHAN and R. KRÄUSEL I shall therefore suggest that our wood be referred to the more comprehensive form-genus *Cedroxylon*. The presence or absence of marginal tracheids in the rays is a somewhat variable character; with regard to the recent *Cedrus* spp. E. STRASBURGER (1891) states that they may or may not be developed in the secondary xylem of the same species, and also that they vary in frequency in various region of the very same individual.

If the anatomy of the cortex had not entered into the picture, our fossil might be referred to *C. Penhallowii*, without any other reservations than those caused by the geographical distribution, and the probably somewhat different geological age. The structure of the cortex agrees in most respects fairly well with that found in recent *Cedrus* sp., hence the abundance of the crystal bearing fusiform elements with resistant walls, presumably cutinized in the fossil as well as in the recent species (J. A. BORGMAN (1879) and W. NOELLE (1910)). The last named author remarks

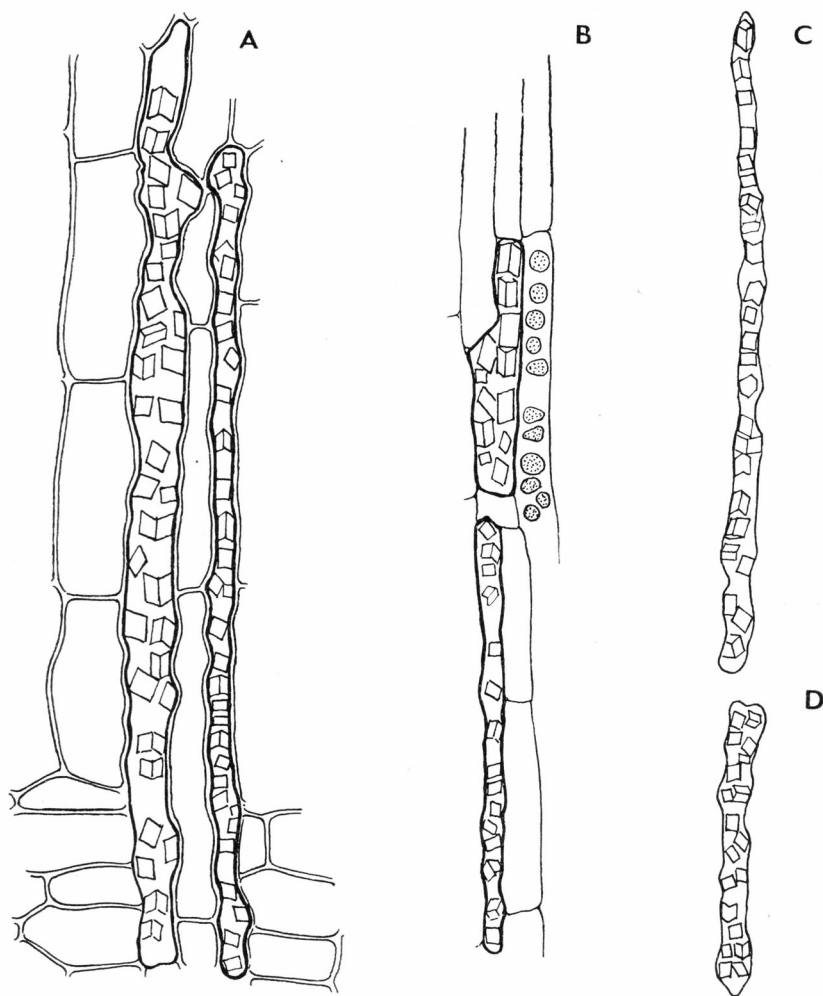


Fig. 6. *Cedrus atlantica*. A, B, C, and D, crystal-bearing fusiform cells from cortex; B, also showing part of a sieve-tube, C and D, after treatment with hydrochloric acid. (A—D $\times 280$).

under *Cedrus Deodora* "In der secundären Rinde finden sich bei dieser Zeder Kristallzellen in solchen Mengen, wie kaum bei einer anderen Coniferenwurzel", Fig. 6, A—D show such crystal-bearing cells from the cortex of the recent *Cedrus atlantica*; those figured in C and D have been treated with dilute hydrochloric acid. The crystals are here of course dissolved, but their outlines are discernible because of the resistant coating (also cutinized) which have closely jacketed the crystal. On the other hand, the cortical groups of sclereids in the fossil deviate greatly from what is found in the recent *Cedrus* spp. O. NOELLE (l. c.) states that they seldom occur in the root in *C. atlantica*, and that they are lacking

in the cortex of the root of both *C. Libani* and *C. Deodora*. I too found groups of cortical sclereids in the root of *C. atlantica*, but they were not very numerous and only of a size in no way comparable with those occurring in the fossil (roots of *C. Libani* and *C. Deodora* were not available for comparison). Some East Asiatic species of *Abies* are on the other hand according to W. NOELLE characterized by having a cortex with "Sclereiden in mächtigen, tangentialgedehnten Platten, die in etwa gleichen Abstand voneinander liegen", which may very well fit in with this character of our fossil but, as known, the *Abies* spp. show resin lacunae in the cortex which it was not possible to demonstrate in the former.

To all appearances our fossil may be considered to be a root fragment of an Abietinian tree showing analogies, in the structure of secondary xylem, with fossils described under the name of Cedroxylon. Among the recent types, our fossil shows the greatest similarity to *Cedrus*; among fossil Cedroxyla it seems closely connected with the West American *Cedroxylon Penhalldwii* nov. comb. R. KRÄUSEL (*Sequioxylon* P. JEFFREY, *Cedrus* P. (JEFFREY) BARGHOORN and I. W. BAILEY). However as the characters derived from the anatomy of the phloem cannot be taken into account in the comparison, as the sample of *C. Penhallowii*, according to the description given, has not retained any cortex and therefore the full identity is impossible to determine, I think it necessary – at least provisionally – to refer it to a new species:

Cedroxylon saviarqatense n. sp.

Geological age: Danian.

Locality: The Saviarqat-delta on the north coast of the peninsula of Nûgssuaq. West Greenland.

***Aphloioxylon groenlandicum* n. sp.**

A piece of fossil wood, ca. 5 cm. long, with a well preserved cortex, making a sector of approximately one third of an axis ca. 8 cm. in diameter; the other two-thirds were presumably broken off when the piece was collected. However, the central part is preserved making it possible to ascertain that a medulla is lacking, and that the piece consequently must originate from a root.

Under the pocket lens the transverse section (Plate VI, Fig. A) shows a densely and finely pitted secondary xylem of a markedly diffuse-porous type, with rather faintly pronounced growth-rings, 2 to 3 mm thick; it is traversed by numerous rays which evenly increase from the center towards the cambial zone, and of which the broadest are up to 1,5 mm in tangential extent in their peripheral part. The ray tissue occupies between one third and one half of the area.

The broadest rays of the xylem are terminated in the cambial zone by an inwardly bent curve; the innermost part of each phloem-ray is thus (Plate IX, Fig. C, and Plate XI) embraced by two protruding parts of xylem. In the cortex, which shows a maximum thickness of 5 mm, the broad rays can be followed to some distance from the periphery. While the colour of the rays in the xylem under the pocket lens is uniformly black and thus forms a distinct contrast to the greyish colour of the interjacent wedges, in the cortex the core of the rays appears as a radiating streak of a brownish colour. In the cambial zone these streaks are somewhat narrower than the outermost part of the corresponding xylem-rays, and in transverse section (cf. Plate VI, Fig. A, and Plate XI) they are very frequently bordered by two white streaks, one on each side. Starting from the cambial region, the white streaks extend outwards into the zone where the broader innermost parts of the cores stand out with almost parallel sides. Generally these streaks are connected with and extending from, a white spot which completely occupies the area of the last phloem and is consequently located in the space between two rays. The white spots are due to the calcite filling up the lacunas, developed by dissolution of the less resistant tissue of the last formed phloem. The brown core wedges out in the outward direction and where the flanking white streaks are fading, an area of black tissue, also a part

of the ray, is seen on each side of the core; these parts generally broaden towards the periphery (Plate XI), thus giving the total ray a somewhat fan-shaped outline.

The surface of the cortex is uneven and in transverse section appears to be made up of protruding arches 3—10 mm wide, between which furrows cut their way as deep as abt. 2 mm below the surface (Plate VI, Fig. A). A conspicuous black border layer, often running concurrent with the projections, but not always continuous, divides the cortex into two zones: the outer zone appears under the pocket lens as a dark-coloured, almost homogeneous tissue, but for a faint pattern of light spots and fractions of the brown parts of the phloem-rays; in the inner zone the alternation of rays and phloem parts produces a more marked pattern, mainly due to the white spots and streaks.

The surface consists of a thin black layer of the same type as that forming the border between the outer and the inner zone of the cortex and like this, is presumably a phelloid layer. The piece clearly shows a formation of scale bark; by means of breaks along the phelloid layer strips of the cortex of a width corresponding with the protruding arches mentioned above are probably peeled off. The length of the strips could not be ascertained.

Cortex and xylem can be easily separated in the cambial zone. Seen under the pocket lens, the traces of the rays in the surface of the xylem appear as axially stretched depressions about 10 mm long and 0,5—1,5 mm broad. As mentioned, the cambial layer within the phloem-rays has an inwardly bent curve which encloses the innermost part of the rays; as a result, an axially directed brownish, double edged streak — representing the core of the ray — may be visible in the middle of the depressions, whenever the connecting part of the cortical ray-tissue with the xylem is preserved. The somewhat projecting parts of the xylem located in the space between the rays frame these as anastomosing lines. The white parts of the transverse section may appear, partly as light streaks flanking the rays, and partly as white, vertical streaks on the crests of the frames, corresponding to the white spots seen in transverse section replacing the last formed phloem. In the transverse section the polished surface of the sample shows some peculiar features, which are presumably to be considered as tissue anomalies. In outline, they are either elliptical, or they appear as wedge-shaped parts of the wood which may be of considerable extent. The wedge shown in Plate VII, Fig. A, measures ca. 20 mm radially and at the cambium has a width of ca. 5 mm; a patch of elliptical outline which breaks the course of the xylem-rays not far from the middle of the piece, measures abt. 3×2 mm. These formations are conspicuous on account of their uniformly black colour, due to the absolute domination of the parenchyma which they contain. The black wedge just men-

tioned, rather gives the impression of being an abnormally broad ray which has arisen by aggregation of many narrower ones (Plate VII, Fig. A); the elliptical patch might be regarded as a medullary spot.

This fossil too, has been preserved by calcification and the crystalline matrix makes photographic reproduction of the microscop slides rather difficult with higher magnifications. These conditions made themselves especially felt with longitudinal sections, where the refraction of the crystalline filling of the vessel lumina has a very disturbing effect, particularly on those parts below the surface of the section and which it was found impossible to reproduce.

Attempts to remove the calcite by means of acid treatment were successful to only a limited extent. In the fossil the submicroscopic particles of the cell walls are either wholly or partly disaggregated. When the structural details of the wall could be reproduced as distinctly as shown by the drawings, it is mainly because the submicroscopic particles of the wall tissue, although separated, are fixed in the calcite matrix; but partly also because the various shades of brown found in the different layers of the cell-walls caused so marked contrasts.

The middle lamella, and the innermost layer of the secondary lamella which borders the lumen, are generally much darker than the main part of the cell wall. This part is most often totally replaced by finely crystalline calcite, especially in the more thick-walled elements (i. e. the fibres of the xylem and phloem as well as the sclereids of the cortex), so after treatment with dilute hydrochloric acid, there is only a very fine brownish powder left, with but few recognizable particles of tissue. Better results were obtained by etching thin cuts, fastened to the glass with hardened balsam. In cuts treated in this way, some parts of the tissue where the decay is less advanced, will be preserved in situ. The perforation plates of vessels, as well as the overlapping tips of tracheids have commonly occurred as such more resistant components, the form and pitting of ray-cells also stand out very well. In the latter case however, the substance of the walls is highly dissolved, and the contours of the lumina are determined almost exclusively by the rather compact dark-brown to black cell content, lining the periphery of lumen and also filling the pits of the cell wall. The photos in Plate IX, Fig. A and B, showing parts of rays in radial section, have been taken from cuts thus treated.

Anatomical Description of Xylem.

Transverse sections of the xylem, observed under low-power magnification, show that the growth-rings have somewhat indistinct boundaries (Plate VI, Fig. A and Plate VII, Fig. A). Their diffuse tangen-

tial outlines are due to some extent to the rather uniform distribution of the vessels, but may also be ascribed to the fact that the border layers in various parts of the same two growth-rings can appear with different sharpness, even within the space between neighbouring rays. This is because in some spaces the difference in diameter between the last formed vessels (and vessel-like tracheids) in one growth-ring, and the first formed conductive tissue in the subsequent one, may be very small and the

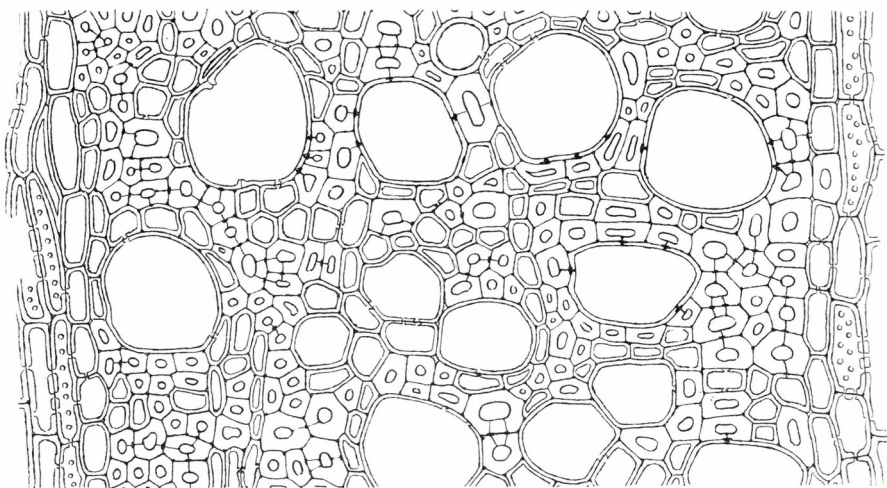


Fig. 7. *Aphloioxylon groenlandicum*. Transverse section of xylem. An area between the margin of two multiseriate rays; tangential tracheidal bands consisting of elements more thin-walled than the fibre-tracheids, and parts of a uniseriate ray are conspicuous. ($\times 325$).

boundary consequently obscure, while in other cases it is distinct (Fig. 8 A). The autumn-wood therefore does not appear as a continuous and uniform border-layer, with the features characteristic of such. In the photo showing part of a transverse section (Plate VII, Fig. B), the borders of the middle ray-interval stand out fairly well. In transverse section vessels and vessel-like tracheids cannot be distinguished; in the narrower last formed part of the growth-rings illustrated, these elements are only about half the width ($40-60 \mu$) of those in the inner part where the vessels are normally $90-100 \mu$ in diameter, but can reach up to 120μ . In the transverse section the elements of the vertical conducting tissue generally appear solitary but they pair off of course where they are overlapping. They are particularly thin-walled, and thus contrast strongly with both the xylem-fibres (Fig. 7 and Fig. 8, A and B) and the thick-walled fibre-tracheids; the latter are rather common and mainly distinguished by their size from the xylem-fibres. The more thin-walled narrow elements which in the transverse sections (Fig. 7, Fig. 8, A and B, Plate VIII, Fig. A) are seen partly to form a network of tangential and

radial bands crossing each other, are parts of two quite different kinds of xylem elements. The radial rows are short rays, often terminated radially by bending round the outer side of a vessel, and here sometimes joining elements of one of the tangentially orientated groups which will prove to consist of tracheids. The relatively thin-walled elements flanking the broad rays may partly be referred to the ray-tissue and are consequently parenchymatic, partly they are of the tracheidal type.

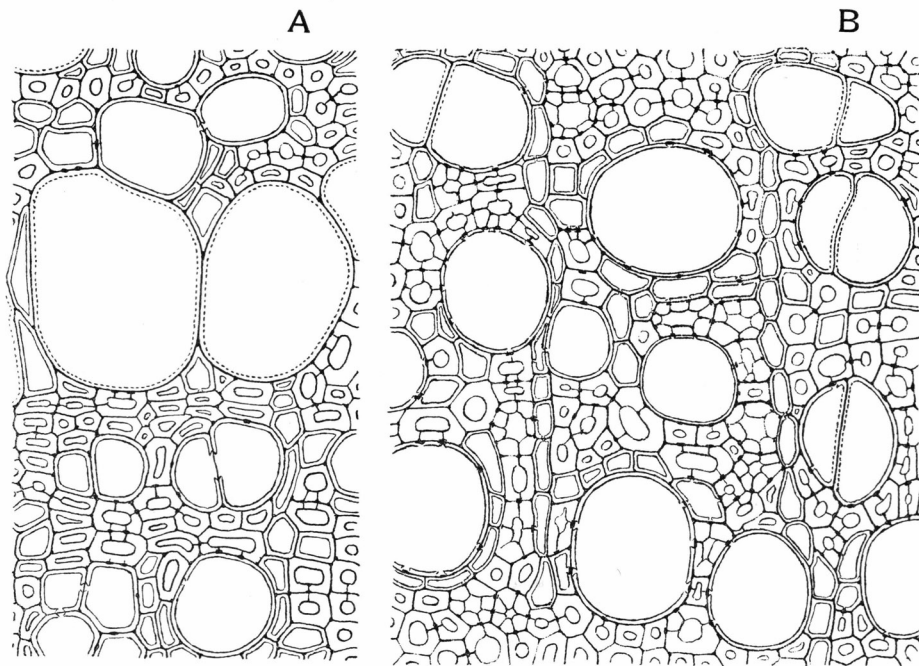


Fig. 8. *Aphloioxylon groenlandicum*. Transverse sections of xylem. In A with the well-defined border of a growth-ring, in B, where the border is scarcely visible, two uniseriate rays are discernable; the tangential tracheidal bands are also very prominent. (A and B $\times 325$).

The broad rays appear with a width of up to 25 cell-rows, and can be recognized as being built up of cells of different length and width. Apart from the somewhat discontinuous layer of border-cells which in the transverse section are isodiametric or of a somewhat radially stretched outline, the elements of the ray tissue are arranged in groups of short cells, alternating with groups of decumbent cells showing long and narrow outlines; the rays are in fact heterogeneous (Plate VII, Fig. B and Plate VIII, Fig. A). Most of the ray-cells are filled with a more or less homogeneous, black material.

The bordered pits in the wall of the xylem fibres, and the fibre-tracheids show the pit-chamber as a small brownish black, lenticular

thickening of the middle lamella, completely filled with dark material: these features are seen in both transverse and longitudinal sections. The pit aperture, forming an extended, highly flattened fine canal, from ascending to almost vertically orientated and running from the pit chamber to the cell lumen (Fig. 7 and Fig. 8, A and B), is also dark-coloured and consequently easily distinguished. The pitting in the side walls of the vessels and vessel-like tracheids could be reproduced only in a few places in the drawings cited, the secondary layers of the walls have to a great extent been dissolved; in such cases the supposed thickness is as indicated by a dotted line.

In the tangential section of the xylem the rays which attain a height of about 15 mm and a width of 1.5 mm are very prominent. They are frequently traversed by combined strands of a few vessels and fibres, in which case (Plate VIII, Fig. B) they assume the character of "aggregated rays of the oak type" (N. E. DADSWELL and S. J. RECORD, 1936). The heterogeneous nature of the broad rays is also discernable in the tangential view (Plate VIII, Fig. B); the border-cells appear rather strongly elongated axially (cf. for instance Fig. 11, A and Fig. 13, A; Plate IX, Fig. A and D) and locally form an almost continuous cover of sheet-cells which continue into the edges of the broad rays as protruding wings 1—2 cell-rows broad (Fig. 9, D). Consequently, our fossil wood is characterized by possession of heterogeneous parenchyma rays of Kribs' type B. Not all of these multiseriate rays attain the maximum width; as is seen from the photo Plate X, Fig. A in addition there are others which are essentially narrower and lower, but no actual transition to the uniseriate rays (Fig. 9, A—C, E, F, G) is found. Rays of the last type are always only one cell-row broad throughout their generally limited radial course, while in height they may vary from one to many cell-rows. Their walls are provided with numerous simple pits, and their lumina generally contain very little of the dark substance so frequently filling out the cells of the multiseriate rays.

The perforation of the vessels is exclusively scalariform; the perforation plate is tangentially ascending, consequently it appears in the tangential cut in section (Fig. 10, A). The bigger conducting elements of the spring-wood have few bars (3—10), while the smaller ones, especially those contained in the later formed part of the growth-rings, have up to 30 bars. In the latter the pit membranes are commonly preserved, and the gaps between the bars consequently closed (Fig. 11, A and D); in such cases it is really a case of vessel-like tracheids differing from the other tracheidal elements of the xylem, as regards shape and thickness of the wall as well as pitting style, also the types represented in Fig. 11, B and C approach the vessel-like tracheids with regard to wall thickness and pitting. In some cases the tracheids may approach the fibres

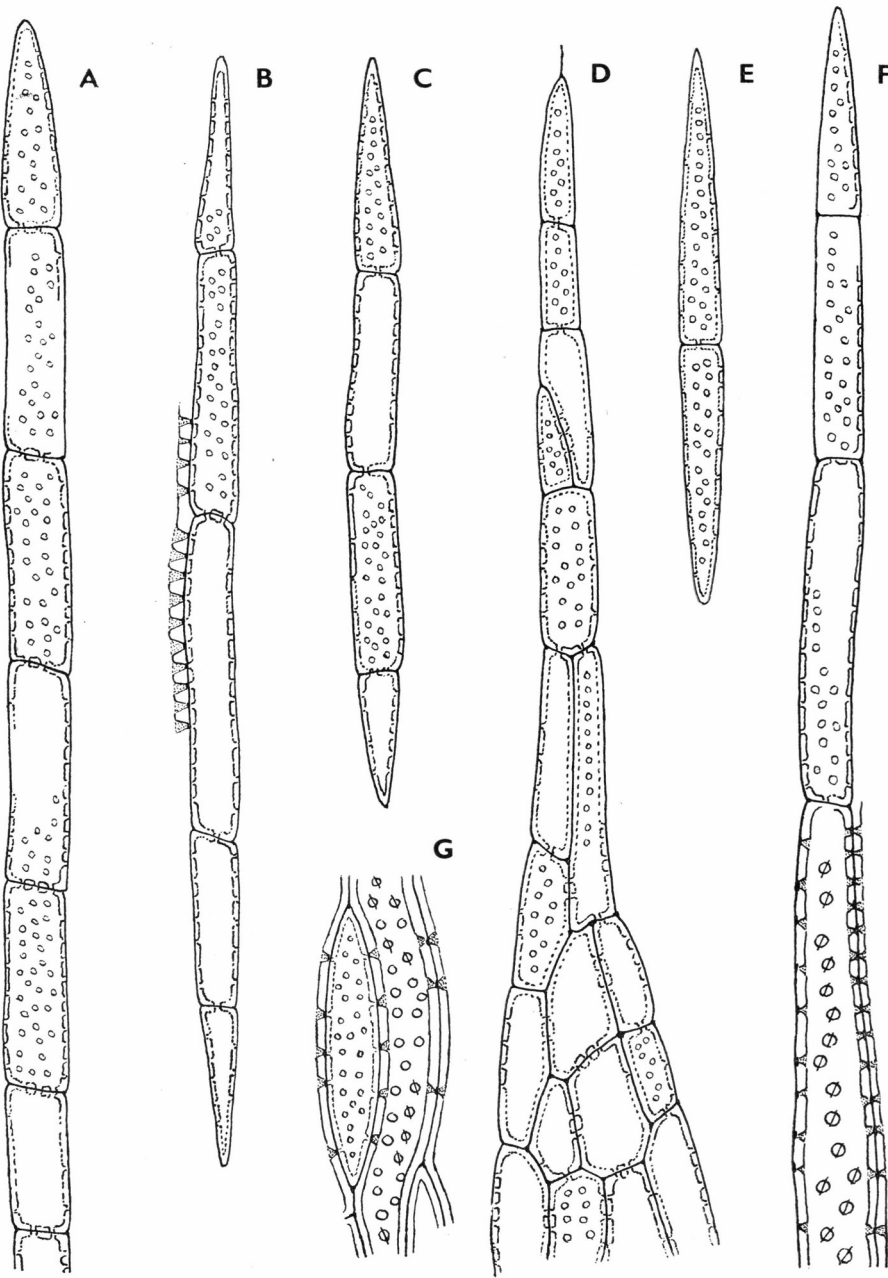


Fig. 9. *Aphloioxylon groenlandicum*. Tangential longitudinal section of xylem. A, showing part of a rather high uniseriate ray; B, C, E, F, and G, lower uniseriate rays in full axial extension. In D is figured the wing at the tip of a multiseriate, heterogeneous ray. (All figures $\times 430$).

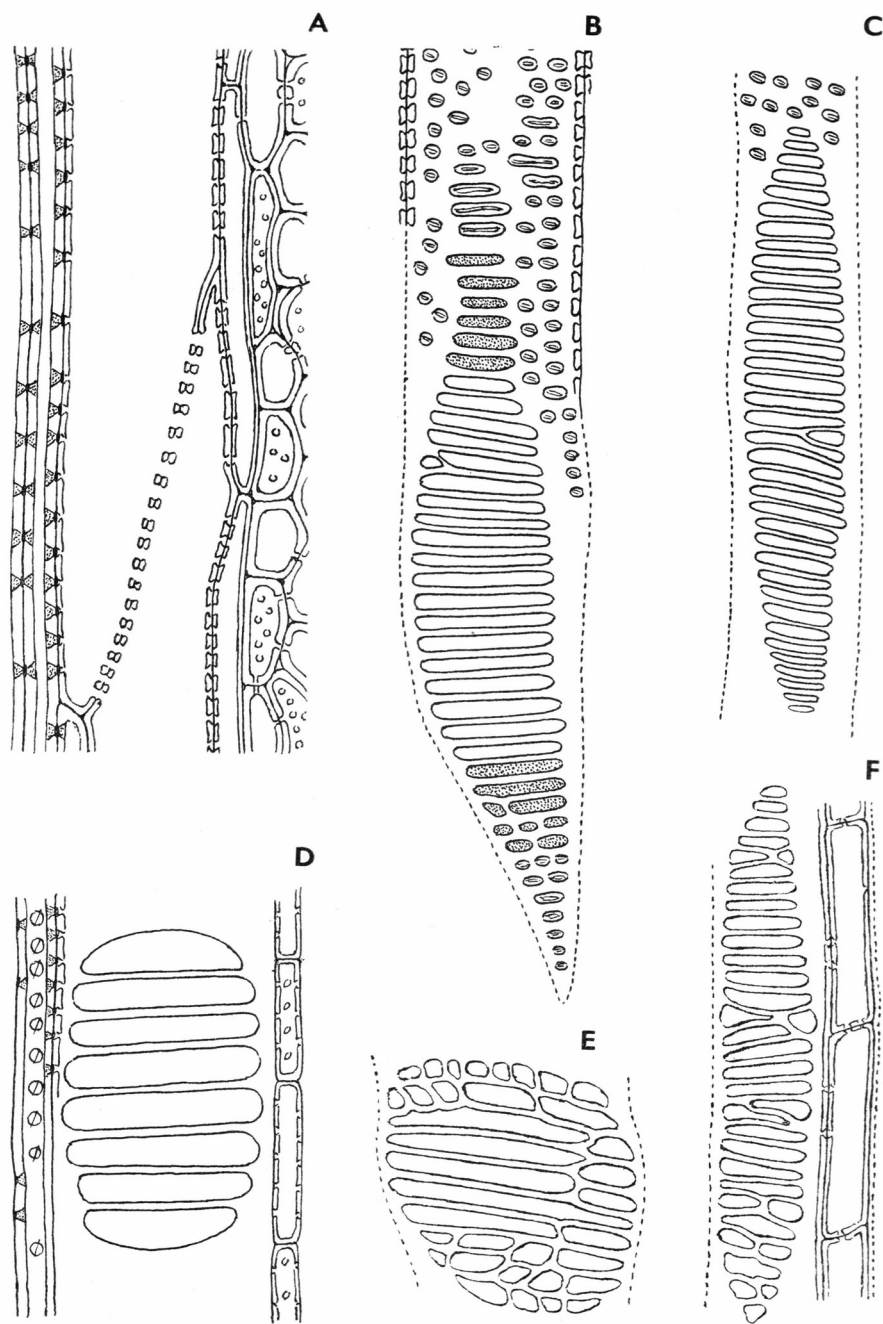


Fig. 10. *Aphloioxylon groenlandicum*. Perforation plates of the vessels; A, shown in tangential section; B, (drawn from an etched slide), C, D, E, and F, as viewed in radial sections. (All figures $\times 430$).

in structure; the example in Fig. 12, D gives the tip of such an element in which the resemblance to a xylem-fibre is obvious ("Faserähnliche Tracheiden" and "Gefässähnliche Tracheiden" according to De Bary).

The vessel members, particularly easily measured in tangential sections, attained up to 600—800 μ in length from tip to tip in the case of the broad vessels; the narrower vessels, and vessel-like tracheids in the last formed xylem of the growth-ring, are longer and measure 1000—1200 μ .

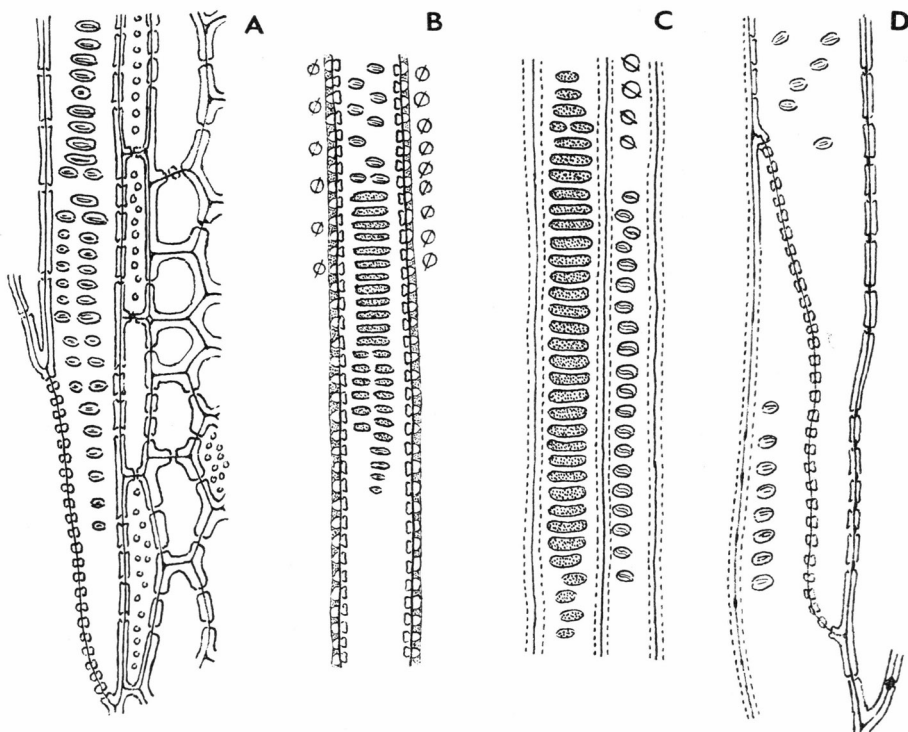


Fig. 11. *Aphloioxylon groenlandicum*. A and D, parts of broad, decidedly vessel-like tracheids; A, joining the sheet-cells at the margin of a multiseriate ray. B and C, parts of narrower tracheids, the narrow, bordered, and radially extended pits are aggregated in scalariform pit areas; in the figures the pit membrane is shown finely dotted. A and D, from a tangential longitudinal section, B and D, from a radial longitudinal section of xylem. (A, B, C, and D $\times 430$).

In longitudinal section too, the bordered pits stand out distinctly on the rather thick walls of the xylem-fibres. As they are found in almost equal numbers in the radial and the tangential walls they appear in both radial and tangential sections in side elevation as well as front view. The pit membrane is most often indistinct; the greatest diameter of the pit chamber is about 12 μ , and appears in front view as a black disc of this size and as an elliptical thickening on the middle lamella in side

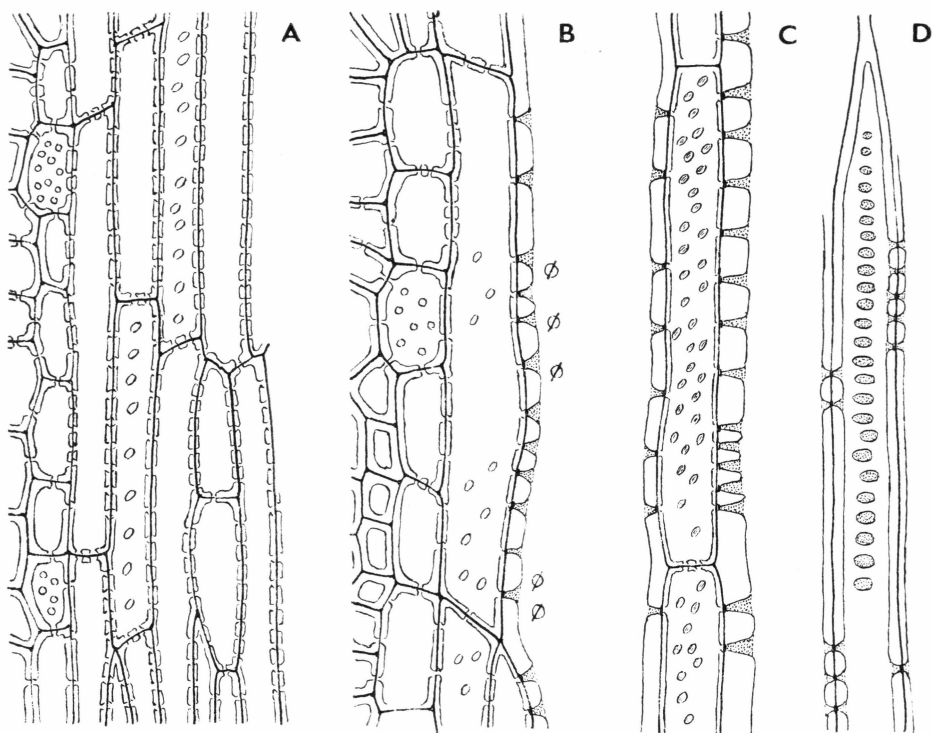


Fig. 12. *Aphloioxylon groenlandicum*. A, B, and C, elements from the tangential bands of thin-walled tracheids of the xylem; in A and B the tracheids are bordering the margin of a multiseriate ray; C, thin-walled tracheids bordering thick-walled fibre tracheid (tangential section); D, an element intermediate between a thick-walled tracheids and a fibre-tracheid. (All figures $\times 430$).

elevation (c.f. transverse sections). The pit aperture, which is considerably longer than the pit chamber is wide is seen in front view as a fine dark steeply ascending line and, on account of the dark material, in side elevation appears as a triangular brownish figure radiating from the pit chamber. The wall substance of the secondary lamella, with the exception of the innermost layer which also coats the pit aperture and pit chamber is mostly dissolved and replaced by calcite; the parts of the fibre-wall located between the pits are therefore hyaline and contrast very well with the apertures appearing as distinct triangular brownish parts of which the tips are directed towards the lumen of the fibre (Figs. 12, B, C, and D, Fig. 13, B and C, Fig. 14, D).

It has not been possible to determine with certainty whether all or at least some of the xylem fibres developed originally as "septate fibres" (W. SPACKMANN and B. G. L. SWAMY, 1949). The type of septae in question described by these authors always appears as a very thin mem-

branes without connection to the primary wall and middle lamella of the initial cell, so they may have been dissolved during the fossilisation of our wood; in some cases such formations do seem to be indicated.

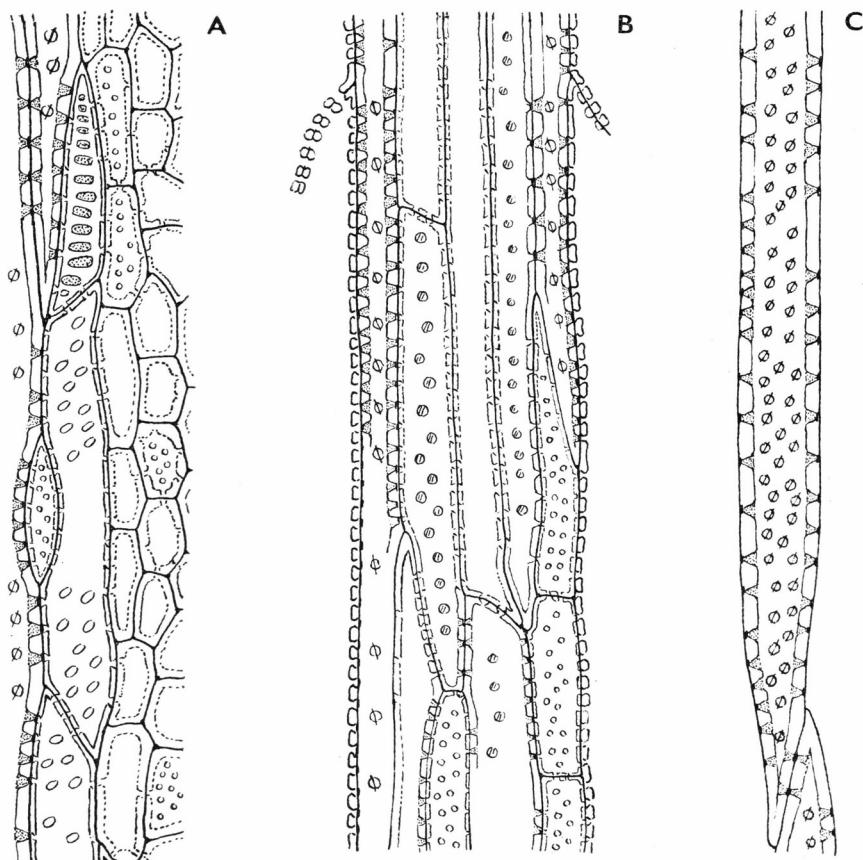


Fig. 13. *Aphloioxylon groenlandicum*. A and B, thin-walled tracheids; in A is shown the end of a vertical strand of tracheids, the element at the tip of the strand with a somewhat diverging form of pitting, in B (to the right in the figure) is seen part of a uniseriate ray (tangential longitudinal sections). C shows part of a broad, thick-walled fibre-tracheid. (A, B, and C $\times 430$).

What are seen in transverse sections as short tangential strands of thinner-walled cells, in longitudinal sections appear to consist of tracheidal developed elements; especially in tangential sections in which, according to the orientation of the strands, there is the greatest possibility of finding groups of them, they are easily perceptible. If only one such element has issued from an initial cell, it will be fusiform with pointed ends, but during its further development the initial cell may be divided by one or more transverse walls, i. e. real walls in which the middle lamella joins that of the longitudinal wall, and thus forms a row

of shorter tracheids. The total length of such a row normally corresponds very well to what may be considered as the length of an initial cell. With regard to thickness of the wall and the pitting style these elements in some cases resemble the xylem-fibres, and in others the vessel-like tracheids; in the case of the thinnest walled elements of this type, which are found especially where they join the sheet-cells of the parenchyma rays, the pit border is but little pronounced, and the outline of the aperture about as large as the pit chamber. However, these elements also have the oblique, ascending pits with elliptical outlines, characteristic of the tracheidal type (Fig. 12 A, and B); in the Fig. 13 B where it has been possible also to reproduce details of uniseriate rays the difference in pitting style between the elements of this and the tracheidal elements is conspicuous.

In the radial section, the oblique perforation plates of the vessels are seen in front view (Fig. 10, B—F).

As already mentioned, the big vessels show but few bars, and the smaller ones a greater number, up to 30. The bars are slender and sometimes bifurcated, in a few cases forming an almost reticulate perforation (Fig. 10, E). Where the vessel is elongated beyond the perforation, the cap shaped part may show the perforation plate continued as a row of bordered pits decreasing in size towards the apex of the vessel. A fine dotting of the pit chamber here indicates, as in Fig. 11, B and C, the presence of a membrane. The pitting style of the vessel-wall is alternating but, as the secondary layer is partly dissolved and the lumen filled with calcite, the pits do not generally stand out clearly in the non-etched slides. The part represented in Fig. 10, B was found in a slide etched with dilute hydrochloric acid. Here the walls are almost intact and the pits are conspicuous. Where the vessel-wall borders the axially stretched sheet-cells of the broad rays, the pitting is rather pronounced with somewhat transversely stretched half-bordered pits which correspond to those of the parenchyma cells of the rays. The pits of the vessel-wall are otherwise short elliptical in outline, and in fact are usually rather closely spaced.

Sometimes the lumen is blocked up by tyloses (Plate VIII, Fig. C), some of the thyllae having a very thin wall, while others have a thicker, finely pitted wall. As far as can be seen from the transverse section, the formation of tyloses may be connected with, or at any rate furthered by the presence of such anomalous tissue parts as represented in Plate VII, Fig. A. In some vessels the calcite filling is of a uniform yellowish brown colour.

In radial section the heterogeneous construction of the xylem-rays stands out very distinctly (Plate IX, Fig. A and B). The cover of the axially orientated sheet-cells, in the broader rays at any rate,

is almost without interruption. No matter what the orientation of the radial cut relative to the ray parenchyma, it consequently always will be possible to see rows of comparatively high cells in the upper and lower part of the radial section of the ray, and adjoining the layer of sheet-cells, rows of the bordering thin-walled tracheids described above (Fig. 11 A, Fig. 12, A and B, Fig. 13, A).

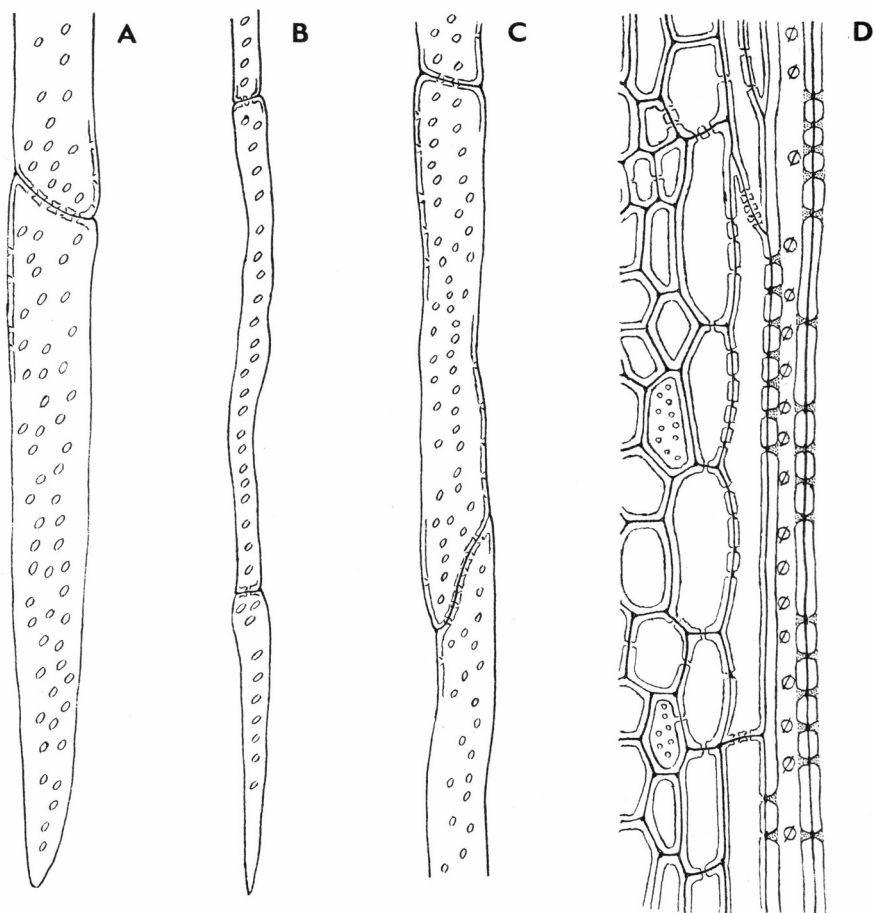


Fig. 14. *Aphloioxylon groenlandicum*. A, B, and C, isolated thin-walled tracheids isolated and drawn from an etched slide. D, margin of a multiseriate ray, bordering thin-walled tracheids and fibre-tracheids (tangential section of xylem). A, B, C, and D $\times 430$.

The walls of the ray-cells are rather thick with a fine, though distinct, pitting but where the sheet-cells border on a vessel or a vessel-like tracheid, the pits are elliptical and procumbent (Fig. 15, F, and G) thus corresponding with the pits in the wall of the bordering elements of the conductive tissue; in all other cases the pits are circular.

A few cells from one of the short, uniseriate rays are seen in radial section in Fig. 15, E; the ray figured here has a height of 2 cell-rows and is accordingly in agreement with what is shown by the tangential section, Fig. 9, E.

Occasionally, and most commonly in parts of the anomalous xylem, it is possible to demonstrate that some of the cells of the heterogeneous rays have been crystal-bearing, especially in the case of the very short ray elements; the rather difficult search for crystals (i. e. pseudomorphs after calcium oxalate) has been facilitated by paying special attention to such complexes of cells which appear to have arisen by division of ray-cells of normal size, i. e. cells considerably smaller than the surrounding elements. The etched slides have also been of importance in this connection; the pictures in Fig. 15, A, B, C, and D are drawn from such slides. The middle lamella of the cells is here partly and the secondary lamella totally dissolved, the interior shape as well as the placing of the pits can on the whole only be seen because the dark cell-content has formed a cast of the lumen. The crystals were formed in "pockets" i. e. within a thin jacket, the character of which cannot be further determined, fitting tightly round the crystal; the jacket has been preserved as a dark-coloured membrane maintaining the shape of the crystal it originally enclosed.

Anatomical description of phloem.

As the cell-tissue of the cortex is rather well preserved (Plate VI, A), it has been possible to recognize details not only of the main features of the very peculiar anatomy, but also some details of the histology which are of importance for the systematic placing of the fossil.

In the transverse section (Plate XI) the cortical prolongations of the broad xylem-rays appear, as already mentioned, as outwardly broadened formations. The core of the ray, consisting of especially thick-walled, frequently crystal-bearing sclereids with dense and fine pits is seen as a wedge directed outwards: in the core the growth increments are marked by layers of thin-walled cells, most of which are also crystal-bearing.

The sclerenchyma wedge is bordered on both sides by a tissue of thin-walled elements of a pronounced meristematic character; in the cambial region this tissue seems to correspond with the border-cells of the broad xylem-rays (Plate IX, Fig. C) — and consequently has a thickness of only one or a few cell layers. After the third growth increment of the cortex (Plate XI) which can be easily identified, not only by the mentioned peculiarities of the sclereidal wedge, but also by the position of the innermost layer but two of obliterated sieve tubes these border-cells form a dilating meristem. In the fossil the cells in the inner parts, i. e. the latest formed parts of the phloem, the border-cells are partly dissolved,

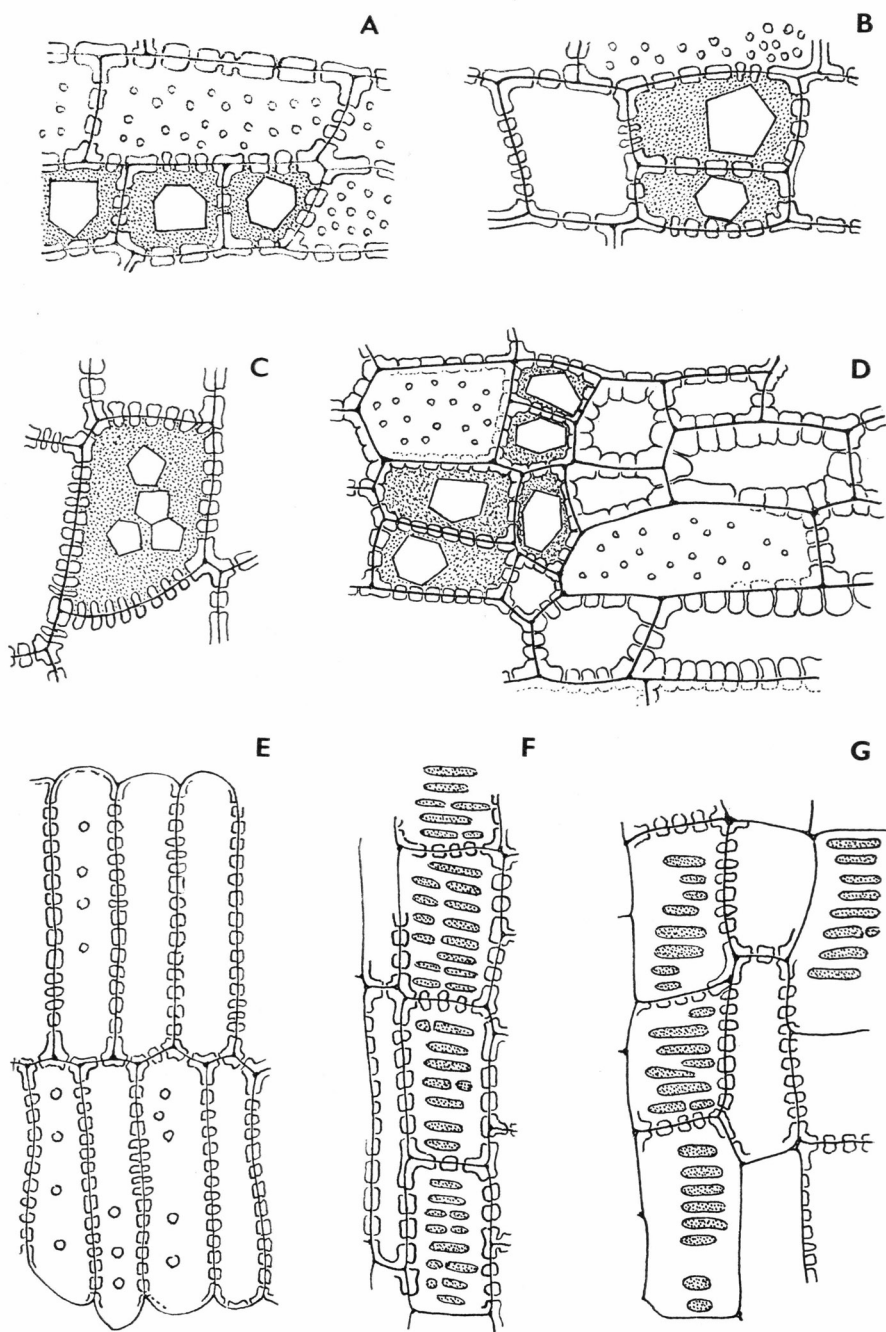


Fig. 15. *Aphloioxylon groenlandicum*. From radial sections of xylem. A, B, C, and D ray cells containing pseudomorphs after calcium oxalate crystals. E, part of a two-storied uniseriate ray. F and G, ray cells with intervascular, half-bordered pits. (A, B, C, D, E, F, and G $\times 430$).

partly separated by maceration, and sometimes occur loosened from the compound of ray-tissue. On the right of the photo, Plate XI, is shown a space between two rays, where the phloem of the latest formed growth increment has been partly dissolved and the cavity filled with calcite. On the left of the photo are shown some parts of almost intact sieve tubes with accompanying parenchyma.

Plate X, Fig. B shows, in tangential section, part of a ray in which a pronounced growth of the flank-cell tissue has taken place. In the tangential view the sclerenchyma wedge is seen to be double-edged; where the border cells are dissolved, as is often the case in the innermost parts of the phloem, the wedge is isolated between the strands of the phloem elements (Plate XIII—here mainly parenchyma).

As the narrower (2—5 cell rows broad) rays of the heterogeneous type do not seem to have such a core of sclerenchyma in their cortical prolongation, they are barely visible in the dark coloured surrounding tissue: whether there has been cortical prolongation of the uniseriate xylem rays cannot be determined, but it is not probable.

As already mentioned and shown on Plate VI, Fig. A, the fossil possessed scale bark. Towards the phellogen — and obviously anticipating its formation and activity — the sclerenchyma wedges of the broad older rays are split up tangentially in a very peculiar way, so that they do not prevent the continuity of the phellogen. This phenomenon is represented in Plate XII. In the xylem rays on the left of the figure the merimastic border-cells have undergone a very considerable division in both tangential and radial directions. The dividing cells have caused a splitting of the sclerenchyma wedge, which probably began in the layers of the more thin-walled cells in the ray, which mark the borders of the growth-rings. In the obviously somewhat younger ray to the right of the figure, the sclerenchyma wedge is still intact. Plate VI, Fig. A, shows a layer which appears black exhibiting only few histological details; it was evidently formed of very thin-walled elements and is to be considered as a detachment layer: immediately within and outside this layer are found sporadic remains of a layer which was composed of small, rather thick-walled cells.

Remains of a similar layer can be traced within the outermost black layer in the figure cited, and this too must consequently be interpreted as the remains of an earlier formed phelloidal layer.

Sclerenchyma is abundant in the tissue developed by the meristematic border-cells of the rays; but as the secondary lamella in these presumably originally lignified elements, is generally dissolved and replaced by a calcite filling, their sclerenchyma nature is not very clear in the photographs. The Fig. 16, C and D shows parts of the dilating meristem in action; elements of the sclereidal wedge of the phloem-

rays are to the left of the figures; to the right is seen the later formed tissue consisting partly of sclereids with a somewhat varying wall thickness. The fibres of the phloem are of a rather peculiar na-

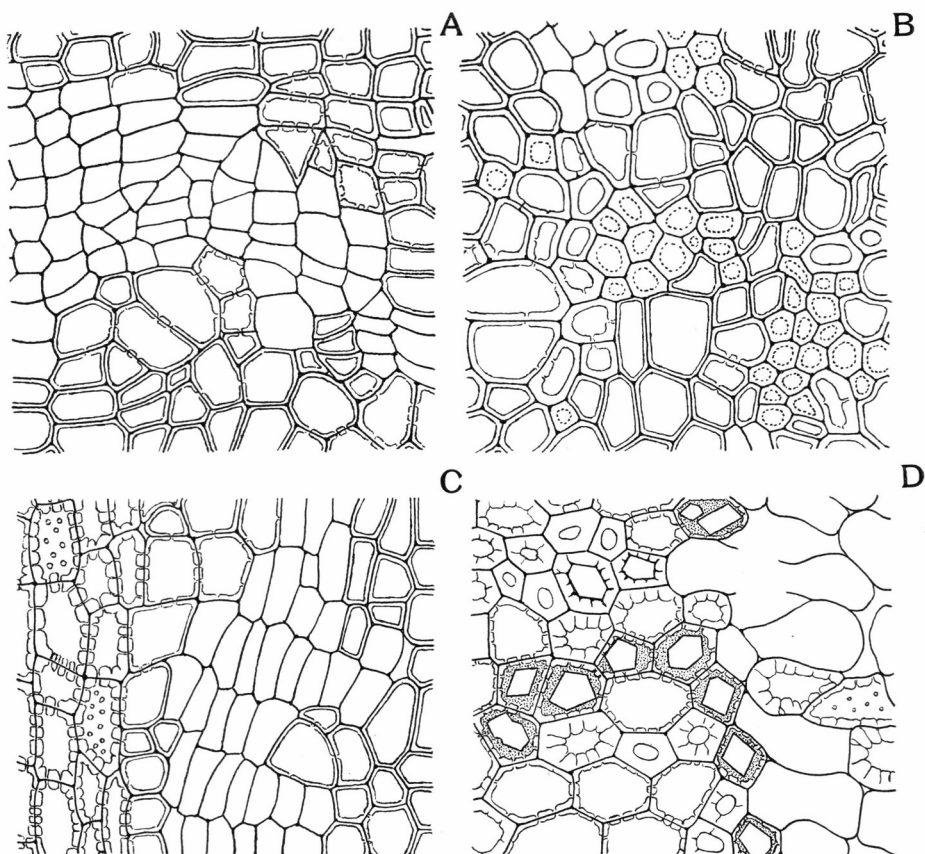


Fig. 16. *Aphloioxylon groenlandicum*. Parts of the cortex. A, B, C, transverse sections; D, tangential longitudinal section. A, part of a local meristem from the scale bark and some sclereids produced by its growth. B, groups of phloem fibres, interspersed in the mainly sclereidal tissue of the scale bark. C, the dilating meristem at the margin of the sclerenchymatous core of a broad ray. D, crystal-bearing sclereids and partly dissolved thin-walled elements at such a margin. (A, B, C, and D $\times 325$).

ture, and vary a good deal with regard to form and size. In Fig. 17, A—H is shown a selection of the most characteristic forms; some are long and rod-shaped, but the types represented in Figs. A, B, C, and E may be assumed to be especially characteristic. As will be seen they are, as the tracheidal elements of the xylem, initially of an elongated spindle-shape and divided by transverse walls into two or more cells; more rarely they are slim and evenly pointed towards the ends, as shown in Fig. 17,

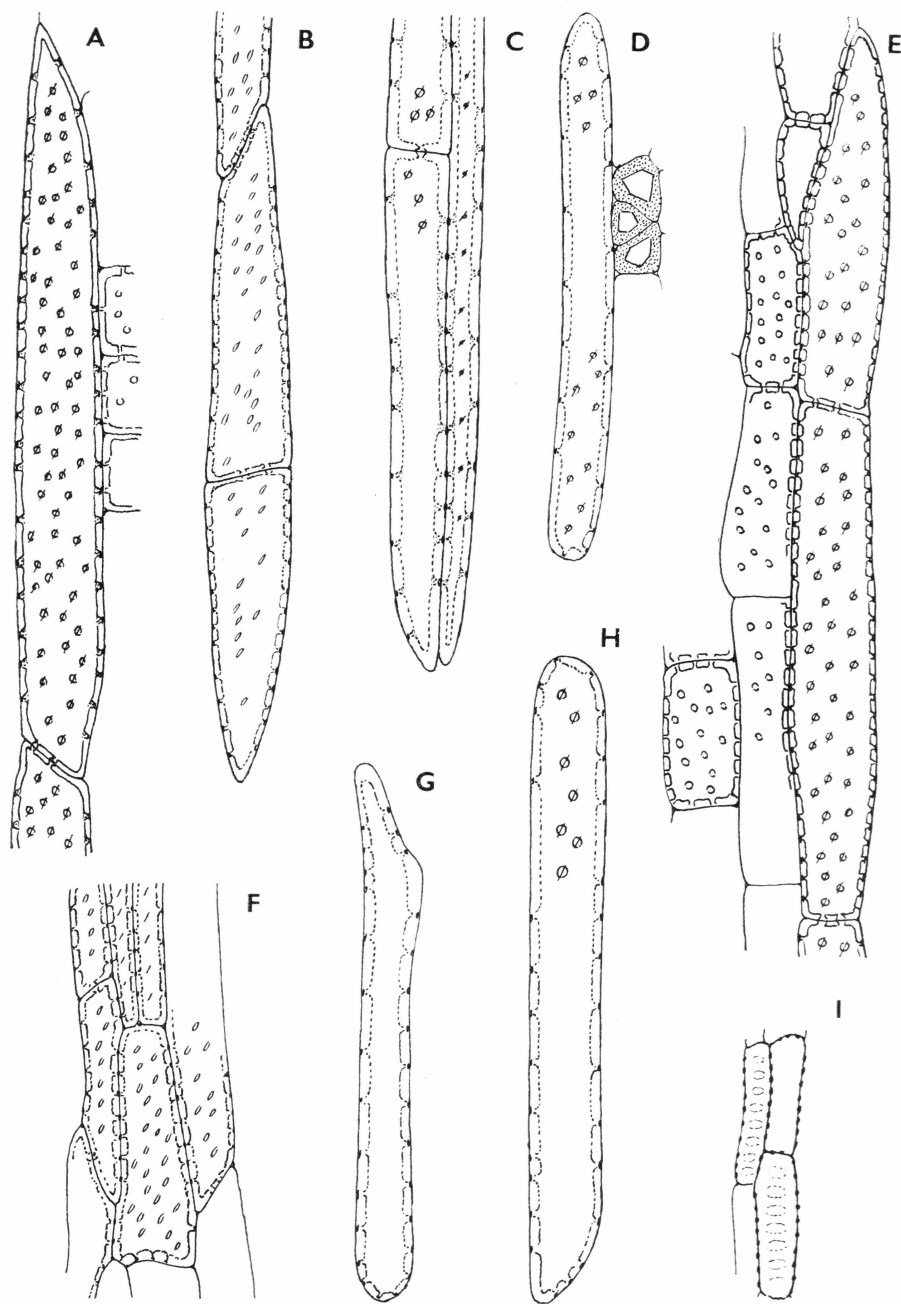


Fig. 17. *Aphloioxylon groenlandicum*. A—H, phloem-fibres of different types. I, phloem parenchyma cells. (All figures $\times 430$).

C; thus assuming the character of typical fibres. As far as it has been possible to ascertain, they always have small, bordered pits with oblique apertures and, most often, a distinctly outlined pit chamber; so in this respect too, they form cortical replicas of the chambered, tracheidal tissue of the xylem.

In the interior parts of the phloem-strands, where the placing of new formation of cell tissue is still rather undisturbed, the fibres are found in small groups, frequently arranged so as to suggest tangential strands; toward the outside their distribution becomes more irregular, and in the outer part of the cortex, i. e. outside the inner phellogen, the course of the phloem-rays can mainly be identified by fragments of the split and strongly dissolved sclerenchyma wedges. Between the wedges the groups of phloem-fibres are seen as light spots (Plate VI, Fig. B); in this figure there are 12 of these spots on the right and the left side of the remnant of the sclerenchyma wedge seen in the centre. Plate X, Fig. C shows such a spot, photographed when highly magnified. The picture represents the outline of a group of phloem-fibres, the contours of its elements being indicated by the primary membrane, and the limits of the lumen by the innermost layer of the secondary membrane; the pits in the wall can also be traced because of the brownish material deposited in them.

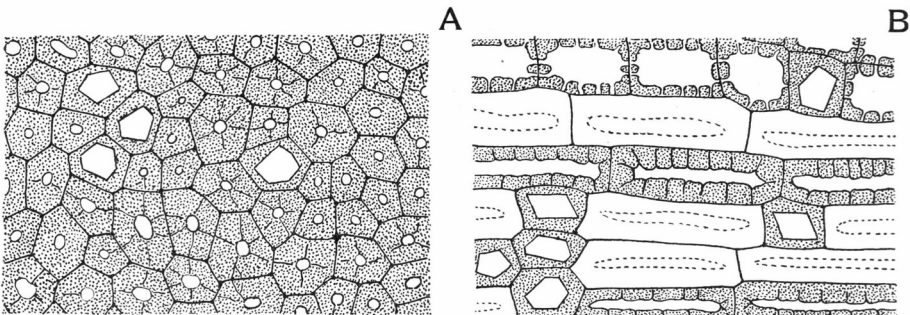


Fig. 18. *Aphloioxylon groenlandicum*. Sclereids from the sclerenchymatous core of a broad phloem-ray; A, figured in tangential, B in radial view. (A and B $\times 430$).

When the arrangement of the fibres is so irregular in this outer part of the cortex, it is connected with the fact that small groups of cells are developing into locally, still more limited meristems by which the growth of the parenchyma has continued in a more casual way probably before the formation of the phelloidal layer delimiting the outer part of the cortex from the inner one. This applies especially to the tissue formed by the meristematic activity of the flank cells of the phloem-rays. In Fig. 16, A is shown a part of such a local meristem, and the tissue originating from the division of its cells; Fig. 16, B shows a group of phloem-fibres, partly disintegrated by the intrusion of sclereids of meristematic origin.

The sclereidal tissues are extremely rich in crystal pseudomorphs. These crystals were also evidently enclosed by a rather resistant coating, now filled with calcite and forming exact replicas of the original crystals. In the sclerenchyma core of the phloem-rays many of the elements contain such pseudomorphs with conspicuous coatings, but where the sclerenchymatic cells of the core have attained the maximum thickness of the wall, the crystal replica has been so closely surrounded that no coating is visible; the crystal is only perceptible as a diaphanous cavity in the uniformly brown cell, the lumen being very narrow. Details in the structure of the wall, such as thickening-layers, are in most cases not discernible (Fig. 18, A and B).

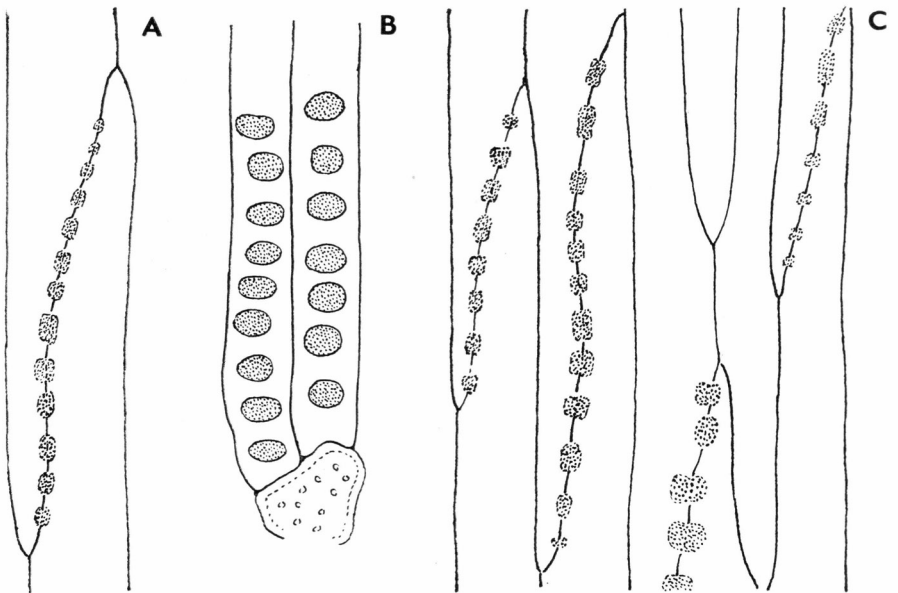


Fig. 19. *Aphloioxylon groenlandicum*. A—C, Sieve tubes, from the innermost part of secondary cortex; the sieve plates are blocked by callus (finely dotted in the figures). (All figures $\times 430$).

The elements of the sieve parenchyma also have a rather characteristic appearance. Fig. 17, I shows such parenchyma cells. They are narrow, measuring only $20\ \mu$ in transverse section, with a somewhat thickened wall, axially elongated ($100\ \mu$ — $200\ \mu$), but chiefly distinguished from the adjoining tissue by having broad pores which in most cases are not easily seen; all the elements being filled with a dark material and also having almost black walls. The pores are most easily perceptible when the cell wall is seen on profile, where the thickened parts separating the pores protrude as small tips.

In Fig. B, Plate XIV such broad pores are faintly visible under the reading glass in some of the elements of the sieve parenchyma mainly to the top left of the figure; also in the photograph Plate XIII they can be traced.

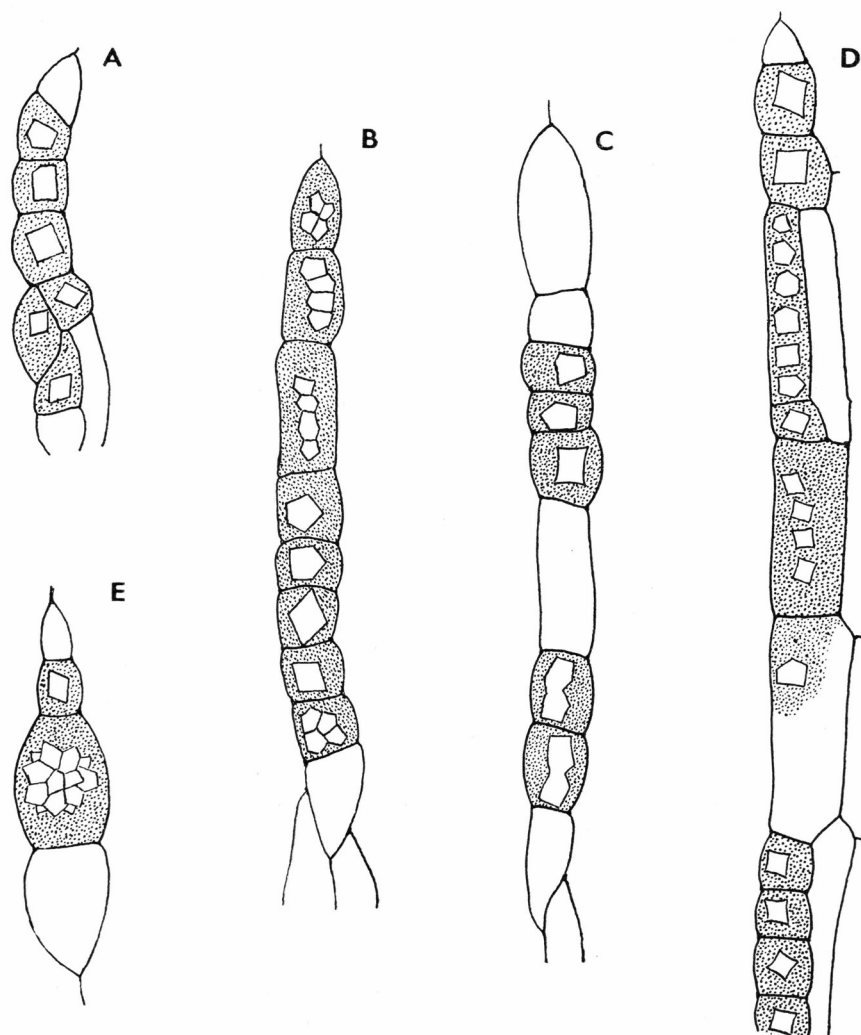


Fig. 20. *Aphloioxylon groenlandicum*. A—D, vertical rows of crystal-bearing cells from the phloem. The calcite pseudomorphs of the original calcium oxalate crystals are enclosed in a solid, but thin-walled coat, the remainder of the lumen filled with a dark substance. (A—D $\times 430$).

The sieve tubes have scalariform sieve plates, 4—6 in the broader tubes with a greater number in the smaller ones; in Fig. 19, A, B, and C are reproduced the overlapping ends of some tubes, the sites of the sieve areas being marked by the very distinct and well preserved accumulat-

ions of callus. In Fig. 19, B which shows such a sieve plate in front view, the sieve areas are marked by dotting, but the diaphragms are in fact totally dissolved.

In the phloem, intermingled with the strands of the other elements, axial rows of crystal-bearing cells are common. Fig. 20, A—E represents such strands, always composed of thin walled cells. Most of these, as shown in the figure cited, contain one or a few crystals (i. e. pseudomorphs of such), while stellate aggregates are rather rare. These crystals have also been coated with a thin but resistant jacket; their shape is sharply defined partly by this almost black coat and partly because the diaphanous calcite pseudomorph clearly protrudes into the brown material which otherwise fills the cells.

Fig. A and B, Plate XIV show some irregularities observed in the broad rays. Reproduced in the figures cited are tangential sections of anomalous parts of phloem-rays; the cells of the core are here locally arranged so as to form an almost circular (A) or elliptical (B) pattern. The correspondance of these anomalies with similar formations in the rays of the xylem has not been proved but is nevertheless probable; Fig. A, Plate XV show a tangential section with parts of anomalous rays bordered by xylem tissue, a proof that such groups of sclereids are at any rate not extraneous to the xylem parts of the rays. Fig. B show a group of sclereids in the margin of a broad xylem-ray. The sclereids in the Fig. A and B, Plate XV are devoid of crystals as far as could be seen.

Summary.

Root wood of a dicotyledonous plant with adhering cortex. Xylem diffuse-porous with minute pores, growth-rings 1—2 mm thick, traversed by numerous broad, multiseriate, markedly heterogeneous rays, in which radial rows of procumbent cells are alternating with rows of shorter to almost square ones, the tangential border of the broad ray with a somewhat discontinuously developed layer of sheet-cells, at the edges continuing the ray as a uniseriate wing; narrower rays of the same heterogeneous type are not infrequent, and numerous uniseriate rays uniformly composed of upright cells, 1—12 layers high and of limited radial extension, very common. In the transverse section of the xylem, the uniseriate rays together with the wings of the multiseriate rays connected with short tangential bands of tracheids, form a more or less pronounced network of rather thin-walled elements. Vessel-like tracheids most common in the last formed xylem of the growth-ring, but uncommon in the spring-wood where vessels attaining a maximum width of 120 μ but most commonly measuring 90—100 μ , and 800—1000 μ in length are dominant; the vessel-like tracheids are usually narrower (30—70 μ) and may

attain a somewhat greater length (1000—1200 μ). Perforation plates scalariform, in the broader vessels with 3—10, in the narrower with 20—30 bars, the vessel-like tracheids exhibit a similar or even somewhat larger number of radially extended bordered pits in their overlapping parts; more or less thick-walled elements, in shape and pitting intermediate between xylem-fibres and tracheids, are found interspersed between the fibres; xylem-fibres thick-walled with distinctly bordered pits on the radial as well as on the tangential walls. The elements of the tangential bands of thin-walled tracheids are formed by division of spindle-shaped initials by means of 1—3 transverse walls. Ray cells rather thick-walled, in their mutual contact the walls finely pitted with simple pits; sometimes they contain pseudomorphs after calcium oxalate crystals, visible because of the thinwalled coat which has surrounded the original crystal. Where border cells of a ray are in contact with a vessel or a tracheid, half-bordered pits of the transverse elongated form connect the elements. As far as could be made out tyloses occur principally in connection with the development of anomalous features in the xylem.

In transverse section the multiseriate rays of the xylem continue into the cortex as rather pronounced fan-shaped formations consisting of a core of crystal-bearing sclereids bordered by a dilating meristem which forms thin-walled parenchyma as well as crystal-bearing sclereids. The periodical growth of the rays may be traced by tangential bands of thinner-walled cells in the sclereidal core. Sieve plates scalariform; phloem parenchyma consisting of narrow, short, and rather thick-walled cells with broadly pitted walls. Groups of phloem-fibres constitute a considerable part of the phloem. These fibres are very variable in shape, most often cylindrical with bluntly tapered ends, but not uncommonly more sharply pointed and thus approaching a normal libriform fibre in form or, like the thin-walled tracheidal elements of the xylem, composed of a spindle-shaped row of cells; their pitting is always of the distinctly bordered type with an ascending slit. Scale bark markedly developed, the detachment layer consisting of thin-walled cells formed between somewhat discontinuous layers of small, thick-walled cork cells, arranged in such a way as to effect the separation of the outside bark into strips. Outside the phelloid the arrangement of the tissues gradually becomes more irregular owing to the activity of numerous short meristems, mainly producing sclereids; the cellular elements here are undergoing dissolution, best preserved are the sclerenchymatous cores of the broad rays and the cells of the phloem-fibre groups. In the phloem crystal-bearing cells are numerous, forming axial rows and containing pseudomorphs after calcium oxalate crystals, coated by a thin membrane, or in some cases a druse. An anomalous development of the sclerenchymatous core of the broad

rays may be met with, the cells being arranged in such a way as to form a circular or elliptic patch, composed of concentric layers in the middle of the core (tangential section); probably they are corresponding with the similar formations in the broad, multiseriate rays of the xylem.

Affinities.

In the last decades especially, the xylem of trees and shrubs representing nearly all the larger and more important units of the Botanical system, has been submitted to a thorough anatomical investigation with a clearly systematic aim. On the other hand, except for cortices of either technical or medical interest, the phloem of adult stems and roots is only incompletely known in most cases.

Notes on the cortex of younger stems, which may be studied on twigs from herbarium material are more common, but in most cases of only little importance for identification of the cortices of mature axes.

For that reason, in my search for a recent analogue to the fossil wood in question, it seemed convenient to start the research by considering the anatomy of the xylem and to use the anatomical data provided by the cortex as an useful supplement, suitable for confirming the results obtained from the xylem structure.

Immediately perceptible characters of our fossil are:

- 1) The very broad and high xylem-rays,
- 2) The diffuse style of pore formation and the rather narrow vessels,
- 3) The faintly defined growth-zones which are not very conspicuous even under the pocket lens.

Using moderate magnification, the following points could easily be ascertained from microscope slides:

- 1) The scalariform perforation plates of the vessels,
- 2) The thick-walled xylem-fibres exhibiting well developed, bordered pits on the radial as well as on the tangential walls,
- 3) Thin-walled vessel-like tracheids and tracheids with a rather thick wall, the latter forming transitional stages to the xylem-fibres,
- 4) The histological characteristics of the xylem-rays:
 - a) the very broad ones distinctly heterogeneous (Kribs' type B) and provided with a layer of sheet-cells,
 - b) the smaller but still multiseriate ones, mainly built up of elements similar to the broadest rays, and finally,
 - c) xylem-rays strictly 1 cell layer broad, 1—12 layers high, with a limited radial extent.

- 5) A system of thin-walled tracheidal elements, which in transverse sections of the xylem give the impression of a rather pronounced diffuse-banded parenchyma.

An attempt at a systematic grouping of types of secondary xylem with rays so conspicuously broad that they are markedly characteristic of a transverse section, has been undertaken by N. E. DADSWELL and S. J. RECORD (1936). The results they obtained were set out in a dichotomous key. As the very extensive collections of wood of the School of Forestry of the Yale University were available for the preparation of the said paper, it is to be supposed that it has been executed on so broad a base that the systematic units essential for our purpose—genera and families—will be represented in the key given by authors. The most characteristic feature of the whole group, i. e. the numerous broad rays, is so easily perceptible on transverse as well as on tangential cuts that it is very convenient for a first orientation; the subdivisions of the key are also well founded on characters more subtle of course, but nevertheless, as my own examination of the systematic units in question has convinced me, sufficient to distinguish the types mentioned.

According to this key a systematic unit which the authors consider to represent a particular family, the “Neumanniaceae”, has a secondary xylem exhibiting the essential characters of our fossil. As indicating a family of plants this name probably is not so well known as it is as a generic name: *Neumannia* (N. RICHARD — not to be confused with *Neumannia*, BROGNIART, Bromeliaceae) which has been in common use and is applied e. g. by Gilg (1925) as designating a genus of the Flacourtiaceae.

As a special family the said genus, on account of anatomical peculiarities and particulars in the development of the flower, was separated by A. VAN TIEGHEM from the Flacourtiaceae and constitutes, according to this author, the only representative of a special family, the Neumanniaceae.

Most authors have in this case not followed VAN TIEGHEM and the systematic unit in question is now usually called not *Neumannia* but *Aphloia* — a name which, according to the available literature, has priority. Although classed among the Flacourtiaceae, most authors claim that *Aphloia* is only remotely connected with the other genera of this family and are thus approaching the opinion of Van Tieghem.

Several species have been described as belonging to the genus *Aphloia*; however the most recent publications (e. g. Flore de Madagascar. Flacourtiaceae by N. PERRIER DE LA BÂTHIE 1936) include only one: *Aphloia theaformis* (WILLD). BENNETT. This is a very variable plant, chiefly with regard to the size and form of the leaves and the size of the rather primitive flowers; it is known from the mountains of South-eastern Africa, from Madagascar and is also found on the islands Reunion

and Mauritius. It grows as a small tree and is used for medical purposes by the natives of these parts of the world; the name in the Malagasy language is said to mean "Change écorce", when translated into French, not as previously supposed (BORY DE ST. VINCENT 1804), "sans écorce" a name also quoted by VAN TIEGHEM; the very special development of the cortex, as will be shown below, justifies the name "change écorce".

In addition to the key, N. E. DADSWELL and S. J. RECORD have given short, but adequate anatomical diagnoses of the xylem of the systematic units in question. From their diagnoses the anatomy of the xylem of our fossil is found to correspond in general characters as well as in histological features, with the family "Neumanniaceae" (=Aphloia). However the said authors do not provide sufficient details to allow a final judgement concerning the identity, or at least the close relationship, of our fossil with the recent analogue. Further information about the anatomy of the xylem in this plant is given by N. W. TUPPER (1939), N. LECOMTE (1922) and by C. R. METCALF and L. CHALK (1930) in their extremely valuable manual: *The anatomy of Dicotyledoneous Plants 1950* (— I. Flacourtiaceae, pp. 122—123).

The data given in the last work are especially of importance. It is here stated (l. c.) "In Aphloia what appears in transverse section to be diffuse parenchyma cells are thin-walled septate fibres. In Aphloia the ground tissue of the wood consists of thick-walled fibres with conspicuous bordered pits, among which are scattered thin-walled septate fibres, which are distributed as single cells or short uniseriate lines resembling diffuse parenchyma — the thick-walled fibres also are septate in *A. myrtiflora* GALPIN but not in *A. maritima* BAKER, the parenchyma like septate fibres have bordered pits and in both these and in the thick-walled fibres the pits are equally numerous in both radial and tangential walls".

As it will appear, these statements relate our fossil to the recent Aphloia to a very considerable extent.

A critical remark may be allowed. What are described as "septate fibres" were shown, lastly by the investigations of W. SPACKMANN and B. G. L. SWAMY (1949), to be of two different kinds. What these authors designate as septate fibres are characterized as "a cell type, distinguished by the fact that the septae are formed after the cambial daughter cell has been lined with the secondary wall. As a result, these septae do not make contact with the vertically oriented primary walls. This is in contrast to the xylem-parenchyma strand in which the septation of the daughter cell occurs in the absence of a secondary wall, i. e. before the secondary layers of the wall are formed, and the primary wall and intercellular layer of the septae are continuous with the vertically oriented primary wall and connected with the intercellular material".

In the recent *Aphloia*, septae of the first type of SPACKMANN and SWAMY can really be met with, and are often quite numerous in the fibres as well as in the thin-walled tracheids; in the latter they are to a large degree replacing the septae of the last named type, in the xylem of *Aphloia* by far not so common as in the fossil.

Details of this delicate nature can of course only be evaluated after the study of recent material, and such material has been placed at my disposal by the courtesy of many individual collectors and organisations. From the botanical collection of the Museum of Lund (Sweden) Mr. TYCHO NORDLIND sent me two twigs of *Aphloia*, both about 5 mm in thickness and labelled respectively: *Aphloia myrtiflora* GALPIN and *A. Theaeformis* (WILLD) BENNETT; from the collection of the School of Forestry of the Yale University I have received two samples of secondary xylem, evidently originating from older trunks and labelled No. 32941 (*Aphloia* BENNETT) and No. 15517 (*Aphloia* (WILLD)) — A. RICHARD)), unfortunately both without cortex. From Madagascar, by courtesy of the French authorities (l'Inspection générale des eaux et forêt. Section de recherches forestières), I succeeded in obtaining samples of both the branches and root of *Aphloia* and in addition — what was of the greatest importance — a part of the base of a trunk with incipient formation of scale bark; this last named and very important material was accompanied by herbarium vouchers.

All the samples of wood from recent *Aphloia* were found to correspond very well with each other in both general aspects and regarding details of the anatomy, although there were slight quantitative variations between the elements of the xylem such as might be considered as normal variation between individuals. Furthermore, comparison of the xylem of the recent *Aphloia* with that of our fossil gave an outstanding impression of close relation.

In the xylem of *Aphloia* are found rays of the two main types described in the fossil: those which are only one row of cells broad and of restricted radial extension and different height, and multiseriate rays up to 25 cell-rows broad, traversing the xylem, heterogeneous with alternating groups of decumbent and groups of higher and broader cells. The broadest and highest rays in particular are more or less completely jacketed with a layer of axially elongated sheet-cells; in tangential section this layer is seen in the upper and lower edge of the ray to be continued as wings, one cell-row broad and of different length. The length of the vessel members and the character of the scalariform perforation plates are very much like those found in the fossil. In recent *Aphloia* also occur, but rather rarely, forms of perforations tending towards the reticular type, similar to those found in the fossil and reproduced Fig. 10, E. Septate fibres, as understood by SPACKMANN and SWAMY,

could not be demonstrated with certainty in the fossil wood, yet such septae can also be absent in the recent *Aphloia* (METCALF and CHALK l.c.). In the sample from Yale University labelled No. 32941 they were found to be numerous, while in the sample No. 15517 they were rather scarce. As it has been found by experiment that such septae disappear even with the more delicate maceration method described by W. M. HARLOW (Botanical Gazette. Vol. 85. 1928), they must consequently be built of a substance which is different from and less resistant than the normal substance of the walls of xylem elements (i. e. probably pecto-cellulose).

The xylem-fibres of the recent *Aphloia* and of the fossil correspond in thickness and pitting of the walls; transitional forms between xylem-fibres and thick-walled tracheids could also be demonstrated in the former, but are not so common as in the latter.

The thin-walled tracheidal septate fibres were found in somewhat varying quantities in the samples investigated, but there was complete agreement between recent and fossil material as regards shape, thickness of the wall and pitting style of these elements; transverse bands of this tissue partly spanning the space between two rays are recognizable in the photo Plate XIV, Fig. C.

In the xylem of *Aphloia* from Madagascar were found a few small medullary spots; larger anomalously developed parts of the tissue could not be demonstrated. In these details the fossil wood differs from recent *Aphloia*, but external influence may have played an important role in the formation of such features. Anomalies in the core of the xylem-rays, as they appear in *Aphloia* (Plate XV, Fig. C), are also found in the fossil, (Plate XV, Fig. A), but in the latter consist of far more thick-walled elements.

As to more notable discrepancies in the anatomies of the xylem in *Aphloia* and that of our fossil it can be said that, the growth-zones are more distinctly accentuated in the fossil and, probably connected with this fact (E. STRASBURGER 1891), the vessel-like tracheids in the summer wood somewhat more numerous. Tylosis could not be demonstrated in *Aphloia*, but as it seems that the blocking up of the vessels in the fossil is restricted mainly in and around the anomalously developed parts of xylem there is a certain coherence between these observations. Crystals in the ray-tissue of the xylem are extremely rare in *Aphloia*, but they occur, while in the fossil they are not uncommon and seem to be most numerous in the anomalously developed parts. The formation of crystals is a very common feature in the Flacourtiaceae (W. W. TUPPER 1934) and thylae, as well as the formation of crystals of calcium oxalate, may very well be induced by external influence (wounding or attack by fungal hyphae).

Sometimes the lumen of the vessels in the dried wood of *Aphloia* is completely filled with a brownish-yellow substance, as is the case in the sample from Yale University labelled No. 32941. This substance swells slightly in water but is not soluble; with a solution of potassium hydroxide it is dissociated into a gritty, viscous mass; with Sudan III—Alcohol it assumes a deep red colour; on the whole its nature seems a little doubtful. K. H. LECOMTE (1922) remarks concerning *Aphloia theaeiformis*: *Petit arbre à écorce mince, brune, écailleuse, finement striée dans la longueur. Decoction aqueuse, brune avec gomme abondante. Gum-secretions are consequently known in Aphloia; M. L. TERRAC (1947) does not mention this fact. The impregnation with calcite has made it impossible to make a more accurate determination of the yellow substance in the vessels of the fossil, and although the content of such an substance in the wood of Aphloia is a feature which has not previously been described, only slight reference can here be made to it.*

In *Aphloia* the cortex in the stems and branches as well as in the root apparently increases in thickness only slowly; in a branch (Madagascar) of about 5 cm. diameter it measured only 2 mm and its surface remained smooth after exfoliation of the primary cortex. The earlier phases in the development are described by VAN TIEGHEM (1899), and transverse sections of the cortex, also from apparently young axes, are described and figured by M. L. TERRAC (1947). The anatomy of the young cortex is consequently well known, whereas the details of the later stage of development, in which the formation of scale bark is of particular importance for comparison with the fossil, have not yet been studied.

Concerning the most advanced phase of development available to him for examination, VAN TIEGHEM states the following facts: *Plus tard encore, il se fait, dans le libre secondaire devenu plus épais, et dehors et dedans, une sclerose progressive des cellules de parenchyma, tant de celles qui sont mêlées aux tubes cribles dans les petits compartiments que de celles qui forment les petits rayons qui les séparent. Les fibres ainsi formées ne forment donc pas de strates tangentiellles, comme dans les Malvacées par exemple, mais sont disposées les unes, celles de compartiments, sans ordre, les autres, celles des rayons, en séries radiales. En même temps la partie externe non sclérifiée des grand rayons libériens se dilate progressivement en éventail vers l'extérieure.* This statement of VAN TIEGHEM is supplemented by H. LECOMTE (1922): *l'écorce de ce bois (i. e. Aphloia) est coupée radialement par des puissants prolongements des rayons de bois.* These authors have consequently drawn attention to some very striking features in the anatomy of the cortex, while not entering into details concerning the more advanced stages of development.

In the sample from Madagascar taken from the base of a trunk, i. e. with the cortex in a more advanced state, these "prolongements" occur as wedges pointing outward, showing parts of sclerenchymatic elements tangentially alternating with parts in which the tissue is composed of groups of thin-walled cells. Crystals of calcium oxalate are fairly common in both types of ray-tissue, with generally only a single crystal developed in each cell. As will be seen by comparing these data given for *Aphloia* with the figures given in Plate XI, in these features too the fossil corresponds very closely with the recent analogue.

The abundant occurrence of sclerenchymateous elements in the spaces between the broad rays in the phloem is a characteristic feature in *Aphloia* as well as in the fossil. In *Aphloia* too, the phloem-fibres are partly arranged in small isolated groups, but partly also in somewhat continuous tangential bands alternating with bands of phloem parenchyma and collapsed sieve tubes.

In the material to hand of *Aphloia theaformis* showing the formation of the scale bark, the cortex has attained a thickness of about 2,5 mm. The detachment layer is formed approximately in the middle of the cortex, i. e. 1 mm under the surface, and runs almost parallel to it. It is composed of very thin-walled cells and bordered on the outer, as well as on the inner side by a few layers of phelloid, consisting of small, rather thick-walled elements. The cortex outside the detachment layer is scaled off in 2—3 mm broad ribbons of various lengths, their dimensions probably to a certain degree being determined by the size and arrangement of the sclerenchymatous wedges from the broad rays, included in them. The colour of the surface is dark brown to almost black, but when a part is scaled off by the loosening of one of the said ribbons, the fresh surface is of a lighter colour. As all the ribbons of scale bark are not all thrown off simultaneously the bark of this tree develops a peculiarly variegated appearance.

The sclerenchyma wedges of the phloem-rays are here of course broken tangentially by the formation of scale bark; yet the development of the dilating meristem on the borders of the rays is not yet far advanced. The "en évantail" appearance of the transverse section of the rays, also stressed by VAN TIEGHEM, is consequently not very apparent, although traces of it could be demonstrated. Neither was the increase in volume of the parenchyma outside the detachment layer by means of secondary local cambia very pronounced.

The fibres of the secondary phloem are of the same type as these found in the fossil (Fig. 17, A—H); as in these the walls in the thick-walled types as well as in the more thin-walled are provided with numerous, small pits, in the most cases with a well developed border and with an ascending slit. The elements of the rather scanty phloem parenchyma

have somewhat thickened walls with broad pores. Axially elongated crystal-chamber spools are particularly prominent in tangential sections of the cortex; these cells are containing single or twin crystals, or less frequently, stellate clusters of calcium oxalate.

As has been demonstrated, the anatomical details of the cortex of *Aphloia* also correspond closely with those of our fossil. Generally speaking, the cortex of the fossil differs from the cortex of its recent analogue mainly in the relatively greater thickness, and the far more pronounced development of thick scales caused by the abundant formation of small, local meristems in the tissue outside the innermost detachment layer, the presence of which implies an increase in volume of the strips of scale bark resulting in a stronger surface relief, as well as the considerable increment "en évantail" of the broad phloem-rays by the dilating meristem on the borders of the sclerenchyma core. Yet these characters may probably be explained by the fact that while the recent material originates from the aerial part of an axis (the base of a trunk—the surface showed a covering of lichen) the fossil is part of a rather old root. The difference in structure in such parts of the same tree can be very pronounced; even in species with an even or almost even bark surface on the trunk the thicker and older roots may show a very conspicuous formation of scale bark, accompanied by a somewhat delayed loosening of the scales. In such cortices the tendency to continued growth may very well be more pronounced.

A fossil wood of a structure identical with or only approaching that of the fossil here described has, as far as I know, not yet been met with. The inspection of other recent types which with some probability might be drawn within the circle of comparison has shown, that none of them possesses a anatomical structure of xylem and cortex more closely allied to our fossil than just *Aphloia*.

The peculiar, rather restricted geographical distribution of this plant and the enormous difference in geological age between the fossil and its recent analogue, of course make a specific identification only based on the structure of secondary wood and phloem, the other parts of the fossil in question (Leaf, Flower, Fruit) being quite unknown, somewhat problematical.

Aphloia is—as already stated by BORY DE ST. VINCENT (1804)—a highly variable systematic unit, and it is not known why real differences in anatomical details are found between the numerous subspecies. A more detailed study of the structural variations of xylem and phloem in these would certainly be of considerable interest; in my opinion the differences in this respect found between the fossil and the material at hand of its recent analogue, are at any rate hardly surpassing what may be regarded as intrageneric variations. Even if the anatomical differences pointed

out—insignificant perhaps but existing never the less—might be considered as being of a certain systematic value, it can probably not be denied that our fossil and the recent *Aphloia* are to be regarded as very closely related, so in a case like this it seems not to be necessary in the nomenclature to give any hint of reservation as to the systematic coherence of our fossil and its recent analogue—based on the similarity of wood structure—by adding the prefix *para* (*par*) to the generic name (J. W. BAILY 1924), formed as usual by the addition of “xylon” or “inium” to the name of the presumably most related recent type, in this case *Aphloia*.

As samples of root and stem of fossil trees and shrubs with cortex preserved are rather rarely to be found, so identification of further finds with our fossil can in most cases only be based on the anatomy of the secondary xylem which in fact in a case like this offer sufficient peculiarities to start a discussion upon. The secondary xylem must therefore be considered the most important part of such a fossil from a palæontological standpoint and must be used in naming even those specimens in which both xylem and cortex are found. A most suitable name for the form-genus in question will therefore be *Aphloioxylon*. But it must be borne in mind, that diagnoses embracing the anatomy of the cortex besides that of the xylem are to be considered as the more satisfactory, giving a far greater probability of correct identification. The comparison of samples of fossil wood consisting only of xylem with specimens comprising both xylem and cortex is justified only to a certain degree and must be regarded with some reservation, especially when the woods in question exhibit characters of only limited systematic value.

As specific name “*groenlandicum*” will probably be adequate, so the whole name should be as follows:

Aphloioxylon groenlandicum n. sp.

Geological age: Danian.

Locality: Igdlorssuarssaq, Nûgssuaq Peninsula, West Greenland.

BIBLIOGRAPHY

Cedroxylon saviarqatense:

- BAILEY, I. W., (1933): The cambium and its derivative tissues. VII. Problems in identifying the wood of Mesozoic conifers. *Ann. Bot.* XLVII. Pag. 145—157.
- BANNAN, M. W., (1936): Vertical resin ducts in the secondary wood of the Abieteneae. *New Phytologist* 35. Pag. 11—46.
- BARGHOORN, E. S. and I. W. BAILEY, (1938): The occurrence of *Cedrus* in the auriferous gravels of California. *Amer. Journ. of Botany*. 25, Pag. 641—647.
- BORGMAN, J. A., (1879): Studier öfver barkens inre bygnad i Coniferernas stam. *Lunds Universitets Årsskrift*. XIV.
- CHANEY, R. W., (1932): Notes on occurrence and age of fossil plants found in the auriferous gravels of Sierra Nevada. *Californian State Div. of Mines. Report of the State Mineralogist* 28. Pag. 299—302.
- CHRYSLER, M. A., (1915): The medullary ray of *Cedrus*. *Botan. Gaz.* 59. Pag. 387—396.
- EDWARDS, W. N., (1944): *Cedroxylon* on the erratic of the Cambridge Greensand by L. Hawkes. *The Quarterly journal of the Geological Society of London*. C. for 1944. Pag. 162—163.
- GOTHAN, W., (1905): Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. *Abhandlungen der Kgl. Preussischen Geolog. Landesanstalt u. Bergakademie*. N. F. Heft 44. Berlin.
- , (1907) Die fossilen Hölzer von Königs Karls Land. *Kgl. Svenska Vet. Akad. Handl.* 42. No. 10.
- , (1910) Die fossilen Holzreste von Spitzbergen. *Kgl. Svenska Vet. Akad. Handl.* 45. No. 3.
- HÖEG, O. ARBO, (1931): The fossil wood from the Tertiary at Myggbukta, East Greenland. *Norsk geolog. tidsskrift*. B. XII. Pag. 363—390.
- JEFFREY, W. J., (1904): A fossil *Sequoia* from the Sierra Nevada. *Bot. Gaz.* 38. Pag. 321—332.
- KRÄUSEL, R., (1919): Die fossilen Koniferen-Hölzer (Unter Ausschluss von *Araucarioxylon* Kraus). *Palaeontographica* LXII.
- And II (1949): — Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferenhölzer. *Palaeontographica* LXXXIX. Abt. B.
- LEXICON OF GEOLOGIC NAMES OF THE UNITED STATES. (1938). Geological Survey Bulletin No. 896. I—II. Washington.
- NOELLE, W., (1910): Studien zur vergleichenden Anatomie und Morphologie der Koniferenwurzeln mit Rücksicht auf die Systematik. *Bot. Zeitung*. 68. Pag. 169—266.
- SHIMAKURA, M., (1937): Studies on fossil woods from Japan and adjacent lands. II. The Cretaceous woods from Japan, Saghalin and Manchoukuo. *Science Report from Tohoku Imperial University* (2. Geologie).
- STOPES, M. C., (1916): An early Type of the Abieteneae (?) from the Cretaceous of New Zealand. *Ann. Bot.* XXX. Pag. 111—124.

- STOPES, M. C. and K. FUJII, (1911): Studies on the structure and affinities of Cretaceous plants. Phil. Transactions Royal. Soc. London. Ser. B. CCI.
- WALTON, J., (1927): On some fossil woods of Mesozoic and Tertiary age from the Arctic Zone. Ann. Bot. XLI. pp. 239—252.

Aphloioxylon groenlandicum:

- BAILEY, I. W., (1924): The problem of identifying the wood of Cretaceous and later Dicotyledons. Paraphyllanthoxylon arizonense. Ann. of Bot. XXXVIII.
- BENNET, J. G., (1838): Plantae Javanicae Rariores (in Adnot. Bixineae).
- BORY DE ST. VINCENT, (1804): Voyage dans le quatre principaux îles des mers d'Afrique. 1801—1802. Vol. III, pag. 115. Collection de Planches, Pl. XXIV.
- CLOS, D., (1857): Révision des genres et des espèces appartenant à la famille des Flacourtiacées. Annales des Sciences Naturelles. Botanique. 4. Sér. Vol. 8.
- DADSWELL, N. E. AND S. J. RECORD, (1936): Identification of woods with conspicuous Rays. Tropical Woods. Number 48. Yale University. School of Forestry.
- DE CANDOLLE, AUG. PYRAME, (1824): Prodromus Systematis Naturalis Regni Vegetabilis. Pars I. Pag. 259 et seq. Paris.
- ENGLER, A. UND K. PRANTL, (1925): Die natürlichen Pflanzen-familien, II. Ausgabe. Bd. 21. E. Gilg.: Flacourtiaceae. Pag. 377—459.
- HUMBERT, H., (1946): Flore de Madagascar. 140^e Famille. Flacourtiacées par Perrier de la Bathie.
- KRIBS, D. A., (1935): Salient lines of structural specialization in the wood rays of Dicotyledons. Bot. Gaz. Vol. 96.
- (1937): Salient lines of structural specialization in the wood parenchyma of Dicotyledons. Bulletin of the Torrey Botanical Club. Vol. 64.
- LECOMTE, H., (1922): Les bois de la forêt d'Analamazaotra. Paris.
- METCALF, C. R. AND L. CHALK, (1950): Anatomy of the Dicotyledons. Vol. I—II. Oxford.
- PARIS, R., (1942): Sur une Flacourtiacée de Madagascar, le Voa-fotzy (Aphloia Madagascariensis Clos. I). Bulletin des sciences pharmacologiques. Vol. 49.
- RICHARD, A., (1830): Bulletin des Sciences Naturelles et de Géologie etc. (Bulletin de Férussae). Tom XXI. Rcf. Numero 65.
- (1838): Flore de Cuba. Phanerogames. Pag. 95—97. Vol. X of Histoire physique, politique et naturelle de Cuba. By Ramon de la Sagra. Paris. 1838—42.
- SOLEREDER, H., (1899): Systematische Anatomie der Dicotyledonen (1899) and: Ergänzungsband (1908). (Bixineae).
- SPACKMANN, W. AND B. G. L. SWAMY, (1949): The nature and occurrence of septate fibres in Dicotyledons. American Journal of Botany. Vol. 36 No. 10. Supplement 1949. Pag. 804.
- STRASBURGER, ED., (1891): Über den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Histologische Beiträge Heft III. Jena.
- TERRAC, MARIE-LOUISE, (1947): Contribution à l'étude des plantes médicinales de Madagascar, de la Réunion et l'île Maurice, Paris.
- TUPPER, W. W., (1934): Preliminary report on the wood structure of the Flacourtiaceae. Tropical woods. Number 38. Yale University. School of Forestry.
- (1927): Woods with conspicuously large rays. Tropical woods. Number 11. Yale University. School of Forestry.
- VAN TIEGHEM, M. PH., (1899): Sur le genre Neumannia considéré comme type d'une famille nouvelle les Neumanniacée. Journal de Botanique. Vol. 13.

PLATES

Plate I.

Cedroxylon saviarqatense. A—D, transverse sections of xylem. A, central part of wood. B, part of wood bored by *Teredo* and showing the greatly variable thicknesses of the growth-rings. C, growth-rings with only a few layers of summer wood; D, with zones of axial traumatic resin canals. (A and B $\times 30$; C and D $\times 60$).

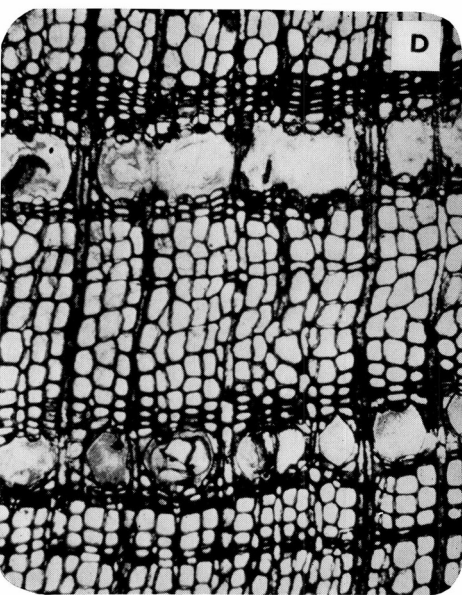
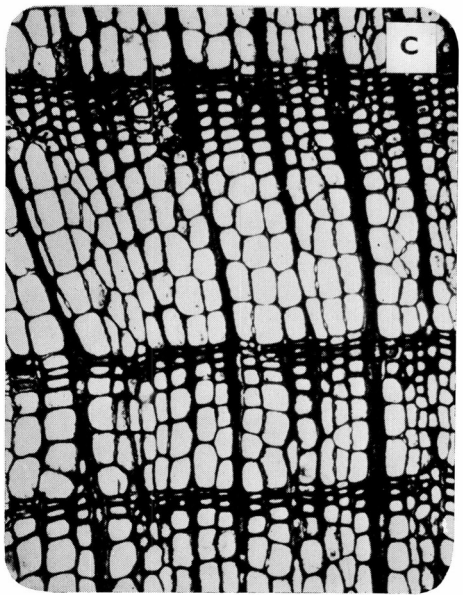
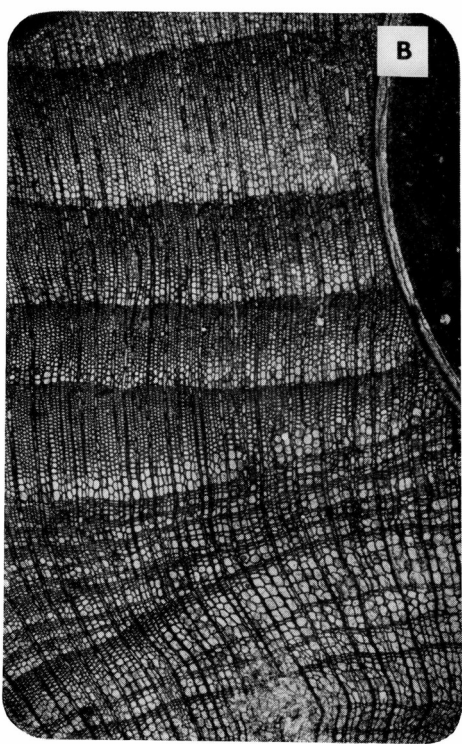
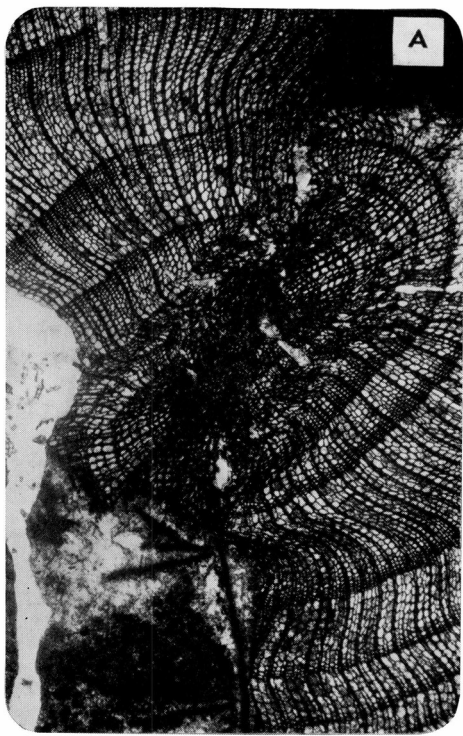


Plate II.

Cedroxylon saviarقاتense. A and B, transverse sections of xylem. A, showing part of a series of growth-rings with broad summer-wood alternating with part of a series exhibiting only few layers of this tissue. B, a radial resin canal emerging outwardly from an axial one. C and D, radial longitudinal sections. C, showing ends of broad tracheids from spring-wood with three rows of alternating bordered pits. D, tracheids from part of the xylem where the spring-wood has merged gradually into summer-wood. (A and B $\times 60$; C and D $\times 210$).

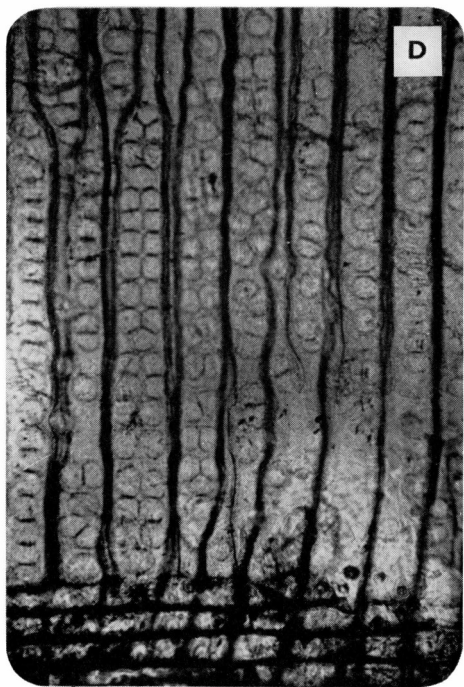
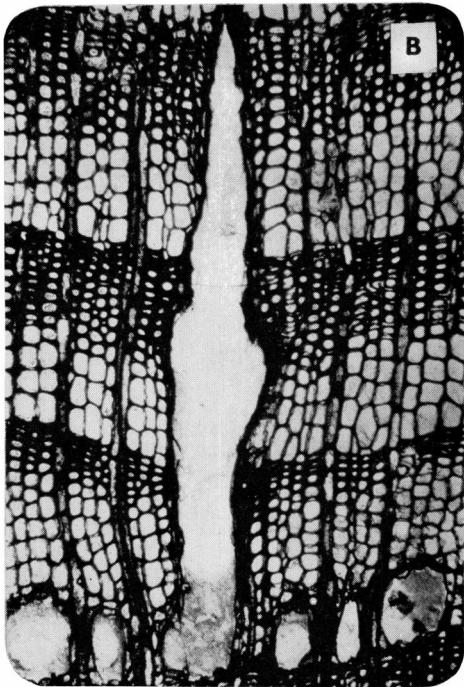
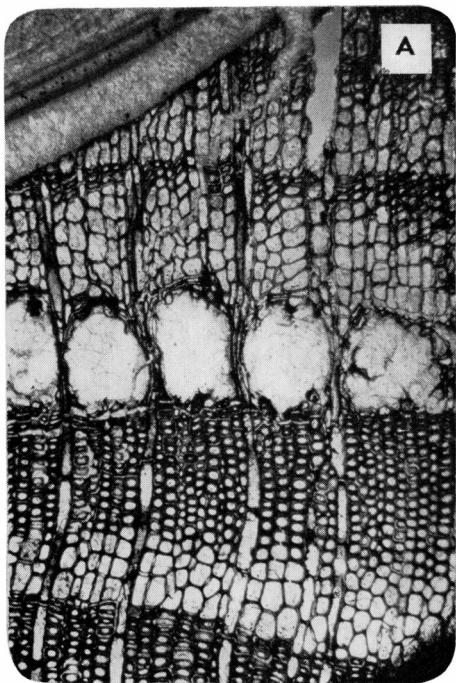


Plate III.

Cedroxylon saviarqatense. Radial longitudinal sections of xylem. A, rays partly showing the pitting of radial walls and the thin-walled marginal cells. B, part of a balsam-cyst and (lowermost to the right) crystal-bearing cells. C and D, axial traumatic resin canals. (A and B $\times 210$; C and D $\times 60$).

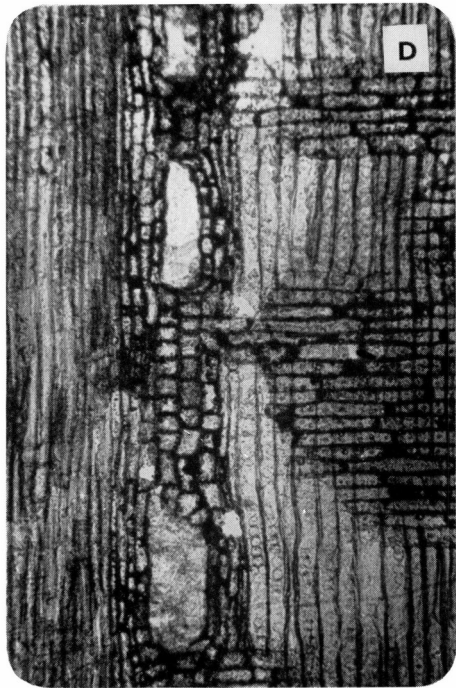


Plate IV.

Cedroxylon saviarqatense. Tangential longitudinal sections of xylem. A, rays traversing spring-wood. B, rays traversing summer-wood, in the latter tangential pitting of the tracheids abundant. C, rays traversing a zone of traumatic resin canals, the rays are coated tangentially with a layer of thick-walled epithema cells on either side. D, radial protuberances from the axial resin ducts in sectional view; in C and D the resinous content of the ducts is partly visible. (A, C, and D $\times 60$; B $\times 210$).

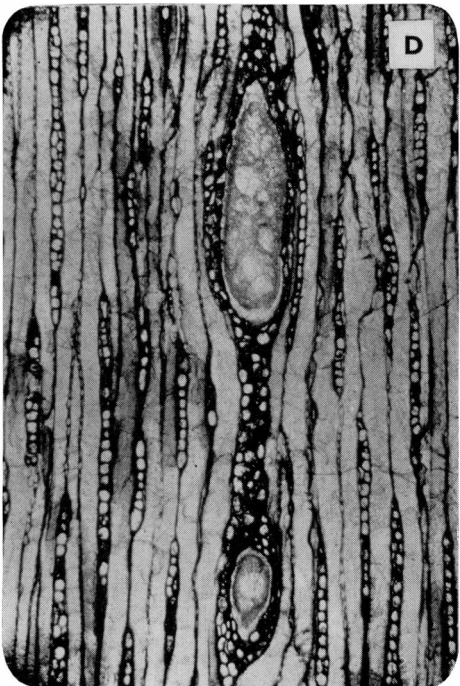
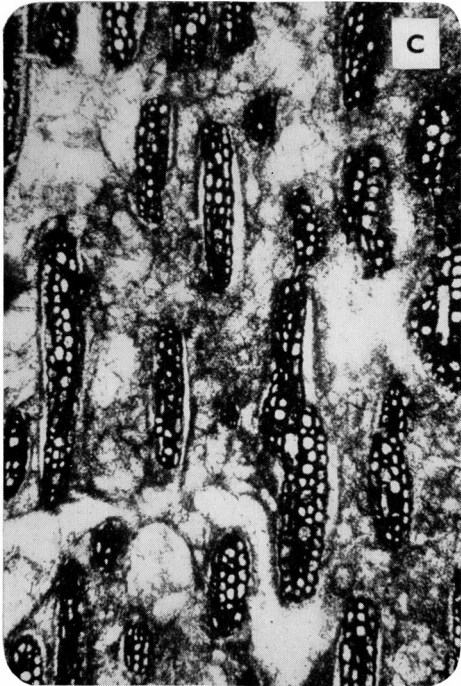
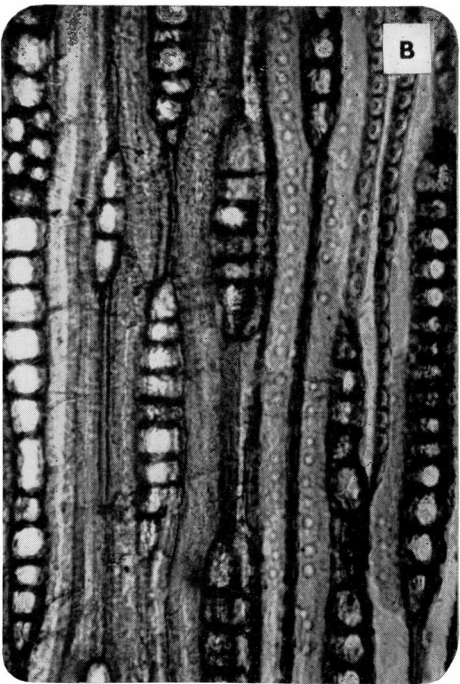
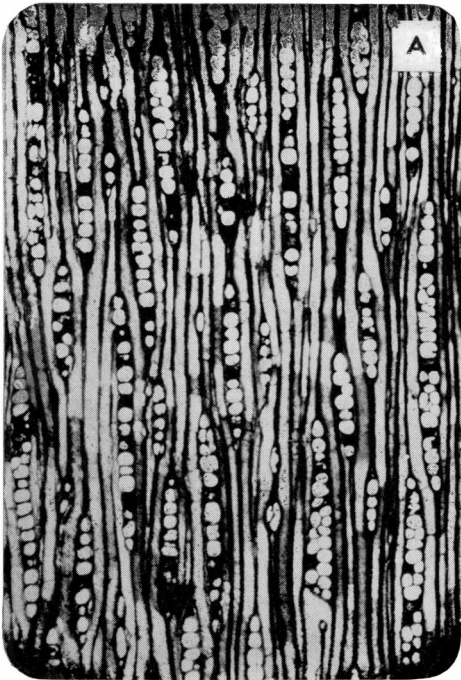


Plate V.

Cedroxylon saviarقاتense. A and B, radial longitudinal; C, transverse section of cortex. In A is shown two medium-sized groups of sclereids, in B (to the left) some cells from the margin of such group, in the centre crystal-bearing cells. C, the cambial zone, a tangential series of traumatic resin canals is under formation, the cortex includes a smaller group of sclereids. (A $\times 30$; B and C $\times 210$).

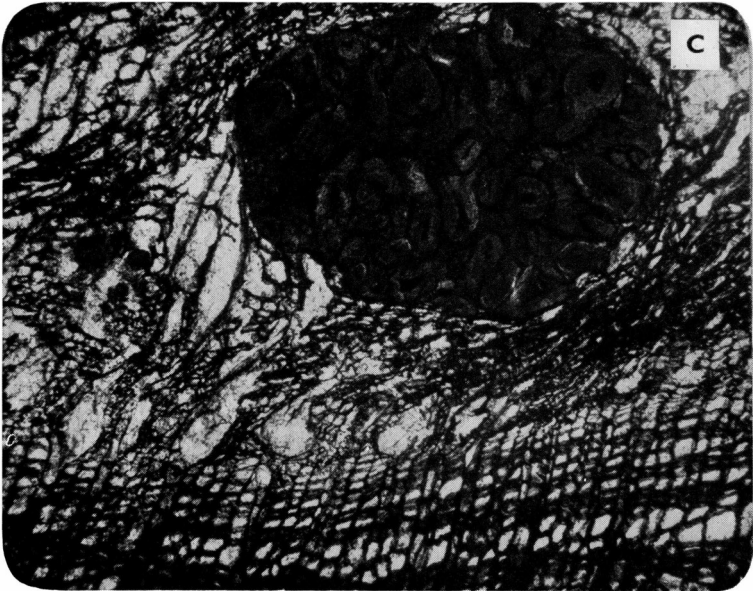
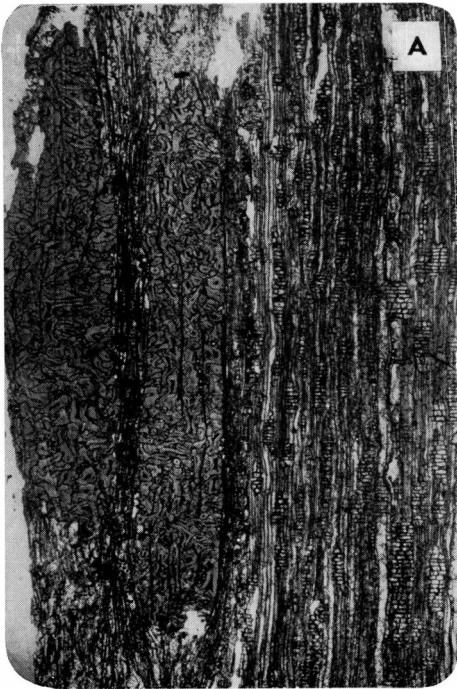


Plate VI.

Aphloioxylon groenlandicum. Transverse sections. A, normally developed xylem, cambial zone and cortex with two successive detachment layers ($\times 10$). B, part of rhytidome with groups of phloem-fibres ($\times 60$).

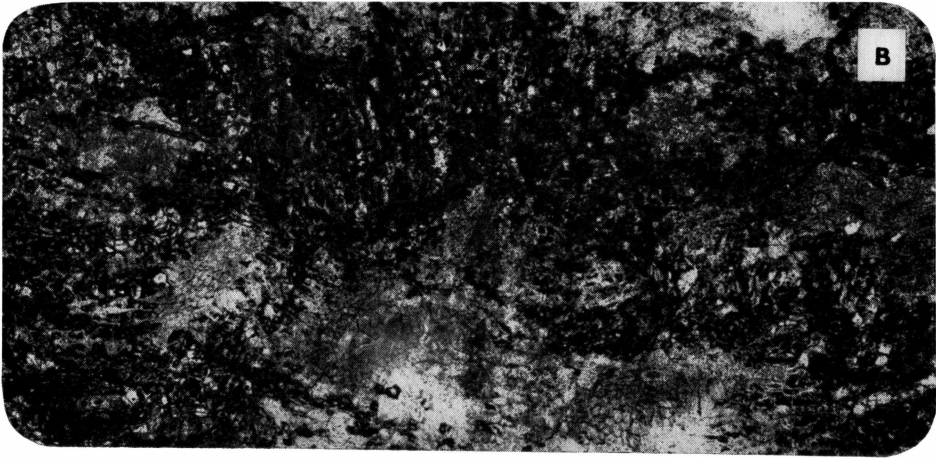
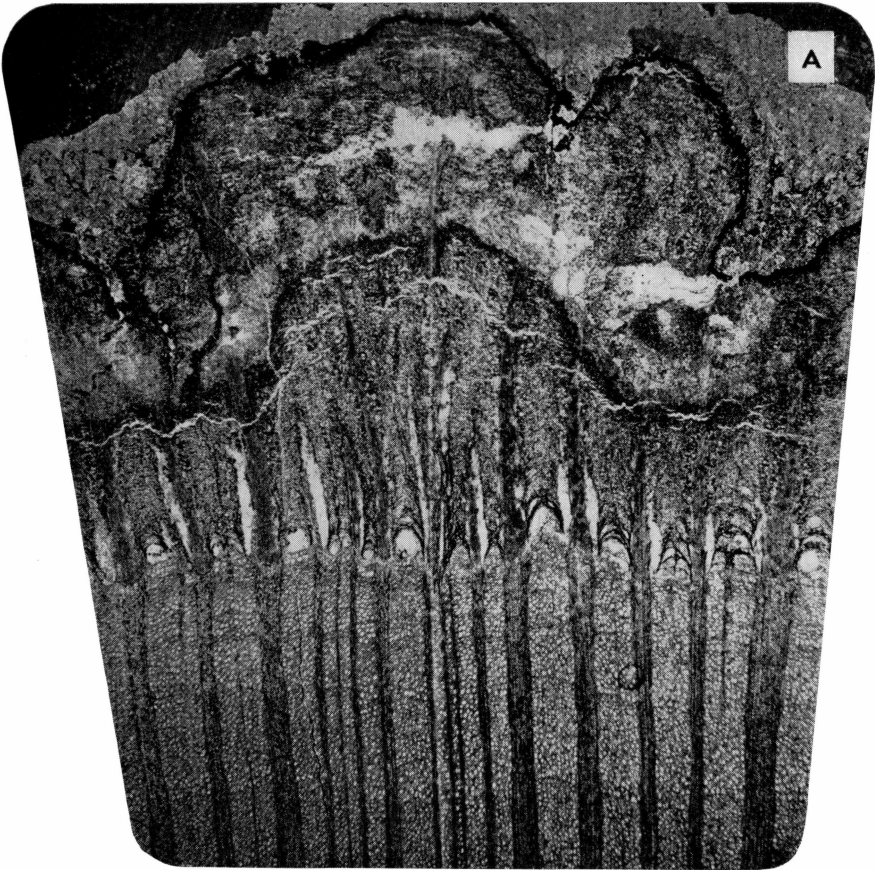


Plate VII.

Aphloioxylon groenlandicum. Transverse sections of xylem. A, an anomalous aggregation of rays and ray-like parenchyma ($\times 10$). B, normally developed xylem, showing parts of two multiseriate heterogeneous rays and part of a growth-ring with well-defined borders ($\times 60$).

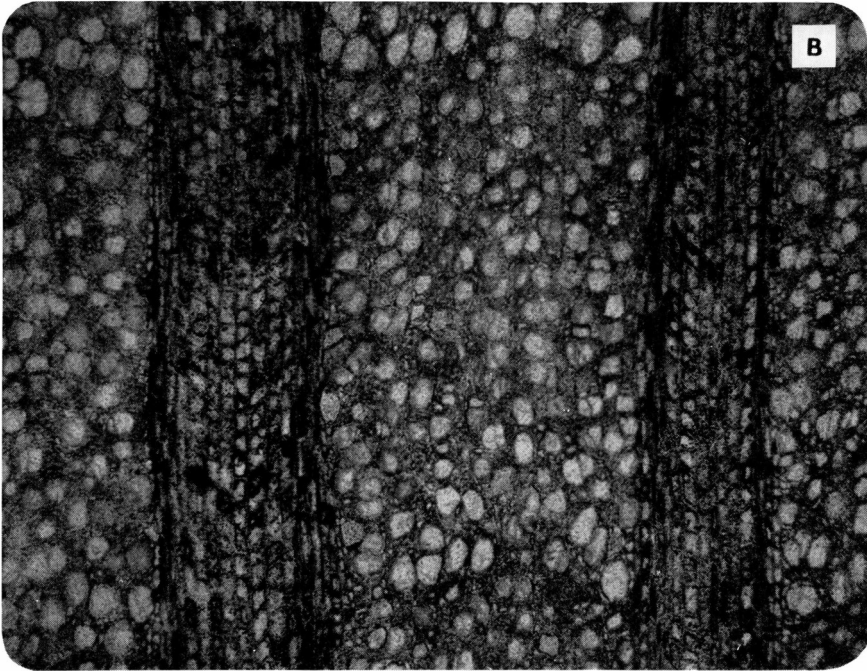


Plate VIII.

Aphloioxylon groenlandicum. A, transverse section of xylem showing parts of two multiseriate, heterogeneous rays, the boundary of a growth-ring, some uniseriate rays, fibres and thin-walled parenchyma-tracheids partly forming tangentially extended groups ($\times 100$). B, tangential section of a multiseriate heterogeneous ray ($\times 60$). C, radial section of xylem., vessels blocked by tylosis ($\times 100$).

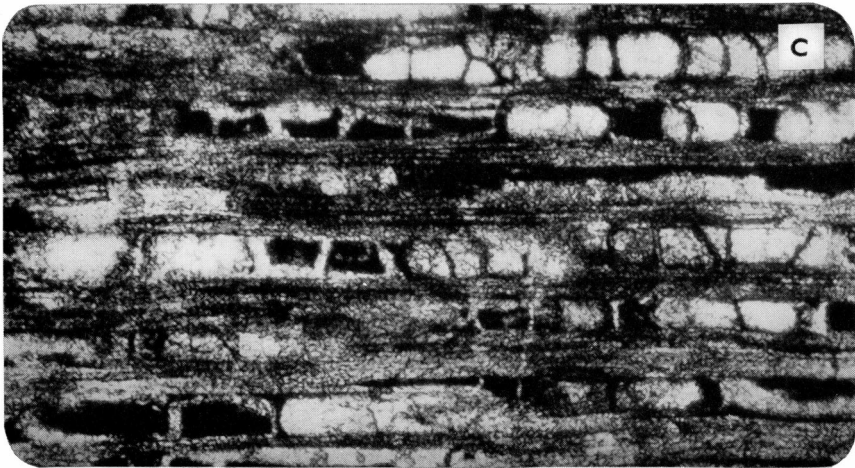
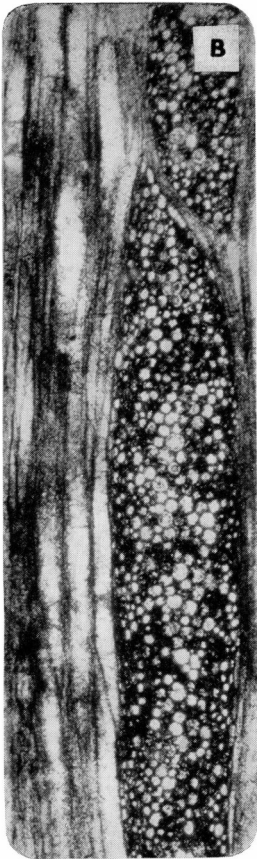
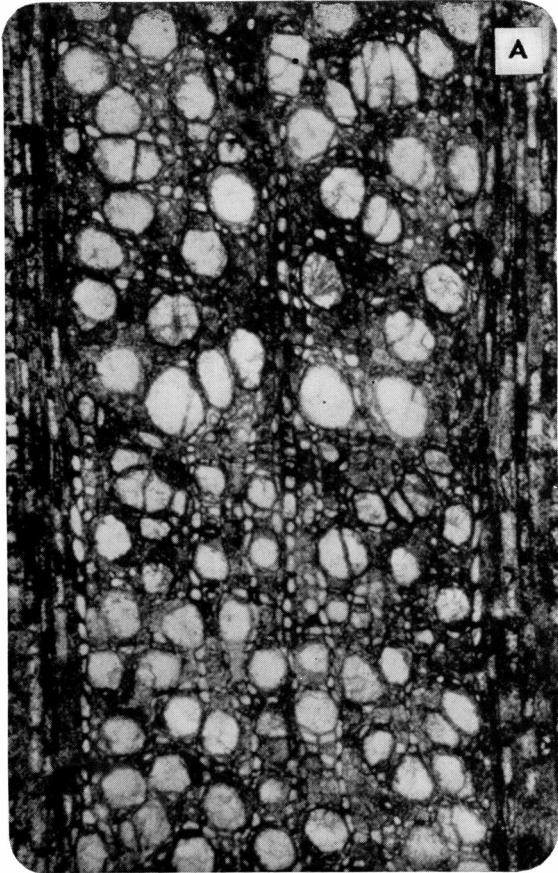


Plate IX.

Aphloioxylon groenlandicum. A and B, radial longitudinal sections of multiseriate, heterogeneous rays, (etched slides, $\times 100$). C, transverse section of the cambial zone showing part of a multiseriate, heterogeneous ray of the xylem and its corresponding part of the phloem; cambium forming an inwardly bent curve outside the xylem part of the ray ($\times 100$). D, radial longitudinal section of sheet cells of a multiseriate ray; to the left thin-walled tracheids ($\times 100$).

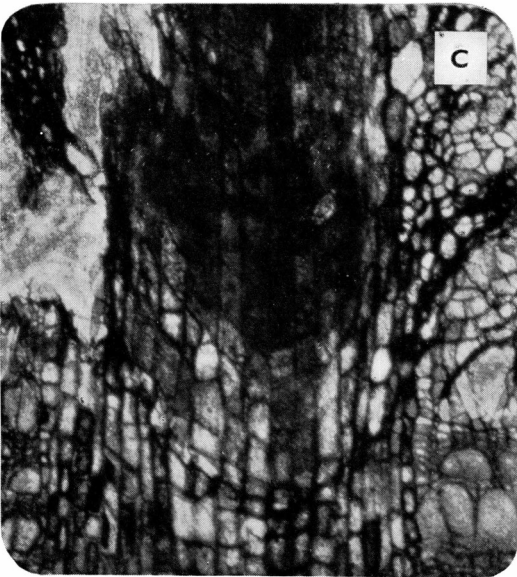
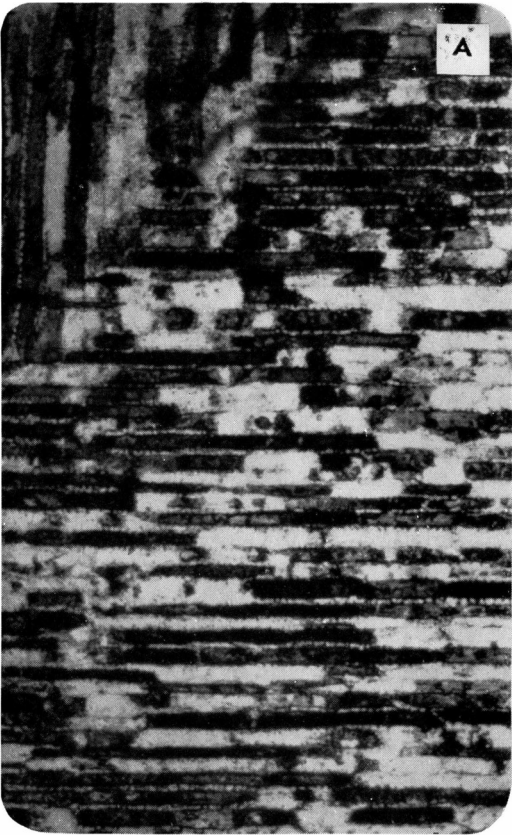


Plate X.

Aphloioxylon groenlandicum. A, tangential section of xylem, multiseriate rays of various sizes and also some uniseriate rays. B, tangential section of phloem showing a ray with its sclereidal core and dilating meristem (A and B $\times 100$). C, transverse section of rhytidoma; a group of phloem-fibres and surrounding tissue ($\times 200$).

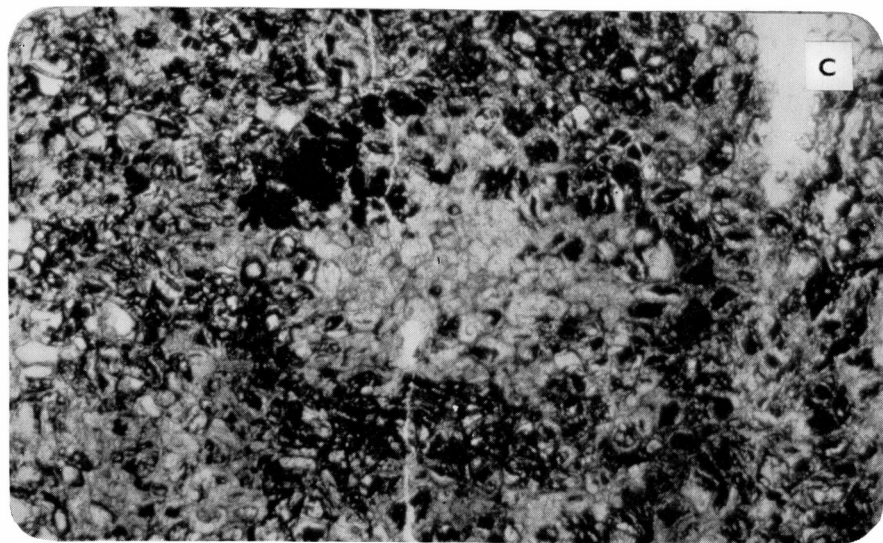
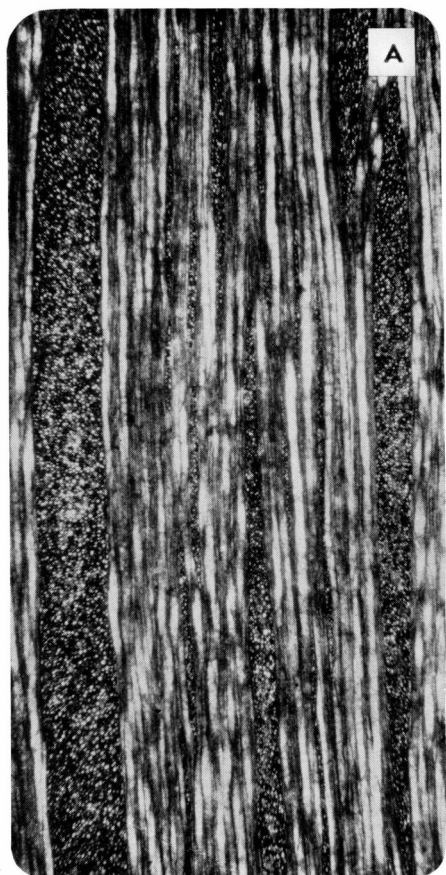


Plate XI.

Aphloioxylon groenlandicum. Transverse section showing outline of xylem at the cambial zone, a multiseriate heterogeneous ray, with a wedge-shaped core of sclereids in the phloem part, while in the abaxial part of the phloem-ray the tissue formed by the dilating meristem is conspicuous. The thin-walled border cells in the inner, adaxial part of the phloem-ray are decomposed ($\times 60$).



Plate XII.

Aphloioxylon groenlandicum. Transverse section of cortex. Sclereidal core of the phloem-ray to the left disintegrated by action of a dilating meristeme while the core of the younger and radially less extended ray to the left is still intact ($\times 60$).

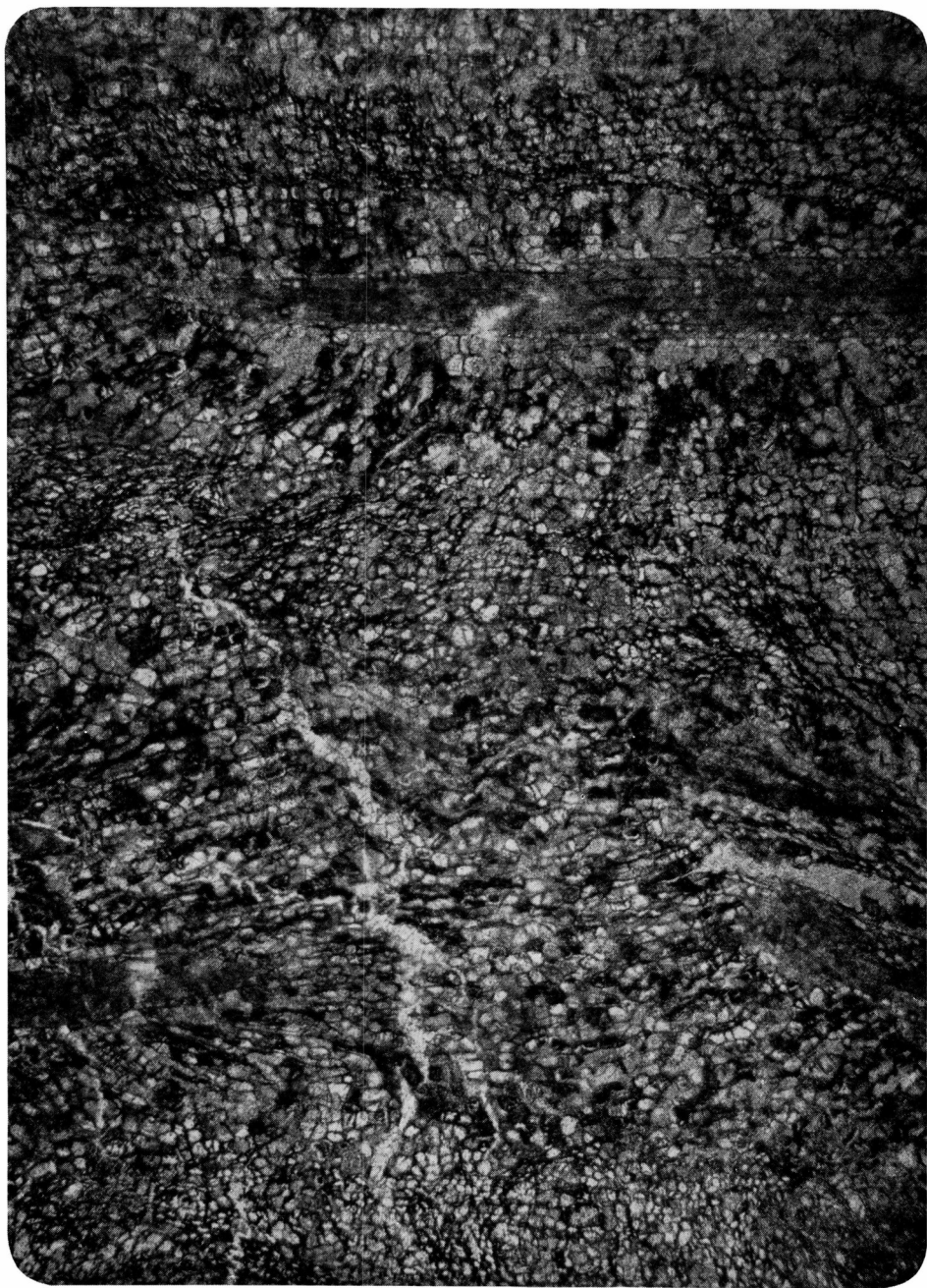


Plate XIII.

Aphloioxylon groenlandicum. Phloem, tangential section. Sclereidal core of the rays intact; sieve tubes and thin-walled border cells disintegrated by maceration and partly dissolved; a group of isolated callus particles have accumulated in the vertical canal formed by dissolution of the sieve tubes. The axial strands segregating the ray tissues are mainly composed of phloem parenchyma ($\times 60$).



Plate XIV.

A and B, tangential section of the cortex of *Aphloioxylon groenlandicum*; anomalous groups of sclereids forming radial strands in the sclereidal core of the phloem-rays ($\times 100$). C, Aphloia (Neumannia) sp. Transverse section of xylem (sample No. 32941 from Yale University School of Forestry) ($\times 100$).

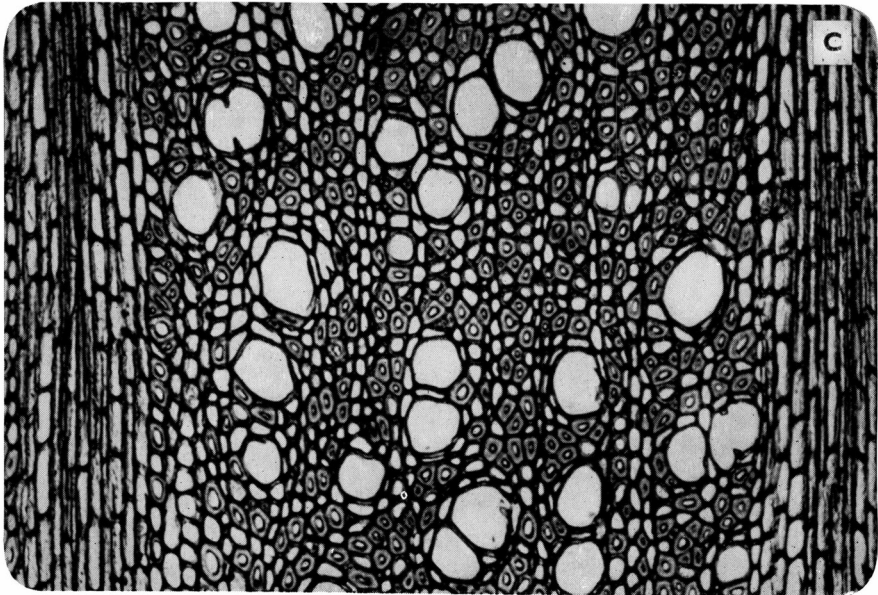
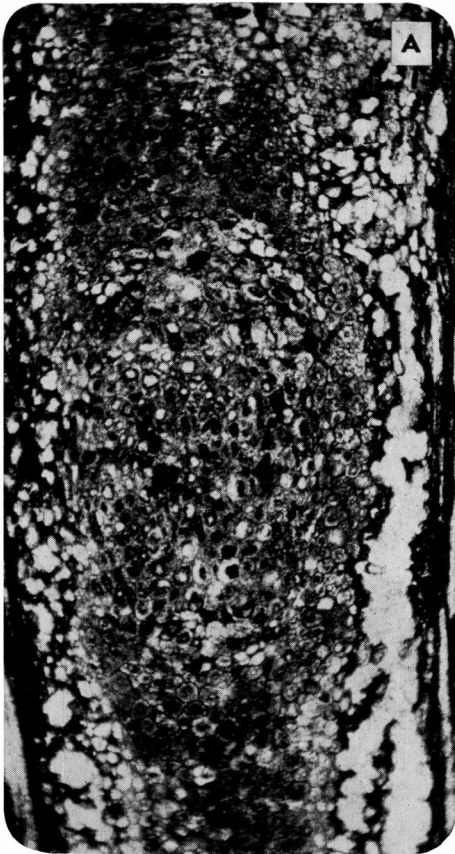


Plate XV.

A and B, tangential sections of xylem of *Aphloioxylon groenlandicum*. Anomalous formations in the multiseriate rays. C, anomalous strands in a xylem ray of *Aphloia* (*Neumannia*) sp. (Sample No. 32941 from Yale University School of Forestry) ($\times 100$).

