FR. J. MATHIESEN

PALAEOBOTANICAL INVESTIGATIONS INTO SOME CORMOPHYTIC MACROFOSSILS FROM THE NEOGENE TERTIARY LIGNITES OF CENTRAL JUTLAND

PART II:
GYMNOSPERMS

Det Kongelige Danske Videnskabernes Selskab
Biologiske Skrifter **17**, 3

1742

Kommissionær: Munksgaard
København 1970

Det Kongelige Danske Videnskabernes Selskab udgiver følgende publikationsrækker:

The Royal Danish Academy of Sciences and Letters *issues the following series of publications:*

	Bibliographical Abbreviation
Oversigt over Selskabets Virksomhed (8°) *(Annual in Danish)*	Overs. Dan. Vid. Selsk.
Historisk-filosofiske Meddelelser (8°)	Hist. Filos. Medd. Dan. Vid. Selsk.
Historisk-filosofiske Skrifter (4°) *(History, Philology, Philosophy, Archeology, Art History)*	Hist. Filos. Skr. Dan. Vid. Selsk.
Matematisk-fysiske Meddelelser (8°)	Mat. Fys. Medd. Dan. Vid. Selsk.
Matematisk-fysiske Skrifter (4°) *(Mathematics, Physics, Chemistry, Astronomy, Geology)*	Mat. Fys. Skr. Dan. Vid. Selsk.
Biologiske Meddelelser (8°)	Biol. Medd. Dan. Vid. Selsk.
Biologiske Skrifter (4°) *(Botany, Zoology, General Biology)*	Biol. Skr. Dan. Vid. Selsk.

Selskabets sekretariat og postadresse: Dantes Plads 5, 1556 København V.

The address of the secretariate of the Academy is:

Det Kongelige Danske Videnskabernes Selskab,
Dantes Plads 5, 1556 København V, Denmark.

Selskabets kommissionær: Munksgaard's Forlag, Prags Boulevard 47,
2300 København S.

The publications are sold by the agent of the Academy:

Munksgaard, *Publishers,*
47 Prags Boulevard, 2300 København S, Denmark.

FR. J. MATHIESEN

PALAEOBOTANICAL INVESTIGATIONS INTO SOME CORMOPHYTIC MACROFOSSILS FROM THE NEOGENE TERTIARY LIGNITES OF CENTRAL JUTLAND

PART II:

GYMNOSPERMS

Det Kongelige Danske Videnskabernes Selskab
Biologiske Skrifter **17,** 3

1742

Kommissionær: Munksgaard
København 1970

CONTENTS

Synopsis

Remains of gymnosperms, which are copiously present in the Danish lignitic deposits, are referable to the recent families *Cephalotaxaceae, Podocarpaceae, Abietaceae, Sciadopityaceae, Taxodiaceae* and *Cupressaceae.* Some of the types are only represented by fossil wood with a more or less well preserved anatomical structure (*Taxoxylon amentotaxoides, Saxegothaeoxylon, Cupressinoxylon callitroides, C. thujoides* and *C. biotoides*). In other genera leaves and pollen grains are found in addition to the wood (*Pinus* and *Sciadopitys*) and in a few examples (*Sequoias, Taxodium* and *Glyptostrobus*) the association of leaves, twigs, cones and seeds are of common occurrence.

Taxoxylon amentotaxoides, Cupressinoxylon callitroides, C. thujoides and *Saxegothaeoxylon miocenicum* represent types of fossil wood not previously described, and the diagnoses of *Taxodioxylon taxodii* W. Gothan and *Cupressinoxylon biotoides* (R. Prill) have undergone some extension.

The age of the flora is regarded as Neogene Tertiary. A marine clay with a molluscan fauna of Middle Miocene age occurs locally in the western parts of the brown coal area where besides pollen and carpolithes only pieces of fossil wood are found, but as most of these are compatible with leaves and other remnants in the eastern localities (Moselund, Silkeborg Vesterskov) the strata could be considered as a continuous series. The character of the pteridophytic flora, described in Part I, does not contradict this.

PRINTED IN DENMARK
BIANCO LUNOS BOGTRYKKERI A/S

II. *Gymnospermae*

This second part of my memoir on the cormophytic macrofossils from the Neogene of central Jutland, of which the first part, the "Introduction and Pteridophytes", appeared in 1965, deals with the gymnosperms. Remains of gymnosperms are copiously present in the Danish lignites and are referable to the recent families *Cephalotaxaceae, Podocarpaceae, Abietaceae, Sciadopityaceae, Taxodiaceae* and *Cupressaceae*. The fossil conifers from the European Neogene, and especially the more common types, are regarded in many cases as being nearly related to, or perhaps identical with, still living species (*Taxodium, Glyptostrobus*, etc.). Recent analogues are mainly to be sought for in floras of North America and the Far East, but also the floras of Australia, and even of the more remote parts of South America have, as will be shown, claimed consideration.

Some of the types described in the following pages are only represented by samples of fossil wood with a more or less well preserved anatomical structure. The existence of some genera (*Pinus, Sciadopitys*) were confirmed by leaves and pollen grains, and there are a few examples of leaves, twigs, cones and seeds (*Taxodium, Glyptostrobus* and *Sequoias*) found in the strata associated with the wood which give support to the exactitude of the generic determination on the fossil woods recorded.

The general type of the gymnosperm flora described is considered as being of Neogene Tertiary age. Most of the species are already known as being widespread in the lignitic floras of central Europe and of so great a vertical extension that they cannot be used for a closer determination of the geological age of the strata. According to L. Banke Rasmussen (1961) a layer of marine origin (a clayish soil enclosing a molluscan fauna of Middle Miocene age) is locally present in the western parts of the brown coal area. The lignites overlying and underlying this clay agree closely in appearance but have not offered determinable plant material other than fossil wood, pollen grains and some common and widely repanded carpolithes. The most common types of fossil wood from the coal layers is compatible with the remains of leaves and other remnants found in the eastern localities (Moselund, Silkeborg Vesterskov) situated at a somewhat higher topographic level. It is possible that the eastern localities represent a geological age a little older than the exploited lignitic layers to the west. The character of the pteridophytic flora, described in Part I, indeed points in that direction.

As many of the Neogene types dealt with here possess a considerable geological extension in time and space references to descriptions of the more common types are very frequent in the relevant phytopalaeobotanical literature. Reference to older memoirs concerning fossils referred to the genera *Sequoia, Glyptostrobus* and *Taxodium* may be found in the very complete lists of P. Friedrich (1883), M. Staub (1887) and P. Menzel (1900).

In the extensive literature dealing with the general morphology, anatomy and geographical distribution of the gymnosperms, extant and fossil, prominance may be given to the memoirs by A. C. Seward (1919), R. Pilger (1926) and R. Florin (1931 and 1963). Details concerning the development and anatomy of the seed are given by K. Schnarf (1937), and the anatomical structure of the secondary wood in relation to systematics has been closely studied by W. Gothan (1905), R. Kräusel (1919 and 1920) and P. Greguss (1955), the latter work dealing only with extant species. In a recent paper (1967) P. Greguss offers a review of the fossil gymnospermous woods found in Hungary from the Permian to the Pliocene.

In many cases it will be convenient to study my plates through a reading glass.

My thanks are due to Mr.Chr. Halkier of the Mineralogical and Geological Museum of Copenhagen and to Mr. H. N. Hansen of the Royal Danish School of Pharmacy for their most valuable collaboration in preparing the photographs for the plates. Mrs. E. Nordmann of the staff of the Institute of Historical Geology has been good enough to draw the figures 6 and 15 and has added a finishing touch to some of my drawings.

For comparison I received from R. Kräusel, Frankfurt a.M. in 1920 a valuable collection of slides of fossil wood from the "Senftenberger Braunkohlenrevier", and from the Museum Ziemi, Warszawa, I obtained through Dr. Z. Zalewska the loan of some interesting slides of fossil wood from the Aquitanian material of Turów, Poland.

Samples of *Amentotaxus* wood were obligingly places at my disposal by the Forestry School of Yale University, U.S.A.

I am highly obliged to the curator af the Royal Botanic Gardens, Kew, Dr. R. Shaw for his efforts in procuring a sample of wood of *Saxegothaea conspicua* for investigation.

Samples of wood of the recent species of *Widdringtonia*, together with herbarium vouchers were kindly presented to the Botanical Museum of Copenhagen University by Prof. N. B. Rycroft, Director of the National Botanical Gardens at Kirstembosch Newlands, South Africa.

I am also greatly indebted to Mrs. H. Helbæk and to Mrs. L. Christiansen of the Mineralogical and Geological Museum and the Royal Danish School of Pharmacy respectively, for their careful retyping of the manuscript.

Dr. Stuart Watt of the staff of The Geological Survey of Greenland has been good enough to revise my translation into English and has kindly read a proof.

The publication of this paper has been made possible by grants from the Carlsberg and Rask-Ørsted Foundations.

Taxoxylon amentotaxoides n. sp.

A sample of fossil wood from the lignite at Salten exhibits the anatomical characters of a *Taxoxylon* (Fr. Unger 1847, R. Kräusel 1949). The fragment was about 5 cm long and 2 cm thick, probably derived from a stem. The peripheral parts were decayed but a central portion about 1 cm thick appeared rather well preserved, of an almost wax-like consistence. Cutting on the microtome was facilitated after hardening in alcohol and very smooth and thin sections could be obtained.

Plate I, A and C show parts of transverse sections; the first figure giving a view of a larger area, while the second only shows a single growth ring under higher magnification. The growth rings appear to be of somewhat variable thickness but the early wood has nearly the same volume in the different rings; the borders are well marked as the transition from late to early wood of the sequent ring is distinct. The more thin-walled elements of the early wood are higly compressed and deformed thus making it difficult to ascertain their original size and shape in the photographs. The tracheids of the late wood are also somewhat radially compressed, but are not so highly deformed. The microstructure of the tracheidal walls is evidently dissolved as the usual double refraction of the wall substance is completely missing and the details of the wall structure (tracheidal pits etc.) are consequently hardly discernable.

Resiniferous elements, conspicuous by their dark brown content, are predominant in the outer part of the early wood and locally form an almost regular tangential zone. They are exceedingly thin walled but, probably due to their compact resinous content, only slightly compressed and deformed thus appearing almost unaltered with an elliptical outline. The tracheids surrounding the resin cells have a considerably smaller diameter than the tracheids of the inner part of the early wood (Fig. 1, A to D) as well as those of the succeeding late wood in which the radial diameter remains almost constant to the border of the ring.

In the transverse section the medullary rays are rather inconspicuous since their elements are compressed and almost dissolved.

Longitudinal sections show the tracheids in a very different state of preservation, as could be expected from their appearance in the transverse view. In many of the tracheidal walls tiny spiral thickenings of the inner surface of the wall are conspicuous (Plate II. A and B) and are most distinct in those elements of the late wood where a tangential cut has exposed the inner surface. In the early wood especially the spirals

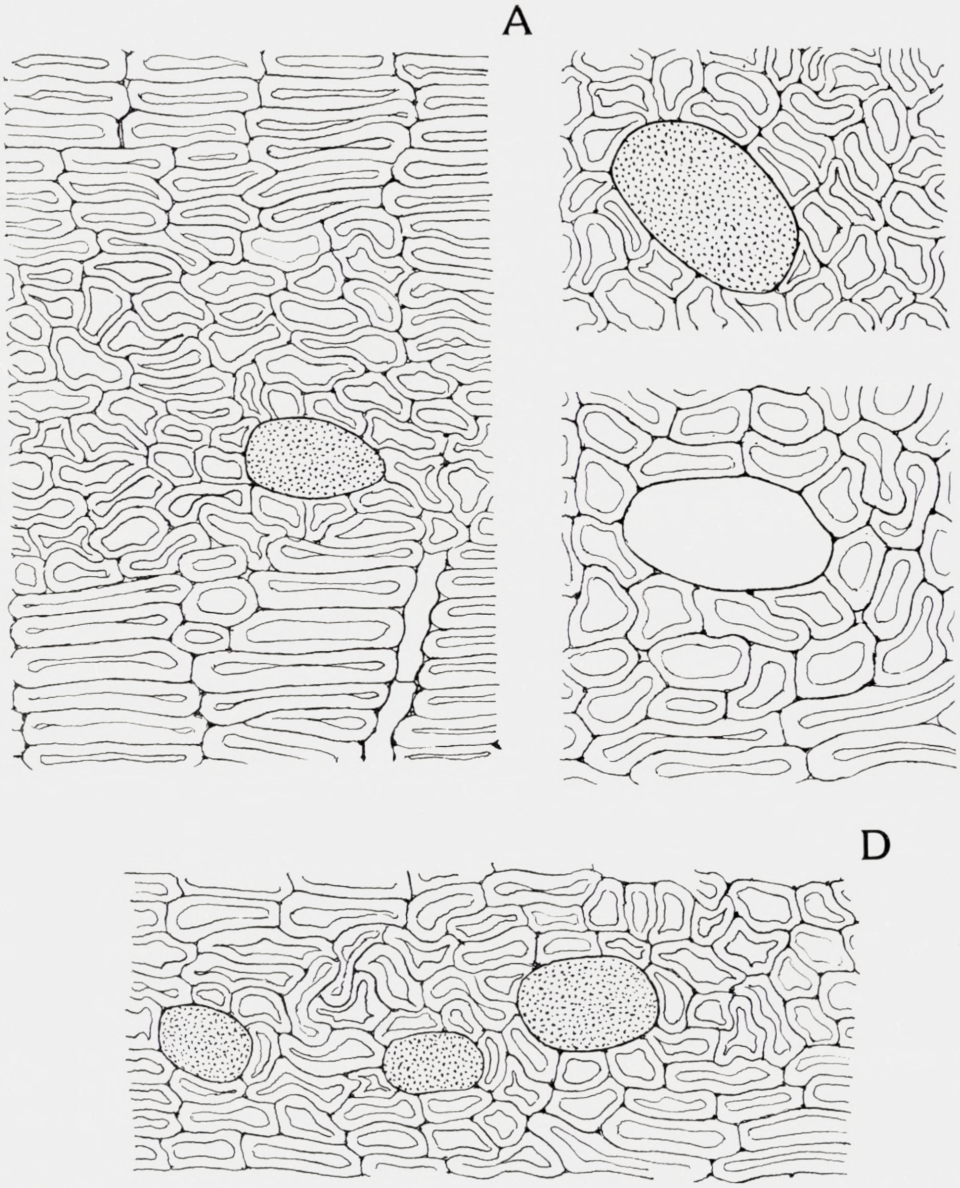


Fig. 1. *Taxoxylon amentotaxoides* n.sp. A–D, transverse sections showing resiniferous xylem parenchyma and surrounding tracheids. (×400). Salten.

are most commonly separate from the rest of the wall and are often found tangled together or forming a coil in the lumen. In such cases their former connection with the wall is only traceable by the scars left in the terminal lamella. In the wider tracheids these thickenings appear as two, delicate, concurrent spirals more or less steeply ascending and when the lumen is compressed they are reduced to zig-zag lines. In the

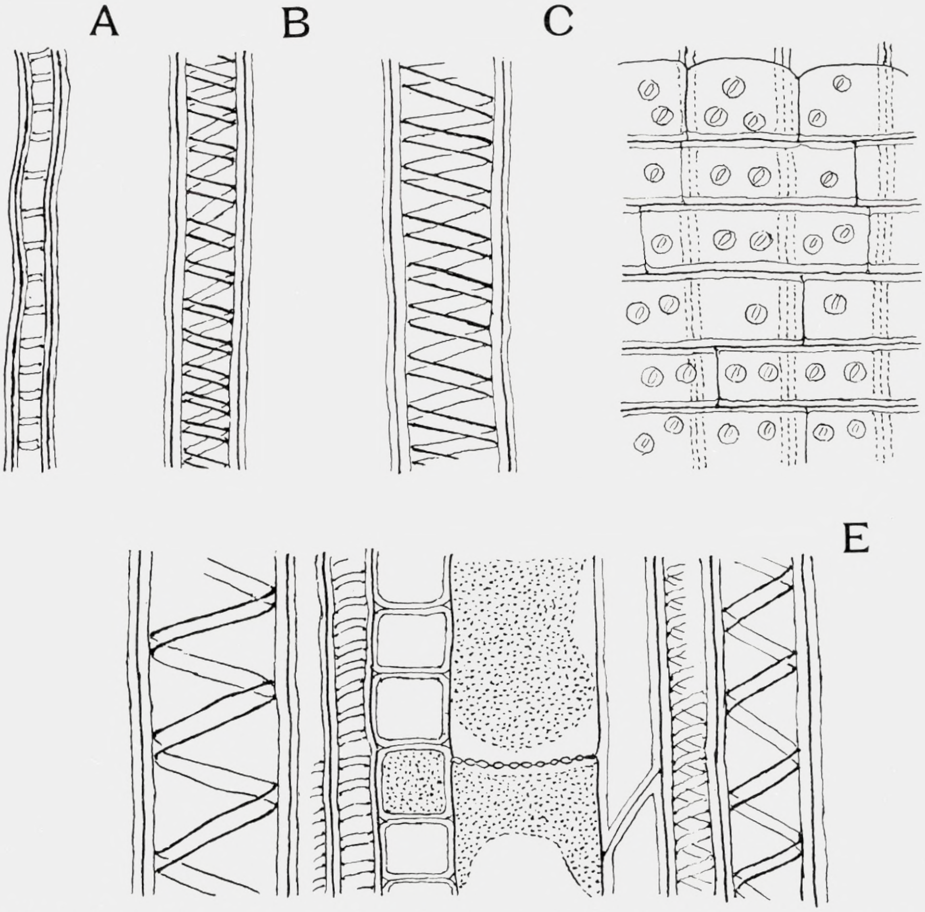


Fig. 2. *Taxoxylon amentotaxoides* n.sp. A–C, parts of tracheids in radial section and E, in tangential section, showing the annual or spiral thickenings of the wall. E also shows a part of a ray and the finely beaded wall separating two resiniferous xylem parenchyma elements. D, cross-field area. (×400). Salten.

narrowest tracheids the thickening sometimes only appears as tiny double rings. The Fig. 2, A, B, C and E show the variations of the spirals.

The bordered pits of the radial walls of the tracheids are only visible where the spirals are dissolved or loosened. They are 14 to 16 μ in diameter and are most commonly arranged in only one row. Tangential bordered pits are rather common.

The irregular radial course of the rays is evidently caused by deformation and it is rare to obtain a large, undamaged group of ray tissue in longitudinal sections that are suitable for figuring. The horizontal walls of the ray cells appear somewhat thickened, with a maximum of 4 to 6 μ, but have a rather uneven profile with thinner and thicker parts irregularly alternating and sometimes showing an intercellular space between the thickening layers of the wall due to disintegration (an 'interstitium'). The tangential walls are thin (1 to 2 μ) and without visible sculpture (Fig. 2, D).

Cross-fields between ray cells and tracheids show one to two, or in the marginal cells sometimes three, circular or elliptical blind pits. Where cross-fields are formed between ray cells and resinous parenchyma the corresponding walls show simple pits; the details are not easy to discern, but the number and shape of the pits seem to vary considerably. The lengths of the resiniferous elements vary from 100 to about 200 μ and are consequently rather short. The transverse walls of the parenchyma cells are partly thin and without sculpture but most often they are somewhat thickened and more or less distinctly bead-like pitted (Fig. 2, E). Transverse sections cleared in a weak sodium hypochlorite solution and stained with vesuvine, show the types of pitting more distinctly.

The medullary rays are most commonly 5 to 12 cells high, but sometimes reach a height of 20 cells. In tangential sections small, triangular, intercellular spaces occur between the adjacent tracheidal wall and the transverse wall of the ray cells.

Diagnosis

A gymnospermous wood of the Taxaceous type. Growth rings well accentuated. In the outer part of the early wood an almost regular, tangential line of thin-walled, resiniferous elements surrounded by tracheids markedly smaller in diameter than those of the adjacent tissue. Spiral thickenings of the inner side of the tracheidal wall normally developed as two very tiny concurring bands. Cross-fields of rays and tracheids exhibit 1 to 3 circular, blind pits, with a variable number of simple pits between ray cells and parenchyma. Transverse walls of parenchyma cells are thin and even, or somewhat thickened and slightly pitted. Bordered pits occur most commonly in single rows on the radial walls and are scattered but rather common on tangential walls.

Affinities

Samples of fossil wood which might be referred with certainty to the Taxales seem to be of rare occurrence. According to R. Kräusel (1919 and 1949) only *Taxites scalariformis* Göppert, of somewhat uncertain geological age, is reliable. Comparing our fossil with the wood of recent Taxaceae and Cephalotaxaceae all details point towards the East Asian genus *Amentotaxus*, the wood of which, according to P. Greguss (1955, p. 147), is characterized anatomically as follows: — *Amentotaxus argotaenia* Pilger — "Latewood portion of the growth increment considerably larger than the earlywood portion, the latter conspicuous for the presence among the tracheids of numerous wide-lumened *paranchyma cells*, not infrequently in whole rows or groups. This disposition of the parenchyma cells and their difference in size from the surrounding tracheids are features so very characteristic as to permit an immediate separation of this species from all other conifers on the basis of the transverse section". The character of the spiral thickenings of the tracheids agrees in the fossil and the recent analogue; in both the spiral thickenings in the tracheids develop as two tiny concurring bands.

In spite of the close similarity between the fossil material and *Amentotaxus argotaenia* some differences may be noted. In the transverse section of *A. argotaenia* figured by P. Greguss (1955, Plate 73) the difference between the tracheids of the early wood and the late wood appears far less marked than in the fossil described here. Another difference is that Greguss mentions the occurrence of numerous round or elliptical pits in the radial walls to the parenchyma cells; these are not clearly seen in the fossil, but this may be caused by the disintegration of the wall substance obscuring such details.

A sample of *Amentotaxus* wood obligingly placed at my disposal by the Forest Department of Yale University, U.S.A., agrees anatomically very well with the sample figured by P. Greguss (1955). However, it is not stated from which part of the axis the sample is derived and as samples of known morphological position have not been available a thorough, detailed comparison, which should also embrace wood from roots and stumps, has consequently not been possible.

Anyhow, the principal characters of the fossil agree so well with those of the recent *Amentotaxus* that the plants from which they originate may be considered as at least being closely related so that the fossil might conveniently be termed *Taxoxylon amentotaxoides* n.sp.

According to a paper by Hui-Lin Li (1952) the genus *Amentotaxus* can be subdivided into four species, the salient characters of which are the form and size of the leaves, and the mutual proportions between the broadness of the two stomatal bands on the under side of the leaf bordering the midrib and the green marginal bands devoid of stomata. The four species are all East Asian and since details of the anatomy of the wood are not available for comparison small specific differences may consequently occur.

The occurrence of *Amentotaxus* leaves in the Tertiary of Europe has been stated several times. A find from the Lower Miocene at Salzhausen (Wetterau, Rhineland) was described by R. Kräusel (1935) who also gives the epidermal anatomy of the leaf. H. Weyland (1937) has mentioned the same species (*A. florini*) from Upper Oligocene layers at Kreutzau near Düren (Rhineland). J. S. Gardner (1883–1886) has figured some leaves as "*Podocarpus Campbelli*" from the Eocene of Great Britain which might be referable to a species of *Amentotaxus*.

Saxegothaeoxylon miocenicum n. sp.

The four samples of fossil gymnospermous wood on which this species is based were collected from the lignites of the Troldhede area (State quarry). All four samples have the same state of preservation, they show tolerably well preserved late wood while the early wood has unfortunately suffered almost total obliteration which, as will appear from the photograph of Plate III, A, has had the effect of making the borders of the growth rings and the transition from early to late wood very conspicuous.

The photographs, Plate III, B and Plate IV, A, show transverse sections more highly magnified. Numerous thin-walled resin cells are seen especially in the compressed early wood, the dark coloured content of the cells making them easily perceptible. The transition from early to late wood is rather abrupt as only in a few places are there tracheids intermediate in size and wall thickness. Two types of late wood elements are discernible; one shows a dark wall while the other, ocurring isolated or in radial groups, shows a bright or only slightly coloured, highly refractive wall. The tracheids of the first type show a far smaller radial extension than those of the second which evidently represents the primary shape. The wall exhibits the normal double refraction in polarized light so that the primary part of the wall as well as the subsequent thickening layers are distinctly discernible while the dark coloured elements have totally lost their double refraction properties as well as the distinctness of the details of the wall structure. It is supposed that they were deformed by shrinkage and disorganization of the microstructure of the wall. In the less altered type there is a certain slight swelling of the wall substance.

The rays are always uniseriate. They confirm the explanation offered on the transformation of the tracheids under fossilization as where they cross a group of bright-walled elements their radial walls are smooth and closely cohering to the bordering tracheidal walls (Fig. 3, A to D), whereas in places where they traverse groups of dark coloured and radially shrunken elements their radial walls are partly separated from the tracheidal walls and are pressed up into folds towards the lumen of the ray cell. By the reduction of the radial diameter of the tracheids in these places the walls of the very thin-walled ray cells have evidently been partly detached, firstly in the centre part of the cross-fields, where the pit has offered a weaker area, subsequently also from the neighbouring parts of the wall, and finally they have been plicated inwards so as to form one or two folds. On the upper and lower borders of the pores the folds often form single loops easily perceptible in the photographs under a reading glass. The thick, horizontal walls of the ray cells have been forced to undergo a similar, radial shrinkage compressing and transforming their pits into tiny tangentially orientated slits.

The bright tracheidal elements (Plate IV, B, D and E) are very conspicuous in the longitudinal sections. D shows elements which have remained almost intact in shape and size while small rings of the fibre in the left of the photograph have undergone a sideward dislocation agreeing with what is found in rotted and machanically treated vegetable fibres, e.g. of *Linum*. B and E show partly intact tracheids in which the transformation towards the dark coloured type has commenced accompanied by an essential reduction in the radial diameter. Most of the tracheids figured in C have undergone such a reduction. Only a few bordered pits are discernible on the radial walls (D) which may be taken as evidence that the apparently intact tracheids have also undergone certain modifications.

A part of a ray passing through a group of transformed but not totally collapsed tracheids is shown in Plate IV, C. The folds on the radial walls here appear as slight vertical configurations, usually only one in each cross-field. In some cases a pair of tiny, vertical stripes forming an x can be discerned corresponding to the folds bordering

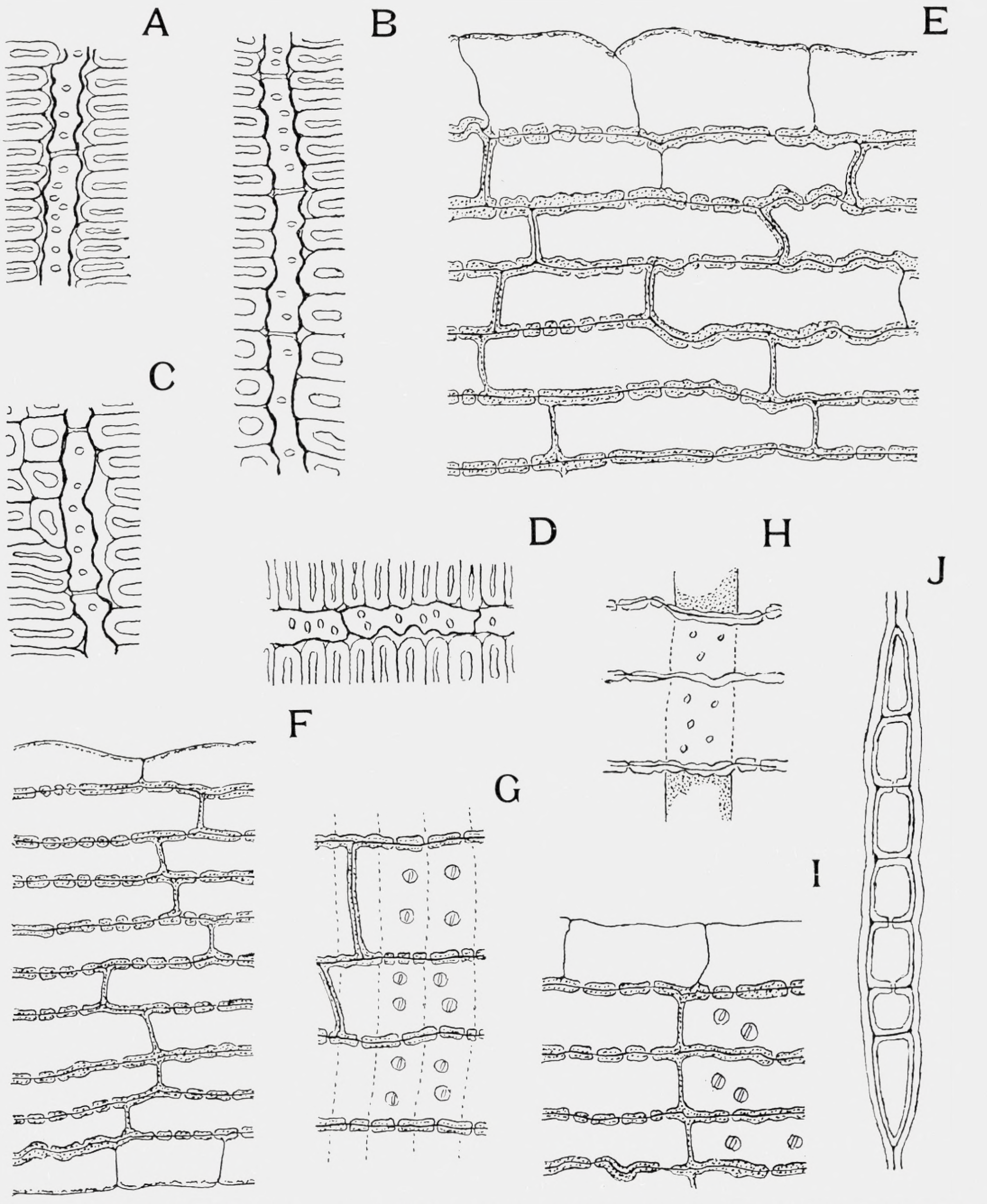


Fig. 3. *Saxegothaeoxylon miocenicum* n.sp. A–D, transverse sections of late wood showing ray cells running through groupes of tracheids with only slightly altered walls. E–I, parts of rays in radial section, H, showing the parts connecting the ray cells with the resiniferous xylem parenchyma. J, tangential section of a ray. (×400). Troldhede State Quarry.

the compressed, cross-field blind pit in the transverse section. Where these pits are slightly less altered the "podocarpoidal" characters are more pronounced than those of the "cupressoidal" type (Fig. 3, G and I).

The horizontal walls of the ray cells attain a considerable thickness, up to 8 μ (4 to 8 μ). They are usually coarsely pitted and in unaltered or only slightly altered parts, such as those figured in Plate IV, C and in Fig. 3, E to H, the pits appear somewhat funnel-shaped, 1 to 2 μ broad. Pits are also perceptible on the horizontal walls seen in transverse sections and may be very conspicuous as is seen in Fig. 3, A to D. Where the horizontal walls are more or less reduced in length by contraction, the pits are radially compressed and appear far less extended often being only perceptible as tiny vertical slits. Under extreme deformation the walls may appear irregularly thickened and so swollen as to obliterate the pitting completely. Fi.g 3, H shows stages of this trans formation. The tangential walls of the ray cells are rather thin and only slightly sculptured or more often quite smooth.

In the tangential section the rays are composed of 1 to 11 vertical rows of cells with thick horizontal and thin radial walls. The walls are especially distinct where the ray traverses a group of relatively unaltered tracheids. Bordered pits on the tangential tracheidal walls are common but difficult to distinguish and are rather small with a diameter up to 4 μ. The elements of the resiniferous parenchyma attain a length of 250 μ, the transverse walls separating them appear to be smooth and unthickened. In the cross-field between parenchyma and ray cells the wall shows from one to five simple pits.

Diagnosis

Growth rings distinct. Rays uniseriate 1–11 cells high with horizontal walls thick, densely and strongly pitted and thin tangential walls smooth or slightly pitted. The cross-fields show 1 to 2 (4) blind pits, circular in outline and of a type intermediate between the cupressoidal and podocarpoidal form. Wood parenchyma resiniferous, thin-walled with 3 to 5 simple pits in the cross-field and transverse walls thin and smooth, Bordered pits in a single row on the radial as well as on the tangential walls of the tracheids. Indentures are not developed.

Affinities

The four samples described represent a type of gymnospermous wood of very peculiar structure agreeing anatomically with the wood of the recent *Saxegothaea*. The genus *Saxegothaea* is commonly referred to the Podocarpaceae but the wood is distinguished from that of the other genera of this family by the very thick, dense and coarsely pitted horizontal walls of the ray cells. *S. conspicua* Lindley was thoroughly studied anatomically by P. Greguss (1955), but F. Beust (1885) had already noted the special character of the ray cells as also had W. Gothan (1905) who l.c. p. 56–57 described and figured some peculiarities of the anatomy of *Saxogothaea* wood. P.

Greguss describes *Saxegothaea* in connection with the wood of the Taxodiaceae mainly because the cross-field pitting in his opinion is of the cupressoidal type rather than the podocarpoidal. At any rate the fossil wood is anatomically closely allied to the recent *Saxogothaea*, and exhibits a well definable xylotomic unit. It is suggested that it represents a special organo-genus *Saxogothaeoxylon* and *miocenicum* would probably be a convenient specific name.

A description of the fossil is nearly covered by that given by P. Greguss (1955) for the analogous recent species. The description is partly contained in his keys for determination (l.c. p. 103–107) and partly in the text which enters into more detail (p. 183). Yet some differences ought to be pointed out. According to his figures the wood of the recent *Saxegothaea* appears more homogeneous than in the fossil described here but the early and late wood may be somewhat variable in volume. According to P. Greguss the rays only attain a maximum of seven stories, but as his sample originates from a branch only 8 years old and 5 cm in diameter the height in the older wood might be greater. As the cross-field pitting of the early wood in the fossil cannot be used for comparison, due to compression and folding, the character of the pitting of this part cannot serve for drawing a parallel.

Saxegothaea conspicua Lindley is at present restricted to southern Chile and Patagonia. The enormous geographical gap from South America to the occurrence of the genus in Tertiary Europa has not been bridged through finds in the intermediate area. The discovery of a fossil plant remain, such as *Saxegothaeoxylon* described here, seems to be of interest as it widens the possibility of demonstrating Tertiary types in the northern hemisphere which now only occur in the far south.

Pinus palaeostrobus (C. v. Ettingshausen) O. Heer.

C. v. Ettingshausen (1855) p. 35, Table VI, figs. 23 to 33. (*Pinitis palaeostrobus*). O. Heer (1855) p. 56, Table XXI, figs. 6a to 8. G. de Saporta (1865 I) p. 74, Table III, figs. 1, A–C; Table IV, fig. 3A. O. Heer (1869) p. 56, Table XIII, figs. 1 to 2. L. Lesquereux (1878) p. 83, Table VII, figs. 2 and 5 to 30. O. Heer (1883) p. 65, Table LXX, fig. 8; Table LXXXVII, figs. 5 and 6.

A dwarf shoot of a species of *Pinus* carrying five needles was found in the fossiliferous clay at Fasterholt. It is so far the only certain evidence of a *Pinus* of this type in the Danish Tertiary flora.

The photograph (Plate V, D) shows the shoot magnified three times. It was not possible to examine the full length of the needles as they were badly damaged on splitting up the hard and brittle matrix, but they have evidently been rather short and did not exceed 4 cm in length. Of the two turned upward in the photograph the right hand needle was broken off at its base and the left hand one was broken a little higher up. The scale leaves that once covered the short, somewhat bulb-shaped, dwarf shoot have left broad scars. The needles are triangular in section with fine, longitudinal stripes on the surface.

The diagnosis of *Pinus palaeostrobus* given by O. Heer (1869, p. 56) runs briefly as follows: *P. foliis quinis, elongati filiformibus, tenuissimis, laxis.* When the needles are described as "flabby" it may be because they often appear bent or curved from which O. Heer concluded that the substance of the needles had been rather soft. O. Heer too noted that the needles may show fine, longitudinal stripes.

Cones or cone scales that could be referred to a *Pinus* of the section *strobus* were not found; the apical of the scales would make them easily recognizable. A badly damager cone of a Pine, referred to "*Pinus laricio thomasiana*" O. Heer by N. Hartz (1909), is recorded from the lignitic layers at Sønderskov (Silkeborg area).

Dwarf shoots referred to *Pinus palaeostrobus* O. Heer are found and described from numerous Swiss localities of Aquitanian age, from Rixhöft (Samland, Kaliningrad region, U.S.S.R.), S.E. France, and outside Europe from west Greenland (Aumarûtigssat, Hare Island and Atanikerdluk) and North America (Castillos Ranch, Florissant, Colorado).

Pityosporites spp.

A few pollen grains referable to Abietinous gymnosperms, probably species of the genus *Pinus,* were separated from the lignitic clay in the brown coal deposit at Silkeborg Vesterskov. The Fig. 14, A to C, shows the types noted.

The pollen grains are elliptical in outline, the largest measuring from 60 to 80 μ in diameter. Each grain has two bladder-like extensions of the exine with a net-like design; the rest of the surface is finely dotted. Two pollen types are recognizable. One (Fig. 14, A) has only slightly protruding bladders, the other (B and C) has bladders more strongly protruding and markedly restricted at the base. The pollen grains of the first type might be referred to the "Haploxylon type" of K. Rudolph (1935) while the second type may be referred to R. Pilger's and K. Rudolph,s "*Pinus silvestris* type". The types are not strictly bound to the two subgenera *Haploxylon* and *Diploxylon* (R. Pilger, 1926); the *Haploxylon* type is confined to the subgenus but the subgenus also contains other types, e.g. in *Pinus strobus,* while not all species of the subgenus *Diploxylon* show the *Diploxylon* type typically developed so that R. Pilger has preferred the term *Pinus silvestris* type in preference to the term *Diploxylon* type.

Remains of *Pinus* species of both the subgenera *Haploxylon* and *Diploxylon* have been found in the Danish lignite deposits as dwarf shoots and wood respectively.

The term *Pityosporites* was adopted by A. C. Seward (1919) for pollen of gymnosperms provided with bladder-like extensions of the exine. Besides the recent Abieteae such pollen occurs in certain Podocarpaceae, but foliage remains referable to this family seem not to have been demonstrated with certainty in the Neogene of Europe (R. Florin 1926).

Pinuxylon sp. cf. ***P. paxii*** R. Kräusel

G. Kraus (1866) *Pityoxylon* sp. R. Kräusel (1919) p. 248, Taf. 18, Fig. 8, 13; Taf. 23, Fig. 5, & Text Fig. 32, 33. R. Kräusel (1920) p. 422, Taf. 28, Fig. 1 to 3; Taf. 36, Fig. 12. R. Kräusel und G. Schönfeld (1924), p, 270. Tafel XXII, Fig, 16 to 18. R. Kräusel (1949).

Among the samples of fossil wood procured from the Torvig State Quarry at Troldhede was a specimen which according to its anatomical structure can only be referred to the genus *Pinus*.

On the whole it is in a tolerably good state of preservation. The difference in thickness of the tracheidal walls of early and late wood elements is not considerable, and the border is only marked by relatively few layers of narrower tracheids so that growth rings must have been rather faintly accentuated. In the present state of preservation the borders of the growth rings are easily recognizable by the layers of collapsed or almost collapsed early wood elements. Plate V, A, shows a portion of a transverse section including some gaps which mark the position of vertical resin canals together with their accompanying thin-walled parenchyma of which there are still some remains. The gaps are rather scarce; their resinous contents have totally disappeared.

Tangential sections show that the wood also possessed normally developed horizontal resin ducts (Plate V, B). Rays enclosing such ducts deviate in form from the simple ones by attaining a broad fusiform shape. The original presence of the resin ducts is most often only recognizable by the occurrence of an irregularly circumscribed lacuna in the middle of the broader part of the ray produced by the solution of the epithema and the surrounding parenchyma. The parenchyma of the simple rays was also found to be mostly dissolved and the rays sometimes have the appearance of that illustrated as Fig. 4, G. The secondary thickening of the tracheidal wall is segregated as steeply ascending spirals and is also partly dissolved.

The drawings D and F in Fig. 4 show rays with almost intact resin ducts, E exhibits a ray in which no resin duct has developed and the resiniferous parenchyma forms a coherent mass.

The figures of radial sections (Fig. 4, A to C) are drawn after the slides have been cleared with dilute sodium hypochlorite solution. Most of the ray parenchyma has disappeared so that what appears as "oëopores" of the radial ray cell walls really only represent the counterparts of the ray pits in the corresponding wall of the bordering tracheids. It is evident that each cross-field between ray and tracheid has possessed only one large "oëopore", elliptical to almost circular in outline. Sections not exposed to the action of dissolving chemicals show the horizontal walls of the ray parenchyma cells irregularly thickened with thicker and thinner parts alternating causing sometimes a coarse poring (Fig. 4, A). Locally the secondary thickening has somewhat disintegrated giving rise to indistinct interstitia. The tangential walls of the ray cells are always only slightly thickened.

The marginal tracheids bordering the upper and lower edge of the larger rays show irregular thickenings on the horizontal and tangential walls which often penetrate into the lumen as small teeth. The small bordered pits connecting the marginal

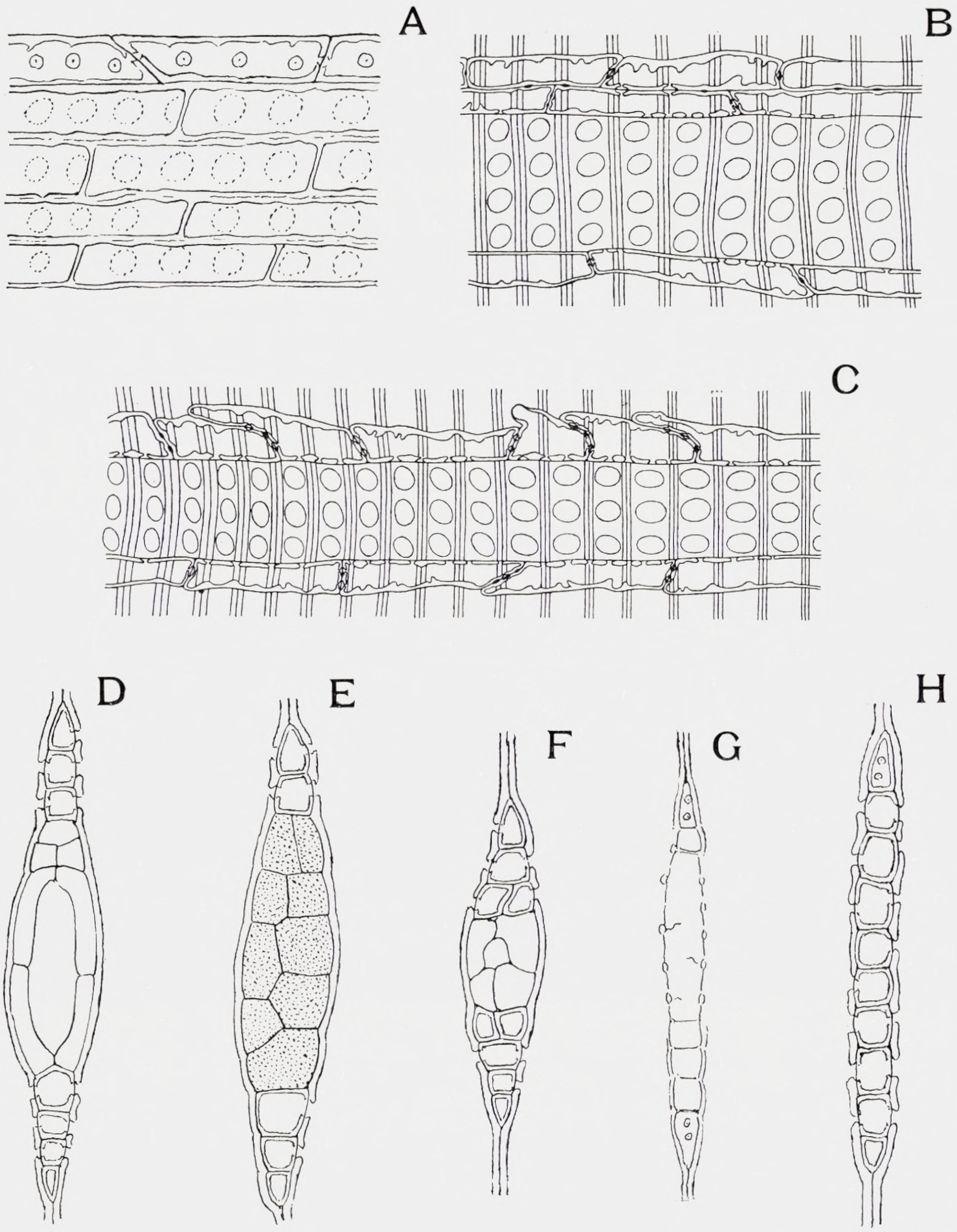


Fig. 4. *Pinuxylon* sp. cf. *P. paxii* R. Kräusel. A, B and C, radial sections. D–F, tangential sections of rays including resin ducts or coherent resiniferous parenchyma. G and H, simple rays; in the ray figured in G the tissue is partly dissolved. (B and C×250, A and D–H×400). Troldhede State Quarry.

tracheids with the vertical tracheidal elements of the wood are mostly rather difficult to discern, but the bordered pits on the tangential, more or less slanting walls are, in most cases, quite distinct. How much of the thickness of the walls of the ray tissue is original and how much is caused by secondary bulging is of course impossible to ascertain.

Among the fossil *Pinus* woods (*Pinuxyla*) the specimen described here shows agreement with the *Pinuxylon paxii* R. Kräusel from the Silesian brown coal, probably of late Miocene age. In the fossil described here as well as in *P. paxii* (R. Kräusel 1920, Plate 28, Fig. 1) the growth rings are only slightly accentuated since the differences in diameter and wall thickness between the tracheids of the early and late wood are insignificant.

According to R. Kräusel and G. Schönfeld (1924) *P. paxii* might be referred to a *Pinus* species of the section *pinaster*. Consequently it is related to the recent widely distributed *Pinus silvestris* L., without being identical with it or, as far as can be seen after comparison with the xylolomical details given by P. Greguss (1955), without being quite identical with any other living *Pinus* sp.

Pinuxylon paxii occurs in the Neogene Tertiary of Silesia and other places in central Europe (Oligocene to Miocene).

Sciadopitys tertiaria P. Menzel

The material investigated was obtained from a fragment of a bore-core about 10 cm in diameter brought up from a depth of about 20 m. The boring was sunk near the Grindsted dairy (central Jutland) in the year 1925. (For details see the publication of H. Ødum and W. Christensen, 1936). The headmaster of the school at Grindsted, Mr. M. C. Nielsen, who examined the material brought up, was struck by the peculiar appearance of a layer, about 20 cm thick of a type of light lignite which enclosed numerous, glossy particles not unlike flattened pieces af straw. A part of the core including this layer was handed over to the Mineralogical and Geological Museum of Copenhagen University for the determination of these fossils.

After boiling part of the matrix with a solution of sodium carbonate the lignite disintegrated and it was possible to pick out the glossy particles. These appeared as rectangular pieces varying in length from 1 to 2 cm, 2,5 to 4 mm broad and 0.5 mm thick, of an olive brown colour. They were finely striped on one surface while the other was showing a broad and rather deep longitudinal furrow still filled by the coaly matrix.

The obtainment of preparations showing surface views made no difficulty. After clearing with a dilute solution of sodium hypochlorite most of the inner tissue was dissolved, and it was then easy to split up the pieces parallel to the flat side. The preparation showed the characters of a leaf.

It proved far more difficult to obtatin transverse sections suitably thin and yet coherent. By clearing the sections under a cover-glass preparations were obtained suitable for drawing; unfortunately it was not possible to keep them as permanent mounts (Fig. 5, A).

The median furrow of the underside represents a stomatiferous band. Here there is a dense covering of short, bluntly-ended hairs which represent papillose protuberances from the outer wall of the epidermal cells. The rest of the surface is smooth, devoid of stomata and in front view appears as composed of longitudinally stretched, rectangular elements with thin and finely pored side walls. By fine adjustment of the depth of focus of the microscope a certain part of the extremely thick outer wall is seen to contain numerous small cavities giving the stratum a somewhat gritty appearance (Fig. 5 C).

A hypodermal layer consisting of coherent tissue of thin-walled, spindle-like elements is found under the epidermis outside the stomatiferous furrow.

The stomata are placed at the same level as the surface of the epidermis. They are individually encircled by a group of 10 to 14 polygonal epidermal cells similar in size and shape to the other epidermal elements of the stomatiferous band but differing from these by their papillose protuberances. The preparations of the surface most often only show the basal, rather thick-walled parts of the papillae (Fig. 5, F), while in the top the thickenings of the wall are commonly dissolved so that only the finely warted cuticle is left.

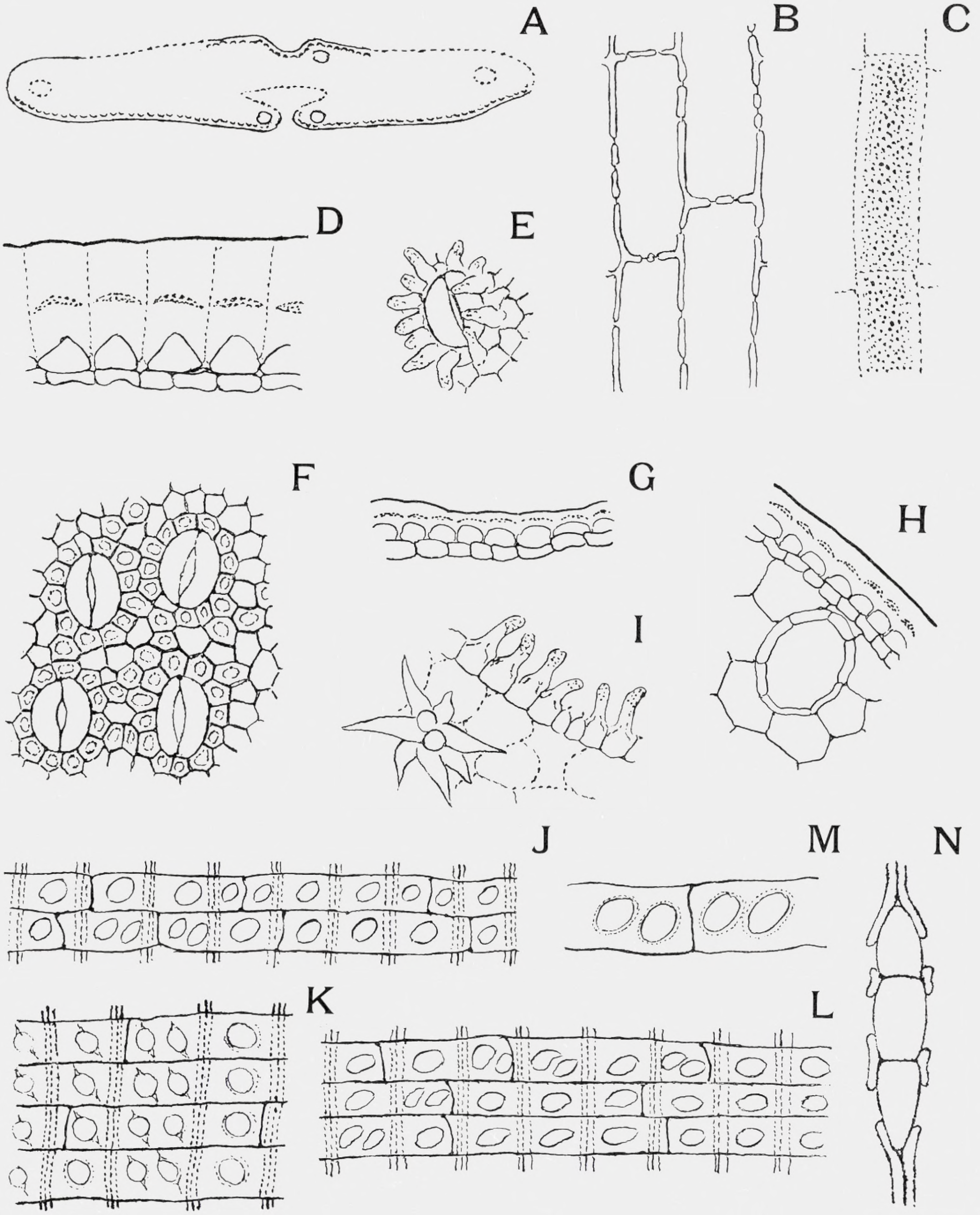
The thickness of the outer wall of the epidermis is apparent from the transverse sections (Fig. 5, D, G and H). The zone of small cavities is seen to form an arch about the middle of the wall. The side and inner walls of the cells normally appear in a state of dissolution in the preparations as well as the elements of the hypodermis. Balsam ducts are traceable here and there but the remains of the star-shaped idioblasts (Fig. 5, I) and the rather large, thin-walled cells of the mesophyll can only rarely be made out. The vein tissue has completely disappeared.

The anatomical agreement of the fossil with the "symphyllodium" (double needle) of the recent *Sciadopitys verticillata* Siebold et Zuccarini is evident. The small cavities in the outer wall of the epidermis are produced by the solution of crystals (calcium oxalate) which are common in the epidermis of the recent species where there is also an arch-shaped crystal layer in the middle part of the outer wall. In the double needle of the recent *Sciadopitys* the hypodermal layer is composed of spindle-like, rather thin-walled elements.

Leaves (symphyllodia) and cones of *Sciadopitys* are known from the Tertiary of central Europe and were first described by P. Menzel (1913) under the name

---

Fig. 5. *Sciadopitys tertiaria* P. Menzel. A, transverse section of a symphyllodium. B and C, surface views of epidermis outside the stomatiferous furrow, C shows the crystal-bearing stratum of the outer wall. D, G and H, transverse sections of epidermis and hypodermis, in the part figured in H a balsam duct is included in the mesophyll. E and F, epidermal elements from the stomatiferous furrow, in the part figured in F seen from the inner side. I, transverse section of a part of the stomatiferous furrow; the mesophyll includes an asterosclereid. (A × 30, B–I × 400). Grindsted.
Sciadopityoxylon wettsteinii K. A. Jurasky. J–M, radial sections and N, tangential section of rays (J–L × 250, M and N × 400). Troldhede.


A
B
C
D
E
F
G
H
I
J
M
N
K
L

Sciadopitys tertiaria. A list of occurrences of fossil *Sciadopitys* in Poland and adjacent territories is given by Z. Zalewska (1960, p. 32). A survey of the fossil *Sciadopitys* and *Sciadopitys*-like leaf types is given by R. Florin (1922) who also has given some important anatomical details. *S. tertiaria* is known from western Germany and Poland (Jarnov) and ranges from the Lower Miocene to the Upper Pliocene. The recent analogue is indigenous to the mountain-forests of Japan and can be grown in northern and central Europe in sheltered places. The parallelism between the recent species and the fossil seems to be very complete.

S. tertiaria appears to have had a considerable extension in Europe, probably occurring in isolated groups in the forests of that time (K. A. Jurasky 1928). It represents an ancient type, a fact already maintained by J. Velenovsky: "Die Gattung Sciadopitys darf nach allen ihren vegetativen und Blütenteilen überhaupt mit keiner der früher genannten Familien (incl. Taxodineae) verbunden werden. Es ist dies ein isolierter Typus, ohne nähere Verwandschaft und höchst wahrscheinlich aus uralten geologischen Zeiten herübergekommen". Fossil remains of *Sciadopitys* had not yet been discovered at the time J. Velenovsky wrote those lines (R. Florin 1922).

The fragments of the symphyllodia, at least when they occur in larger quantities, give a very peculiar aspect to the brown coal. In Germany this type of lignite is termed "Graskohle" (W. Gothan 1936); compare the first impression Mr. Nielsen, the collector of our material, received: glossy particles, not unlike flattened pieces of straw.

Sciadopityoxylon wettsteinii K. A. Jurasky

Four samples of fossil wood, one from the Lystrupsminde quarry and three from the Troldhede district, are referable to this type. Of the three pieces from the Troldhede district one was found in the State quarry and two in the Torvig quarry. The state of preservation proved fairly good save for the rather advanced segregation of the thickenings of the tracheidal walls into their fibrillary components.

The transverse section (Plate VI, A) shows a gymnospermous wood of a rather uncomplicated type. The early wood appears mostly compressed with collapsed tracheids; where the original shape of the elements is traceable it is evident that they do not differ much in size from those of the late wood. The growth rings have thus been histologically almost homogeneous, yet the limits are tolerably well marked. The outline of the tracheids tend to be of the angular type but minute intercellular spaces are not rare. The monoseriate rays are composed of uniformly thin-walled cells which in the slide figured are not very conspicuous.

In longitudinal sections (Plate VI, B and C) the more or less advanced dissolution of the tracheidal walls is evident. In the radial section some bordered pits (arranged in one row) are still traceable; in the middle of the photograph (Plate VI, B) they appear in front view, and to the right som pits of the tangential walls are seen in section.

The two rays in Plate VI, B show the type of the cross-field pitting with one, rarely two blind pits in each field. The outline of the pits is not very conspicuous; the drawings in Fig. 5, J to M will be supplementary to the photographs. The pits appear elliptical, somewhat slanting, broader in the cross-field of the early wood, more slender in the late wood. Through a lens the outline is traceable as is also, in a few cases, the corresponding slit in the tracheidal wall; most often these details are obscured by defibrillous disintegretion of the tracheidal wall which has split up the border and affected a "tailed" outline of the pit.

The cross-field pitting is characteristically of the "oëoporous" type. In the drawing Fig. 5, M it has been possible to sketch the whole of the circumference of the pits.

In the photograph (Plate VI, C) of a tangential section some rays are shown. They are most commonly low, composed of 1 to 3 cell rows, but higher rays occur. The elements are extremely thin walled, the pits are quite small and sometimes confluent.

K. A. Jurasky (1928) has described a fossil wood which he refers to the recent genus *Sciadopitys* under the name *Sciadopityoxylon wettsteinii* n.sp., from the lignite at Düren (Grube Zukunft) situated near the quarry "Marie Theresia" by Herzogenrath near Aachen, the same locality from which the *Sciadopitys tertiaria* of P. Menzel originates, and probably of early Miocene age. The resemblance between the fossil and its recent analogue is indeed very striking, and the description, accompanied by some excellent microphotographs, settles the determination beyond doubt. *Sciadopityoxylon* is distinguished from the collective type *Plyllocladoxylon*, comprising fossil wood represented by the secondary xylem of the recent genera *Phyllocladus, Microcachrys, Pherosphaera, Podocarpus* spp. and *Dacrydium,* by the "ungleichmässige Aussehen der Eisporen und vor allem durch den auch im Frühholz auftreteden weiten Hof". (K. A. Jurasky 1928). These characters are also acceptable to E. J. Slyper (1933).

As the fossil described here agrees very well with *S. wettsteinii,* and the geological age of the two specimens is probably the same, the name *Sciadopityoxylon wettsteinii* K. A. Jurasky can be applied to our fossil.

It should be noted that the growth rings in a sample of *Sciadopitys* wood of Japanese origin are far less homogeneous than those of the fossils described; the early wood being composed of tracheids considerably wider in outline and far more thin walled than those of the late wood and in transverse section of a strictly angular shape.

According to a statement of P. Greguss (1955, p. 147) "Wood parenchyma cells [in *Sciadopitys*] were not seen, not even exceptionally, though some investigators claim their occurrence". Neither were wood parenchyma cells found in my recent Japanese material used for comparison, nor noticed by K. A. Jurasky or occurring in the fossil samples investigated by me. The identity of the other investigators mentioned by P. Greguss is not given.

As was pointed out by K. A. Jurasky (1928) it is of course not strictly demonstrable, but at least rather probable, that all the Tertiary fragments referred to *Sciadopitys* appertain to the same species closely agreeing with the recent *S. verticillata* Siebold et Zuccarini. Cones and seeds are not known from the Danish lignites, but leaves (symphyllodia), pollen (P. Ingwersen 1954) and wood have been identified as appartaining to a *Sciadopitys* sp. According to the commonly admitted rules of nomenclature for fossil plants it is not at the present state of our knowledge allowed to include these fragments under the same species so they have to be mentioned as representing as many organo-genera.

Sequoia couttsiae O. Heer (1863)

Foliage twigs, cones and seeds referable to this type are fairly common in the fossiliferous clay at Moselund. Seeds are also found in the lignitic layers at Fasterholt and here and there in the coal itself.

The diagnosis of *Sequoia couttsiae* (O. Heer 1863), completed by P. Menzel runs: Sequoia ramis curvata-adcendentibus alternis; ramulis junioribus elongatis, gracilibus foliis ramorum innovationumque squamaeformibus basi adnata decurentibus, rigidis, imbricatis, semipatentibus, sulfalcatis, acuminatis, dorse levitur carinatis; foliis ramulorium productionibus, laxe imbricatis, falcato-sublinearibus; amentis masculinis axillaribus, rotundis, e braeteis conferte imbricatis; strobilis globosis vel sub globosis, ad ramulorum apices plerumque solitarie appensis; squamis paucis, peltatis, rhomboideis, medio brevissime mucronolatis, rugosis, seminibus curvatis, compressis, alatis (P .Menzel 1900, p. 91).

Plate VII, A shows a bunch of foliated twigs, two of them terminated by cones. The leaves here are rather scaly, but terminate in a sharp point with a tendency to be inwardly bent. The Fig. 6 shows parts of some isolated twigs in which the foliage is more open and the leaves distinctly acute and falcate.

Anatomically the leaves show an epidermis of axially extended, rather thick-walled elements only interrupted by four, narrow, almost marginal lines of short cells, two on the upper and two on the under side of the leaf, in which the stomata are localized. The guard cells are surrounded by 4 to 5 epidermal elements. The outer wall of the epidermis contains numerous small dots each representing a cavity probably originally filled with a crystal of calcium oxalate. Outside the stomatiferous lines there is an almost continuous hypodermal layer of more or less thick-walled prosenchyma cells, undoubtedly contributing to the admirable preservation of the fossils. By maceration in a solution of sodium hypochlorite the mesophyll is dissolved and the hypodermal layer becomes less conspicuous. Predominantly in the base of the leaf a few peculiar prosenchymatous elements in the mesophyll are found though often difficult to discern in the macerated material. They are stout, short, somewhat irregularly shaped, bluntly tapering and thick-walled, and in some places covered with a thin, finely granular sheet, evidently representing a thin crystal layer.

The cones figured in Plate VII, A, B and D are almost intact. The highly compressed specimen of Plate VII, C might also be related to *Sequoia couttsiae*, The cones are small (10 – 12 mm) with an estimated number of only 20 to 30 scales. The escutcheon corresponds well with the figures given by J. S. Gardner (1883–1886),

P. Menzel (1900) and Z. Zalewska (1960). A few seeds were isolated by splitting up an intact cone. In size and shape the seeds correspond with the figures given by, e.g. Z. Zalewska (1960), and show the characters of the diagnosis.

Some anatomical information was obtained by macerating a cone like that figured in Plate VII, B. Numerous spindle-shaped prosenchyma cells were found embedded in the thin-walled, brown parenchyma which occupies the central part af the scale, a character also found in the cone scales of the extant Sequoias.

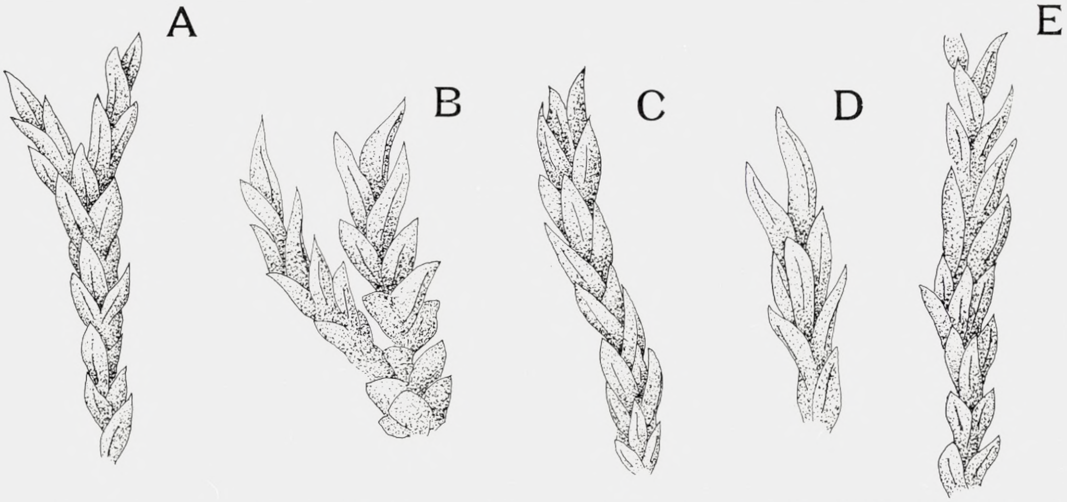


Fig. 6. *Sequoia couttsiae* O. Heer. Parts of foliage twigs (×2). Moselund, Mrs. E. Nordmann del.

A series of seeds agreeing anatomically and referable to *S. couttsiae* are shown in Plate VII, E, F and G. The cuticle of the epidermis appears finely striated with the subepidermal layer developed as a sheet composed of almost isodiametric sclerenchyma cells which are finely and densely pitted and here and there show the outlines of a crystal having filled out the tiny lumen. The main part of the testa consists of axially extended, spindle-shaped sclerenchyma cells (Fig. 7, H), the rather thick walls of which show numerous, quite small but distinct bordered pits.

Remains referable to *Sequoia couttsiae* occur over a wide range and in age reach from the Upper Oligocene to the Miocene (compare, for example, the table p. 76 of Z. Zalewska (1960) covering the localities in Poland and adjacent areas). A number of allied systematic units are described (P. Menzel 1900) but can hardly be maintained as distinct species. The anatomy of the leaf (H. Bandulska 1923, Z. Zalewska 1960) agrees very closely with the anatomy of the extant *Sequoia gigantea* (J. Lindley) J. Decaisne (*Sepuoiadendron* J. T. Buchholz) (R. Florin 1931), commonly regarded as a living analogue. An anatomical character of the *S. giganteum* hitherto, as far as I know, overlooked, is the occurrence of the peculiar stout, spindle-shaped, bluntly pointed prosenchyma elements covered with a thin layer containing minute crystals at the decurrent base of the leaf as well as in the pericyclic layer of the axis. This layer is not directly part of the wall of the prosenchyma cells but is formed in the walls of the adjacent parenchymatous elements, it is not always distinguishable in the fossil as the thin, frail walls of the mesophyll here are more or less destroyed.

The twigs of *Sequoia couttsiae* are generally far more slender and the leaves smaller than in *Sequoiadendron giganteum*. A marked difference is also noticeable in the size of the cones which in the living analogue attain a considerable size (60 × 40 mm) while in the fossil they are always quite small. The seeds almost agree in size and shape but differ in anatomical details. A common feature of the seeds of all Taxodiaceae is the development of a subepidermal layer of small, almost isodiametric, thick-walled sclerenchyma cells, often containing crystals of calcium oxalate, but they are not developed to the same extent in all the genera.

As is shown in Fig. 7, A, B and C the transverse sections of the seeds of the two extant Sequoias differ considerably in outline; the marginal wing is broader in *Sequoiadendron giganteum* than in *Sequoia sempervirens*. Other differences are found in the histology of the testa; in *S. sempervirens* the tissue is markedly heterogeneous, composed of mixed groups of thin and thick-walled elements, axially extended and highly pitted, while in *Sequoiadendron giganteum* the tissue is almost homogeneous with a mesotesta composed of thin-walled, somewhat branched cells. The fossil seeds (Plate VII, E–G), referred to *S. couttsiae*, are very much like the seeds of *S. giganteum* in size and shape being broad winged and with a curved embryo, but they are well defined histologically. The main elements of the testa, including the subepidermal layer of isodiametric sclereids, are far more solid in *S, couttsiae* than in *Sequoiadendron* giganteum (Fig. 7, H and G).

The fossil seeds approach in size and shape the seeds of *Metasequoia* (Z. ZALEWSKA 1960). The *Metasequoia* seeds are easily distinguished from those of *S, giganteum* by having two larger, or a number of smaller, ducts of schizogenous development, but mostly devoid of resin (Fig. 7, D, E and F). The mesotesta is homogeneous, composed of thin-walled elements. Often the seeds show a slight incision in the top so conspicuous that it gives the outline an almost obcordate appearance. Remains referable to *Metasequoia* have not yet been found in Danish lignitic layers.

In a recent paper by O. SCHWARTZ and HEINZ WEIDE (1962) a new interpretation of the systematic interrelation between the genera *Sequoia*, *Sequoiadendron* and *Metasequoia* is advanced in which they are considered so closely related that they are included in one and the same generic unit. According to the rules of priority this generic unit must then be named *Sequoia*.

Some anatomical details concerning the structure of the secondary xylem and the seed seem to have escaped the attention of these authors. As was pointed out by J. T. BUCHHOLZ (1939) the genus *Sequoia* St. Endlicher contains two types differing sufficiently to justify the division into two genera, *Sequoia (sempervirens)* and *Sequoiadendron (giganteum)*. *Metasequoia* seems most conveniently kept apart as a special genus. An adequate solution of this somewhat complicated question would probably

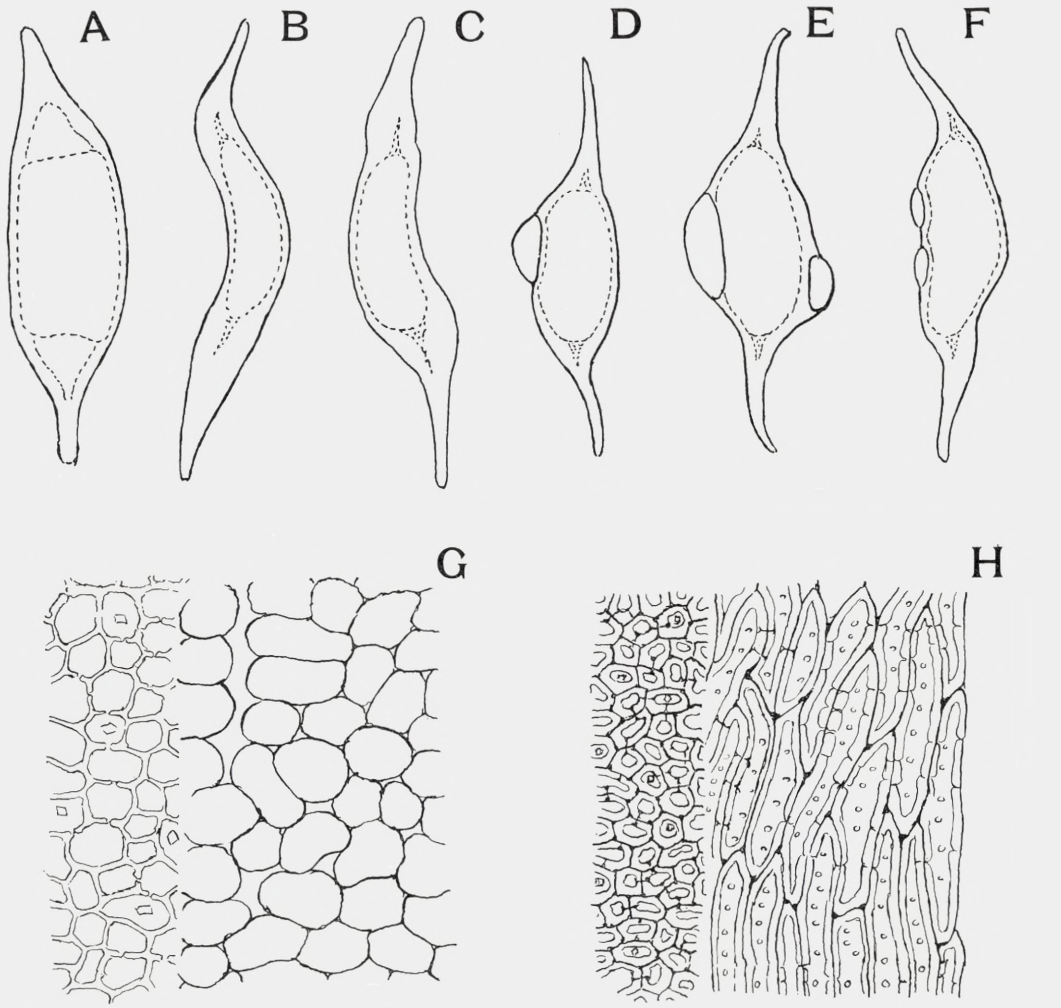


Fig. 7. A–F, transverse sections, drawn in outline, of seeds, A of *Sequoia sempervirens* (A. B. Lambert) St. Endlicher. B and C, *Sequoiadendron giganteum* (J .Lindley) J. T. Buchholz and D–F, *Metasequoia glyptostroboides* H. H. Hu and C. Cheng. G, exo- and mesotesta of *S. giganteum* and H, of *S. couttsiae* (Moselund). H is drawn from macerated material (A–F × 20, G–H × 200).

be to interpret the two types in question as monotypical representatives of as many subgenera, to which might be added the fossil *S. couttsiae* as a third. As for the specific rank of the last named unit the remark of the authors cited (1962, p. 187) seems somewhat arbitrary: "S. couttsiae (O. Heer 1863) umfasst ein Gemisch [?] von S. Langsdorffii und S. Reichenbachii was durch die Originaldiagnose bestätigt wird. Die Vorwendung dieses Binomens ist ebenfalls inkorrekt". The original diagnosis and the corresponding diagnosis by O. Heer in his Flora fossilis arctica (1868) as well as in his Miocene baltische Flora (1869) are verbally identical, and the accompanying figures agree with the text and illustrate the type very well.

Sequoia couttsiae considered as a distinct species has, as is well known, caused some discrepancy. In the paper of P. Menzel (1900) the difficulties are faced and a close study made which terminated in the more elaborate and detailed diagnosis cited above. But relying only on the olde rstatements of O. Heer it should be possible to maintain *S. couttsiae* as a well established species. The numerous and excellent photographs of isolated twigs, cones and seeds published in the paper of Z. Zalewska (1959) justify this interpretation.

Sequoioxylon canadense (C. Schröter) nov. comb.

Sequoia canadensis C. Schröter 1880, *Sequoia wellingtonioides* W. Prill 1913, *Cupressinoxylon canadence* (C. Schröter) R. Kräusel 1919 and Z. Zalewska 1953.

All the numerous samples referable to this type of fossil wood were collected in the Troldhede area. In the lignites of Torvig quarry a number of stumps were found (compare Part I, p. 19). Since the wood of the stumps had only been subjected to compression parallel to the fibres the anatomical structure was but slightly altered and the preservation almost perfect. A sample of such a stump was chosen to represent the type. Unfortunately it has not been possible to secure a whole stump for the Mineralogical and Geological Museum of Copenhagen University since the wood is broken up into concentric flakes, 5 to 10 mm thick, each representing a few growth rings. No traces of bark are left.

Transverse section. The growth rings are of a uniform thickness and well delimited (Plate VIII, A) with a gradual transgression from early to late wood. The rays are composed of one row of thin-walled, radially extended elements. Resiniferous xylem parenchyma is diffuse or somewhat crowded in the late wood. Vertical resin ducts could not be detected.

Radial section. Plate VIII, C and D show tracheids of early and late wood. The broader elements of the early wood have two rows of opposite bordered pits often separated by rather faintly pronounced crassulae. The narrower tracheids of the late wood show only one row of bordered pits. The rays are composed of thin-walled, radially extended cells without any sculpture on the horizontal or tangential walls and are slightly ascending. Indentures are rare and only feebly developed. The cross-field shows 2 to 4 cupressoidal-taxodioidal blind pits. In the photographs the inner borders of the pits are diffuse while the connecting slits to the treacheids are distinct.

Tangential section (Plate VIII, B). The photograph only represents a part with low rays, but the rays may reach a height of 30 cell rows or more. The small tangential bordered pits are visible in some cases with a reading glass. Of salient importance is the structure of the horizontal walls of the resiniferous xylem parenchyma which appear smooth or almost so, in the latter case they only show a fine bead-like structure.

Horizontal resin ducts were not seen in the investigated sections.

Under the name "*Cupressinoxylon wellingtonioides*" R. Kräusel (1919, p. 293) has given a short diagnosis of the species based on a small piece of a branch about 3 cm thick and showing a number of 2 to 4 mm broad growth rings and a few vertical traumatic resin ducts in the early wood of one of the rings. Apart from the last detail the fossil wood of this type from Torvig quarry agrees with the diagnosis.

W. Prill (1913) discusses the systematic relations of his "*Sequoia wellingtonioides*" to other species of fossil wood and the extant Sequoias and places it as closely related to *Sequoia gigantea* J. Lindley (J. Decaisne) (*Sequoiadendron giganteum* (J. Lindley) J. T. Buchholz). *S. couttsiae* is mentioned as a fossil type with a wood anatomy closely connected with what is known about *S. giganteum*. The lack of traumatic resin ducts is no hinderence to referring our samples to the Sequoias since they are not always demonstrable in the two extant species (E. C. Jeffrey 1903).

A. Schenk (1869) is inclined to refer a fossil wood of the type in question to *S. couttsiae*, but his short description is inadequate and not accompanied by figures.

Considering the wide extension in time and space of *Sequoia couttsiae* it seems curious that wood referable to the *Sequoiadendron giganteum* type is not more common in the lignites of Europe. The arctic *S. canadense* (C. Schröter) was regarded by R. Kräusel (1919, p. 296) with some hesitation as a "*Sequoioxylon*" and the specific name *canadense* was finally adopted for the type: ("Cupressinoxylon canadense (C. Schröter) nov. comb., C. wellingtonioides (Prill) Kräusel, das mit Sequoia canadensis Schröter (vergl. Kräusel 1919 b, p. 240) vereinigt werden muss") (Kräusel 1949, p. 116). According to recent investigations it seems to be most convenient to retain the generic name *Taxodioxylon* (Gothan 1905) for fossil wood agreeing with or referable to the recent *Taxodium* and *Sequoia sempervirens* type.

According to the undoubtedly taxodiaceous characters of our fossil it must be admissible to refer the wood of this type to a *Sequoia* (in sensu latiore); the only feature connecting it with the Cupressinoxyla would be the type of cross-field pitting but, as noted above, the pitting is often tending to the taxodioidal type, and as a sole criterion, it cannot be regarded as decisive. The double rows of bordered pits frequently ocurring in the early wood as well as the remarkably high rays also points in the direction of the Taxodiaceae.

The cones, seeds and foliage twigs commonly described under the name *Sequoia couttsiae* are undoubtedly of a *Sequoia*-like appearance and mutually related. Our fossil wood is probably of the same specific origin as the accompanying remains of *S. couttsiae*, but the interdependence with *Sequoiadendron* is not so clearly demonstrable as, for example, is the case with the remains referable to *S. langsdorffi* and the recent *S. sempervirens*, so it seems a little premature to create a new genus. The name *Sequoioxylon* may be retained — at least provisionally — to designate the wood in question.

A sample of gymnospermous wood from the Torvig quarry (Troldhede) shows a peculiar appearance (Plate IX). Short and broad rays of an almost uniform shape and homogeneous structure occupy a considerable part of the bulk of the wood. They are most conspicuous in the tangential section but are also prominent in both the transverse and radial sections, while rays of the normal type are comparatively rare and of a less salient appearance. The rays are composed of rather thin-walled elements varying in size and shape; the horizontal and tangential walls without sculpture, the radial walls showing 2 to 4 cupressoidal-taxodioidal blind pits in the cross-field.

The resiniferous xylem parenchyma appears somewhat diffuse and the horizontal walls are smooth or slightly bead-like pitted. In the early wood there are 2 to 3 rows of opposite bordered pits; crassulae are distinct.

According to these characters it seems permissible to refer this wood to a *Sequoia* but evidently originating from an anomalous part of an axis, probably from a protuberance developed on a stem, a common feature in the extant Sequoias. The shape of the rather small sample supports such an origin since it is curved both radially and tangentially.

R. Kräusel has described and figured an irregular development of the ray tissue in a "Maserknolle" (1919, Taf. 23, Fig. 2 and 4, Taf. 24, Fig. 7, 8 and 11) which he refers to a *Cedroxylon* (*Physematopitys salisburioides* Göppert) (p. 230 l.c. et seq.), the systematic position of which seems a little doubtful.

A protuberance of *Sequoia sempervirens*, kept in The Botanical Museum of the University of Copenhagen, shows an irregular development of the ray tissue not unlike that noted by R. Kräusel but differing greatly from that found in the sample described here, while in a bulb-like protuberance from a "knee" of *Taxodium distichum* multiserial rays were regularly developed. Anomalous wood of *Sequoiadendron giganteum* was not available.

Sequoia langsdorffii (A. T. Brongniart 1828) O. Heer

Foliage twigs and cones referable to this species occur rather commonly in the lignitic clay at Moselund.

In European and Arctic Tertiary deposits, ranging in age from Eocene to Pliocene, remains of this *Sequoia* are common and consequently described and figured in numerous papers. Lists of the relevant literature, compiled by P. Friedrich (1883) amd M. Staub (1887), the latter comprising 94 titles, covers the literature up to the years cited since when may be added those of P. Menzel (1900) and R. W. Chaney (1951).

The foliage twigs are partly preserved as carbonized leaf substance and partly only as imprints (Plate X, A to F). At the base of the twigs there are a few, small, scaly leaves. The samples agree closely with the diagnosis given by P. Menzel (1900, p. 89): "Sequoia foliis rigidis, coriaceis, linearibus, apice oblusiusculis vel breviter acuminatis, planis, basi augustatis, adnato-decurrentibus, patentibus, distichis, confertis; nervo medio valido; strobilis breviter ovalibus vel subglobosis, squamis compluribus, peltatis, mucronolatis".

The decurrent leaf bases are better shown in the camera lucida drawings of Fig. 8, A to E. Both in the structure of the epidermis and in the mesophyll the different appearance of the upper and lower sides of the leaves are very marked. The stomata on the upper side are few in numbers and arranged in axially extended, small groups while on the under side of the leaf there are two broad bands of stomata, one on each side of the midrib, extending from the base to the apex of the leaf.

A hypoderma, composed of rather thick-walled prosenchymatous elements, forms an almost continuous layer on the upper side while on the under side the prosenchyma is more scattered and thus permits ample stomatic communication whereas stomata on the upper side only occur where lacunae are formed in the subepidermal layer.

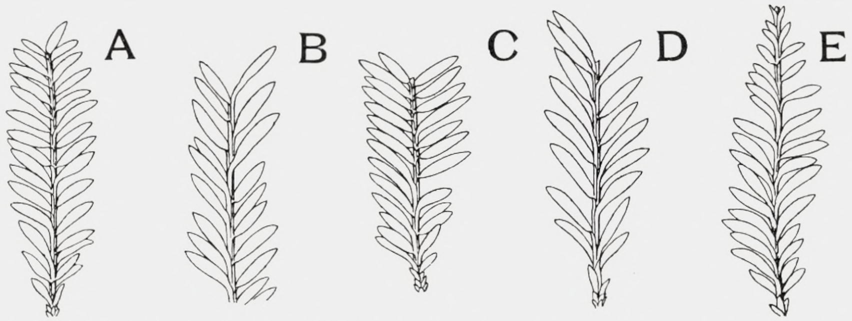


Fig. 8. *Sequoia langsdorffii* (A. T. Brongniart) O. Heer. Deciduous foliage twigs. Moselund.

On both the upper and lower sides the outer wall of the epidermis shows a finely dotted structure, the dots representing cavities from which crystals of calcium oxalate have been dissolved.

The type of foliage twigs figured by Z. Zalewska (1959) as Plate IX, Figs. 2–4, are also found in our material but an anatomical inspection has not been possible.

The cones reproduced in Plate X, G to K are probably also referable to *Sequoia langsdorffii.* They were all collected from the lignitic clay at Moselund. The scales of the mature cone are squarrose and as the interspaces in the fossils are filled with matrix the cones are in most cases impossible to isolate without injury. Plate X shows fractions of the cones. The cones are 15 mm in diameter and the axis about 20 mm long. The number of cone scales is estimated as 30 to 40. The shape of the cone is ovoidal. All the cones were fully developed and the seeds dispersed.

The morphology of the foliated shoots and the anatomy of the leaf of the fossil *Sequoia langsdorffii* appears very much like that of the recent *S. sempervirens* (D. Don) St. Endlicher. According to P. Friedrich (1883) and P. Menzel (1900) the number of cone scales in the fossil is about 50, while only about 20 are found in *S. sempervirens;* the latter should accordingly have smaller cones, but the material I have had access to shows cones of the same type and size as those of the fossil and with a corresponding number of cone scales, so the size may vary considerably.

As a character of *S. sempervirens* R. Pilger (1926) mentions the squarrose cone scales, his Fig. 151 b showing the apperance of a mature cone very like that of the fossils. The inner sides of the cone scales show a fine, fan-shaped striation which is also discernable under a reading glass in the photographs of Plate X.

The seeds of *S. langsdorffii* are lacking in my material, but if it is assumed that the seeds of *S. langsdorffii* correspond morphologically and anatomically with the seeds of the recent analogue they would be easily discernable if present. The seeds of *S. sempervirens* are of a dark brown colour, highly variable in size from 2.8 to 3.5 mm, irregular, inverse conical-prismatic in shape, with a relatively faintly protruding wing. The embryo is almost straight, scarcely conspicuous on the surface of the seed. The testa is mainly composed of rather thick-walled, lignified elements which give a conisderably greater weight to the seed than, e.g. in *Sequoiadendron giganteum*. For comparison reference is made to Fig. 7 which shows transverse sections of the seeds of *S. sempervirens, Sequoiadendron giganteum* and *Metasequoia glyptostroboides*.

According to the authors cited by P. Friedrich (1883) the type shows a considerable variation which has caused the establishment of a series of species. These have been criticized by P. Friedrich and are probably not to be maintained.

Taxodioxylon gypsaceum (N. R. Göppert 1842) R. Kräusel

(*Sequoia gypsaceum* (N. R. Göppert) nov. comb. P. Greguss 1967)

Only one specimen referable to this type of fossil wood has been found (the State quarry at Troldhede). It appears in an excellent state of preservation.

The fossil anatomically agrees very closely with the wood of the extant *Sequoia sempervirens* (A. B. Lambert) St. Endlicher, the well known "Redwood" of the western states of the U.S.A. The very thorough study by I. W. Bailey and Anna F. Faull (1934) allows a detailed comparison to be made between the fossil and its recent analogue.

Transverse section. In the transverse section the growth rings are well marked and narrow with a gradual transgression from early to late wood. The rays are 1 to 3 cell rows broad with thin-walled elements. Resin cells are scarce, mainly occurring isolated towards the border of the growth rings, or scattered.

Radial section. The tracheids of the early wood typically show two (or three) rows of bordered pits with a well-marked torus and distinct crassulae.

The pits tend to be more numerous and crowded towards the overlapping ends of the tracheids. In the early wood tracheids the opposite pitting sometimes changes to become alternating and crowded. The rays attain a considerable height. The tangential and horizontal walls of the ray elements are smooth, or almost so, and indentures are lacking or only faintly developed. The radial ray walls of the early wood show 1 to 2 transverse rows of typical taxodioidal blind pits with an elliptical, radially extended outline; the aperture is never slit-like, but broad elliptic forming a crescent-shaped configuration on both sides of the pits. Occasionally, and prominently in the first formed layers of the early wood, the pits tend toward the circular, glyptostroboidal type with a small or no border (Plate XI, C and D, Plate XII, B and C). The late wood shows the connecting pits with a stunted, slit-like porus.

The transverse walls of the resiniferous xylem parenchyma are smooth or finely pored, exhibiting in the section a bead-like appearance.

Tangential section. The late wood tracheids have numerous bordered pits which are considerably smaller than those of the radial walls of the early wood. The height of the rays is exceedingly variable with rays of 1 to 5 cell rows intermingled with rays 10 to 20 rows or more, and rays of 30 to 40 rows high are a common occurrence. In a few cases a maximum height of 70 cell rows has been noted. The rays are usually uniseriate, but bi-and triseriate rays are not uncommon, and as far as can be stated, occur much more frequently here than, for example in the wood of the fossil *Taxodium* or *Glyptostrobus* (Plate XIII, B and C).

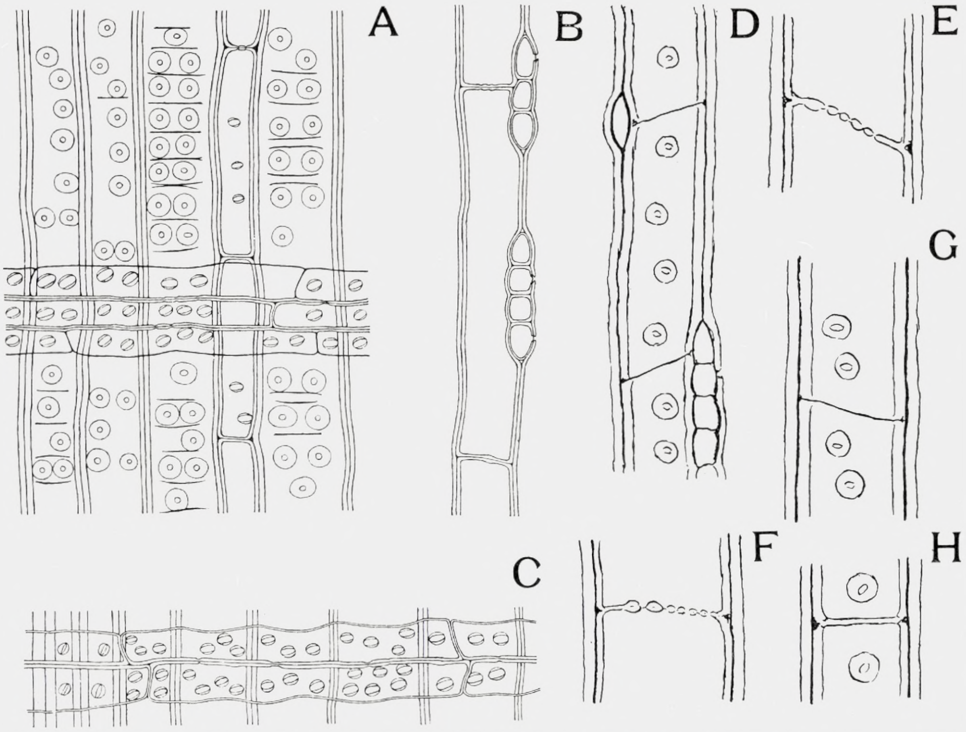


Fig. 9. *Taxodioxylon gypsaceum* (N. R. Göppert) R. Kräusel. A and C, radial and B, tangential section D, G and H, parts of strand tracheids. E and F, horizontal walls of resiniferous xylem parenchyma (A, B and C×250, D–H×400). Troldhede State Quarry.

"Strand Tracheids", i.e. non-resiniferous tracheidal elements divided by horizontal walls, are seen in the late wood (Plate XII, A, and Fig. 9, D, G and H). The horizontal walls are most commonly quite thin while in some places they attain a certain thickness.

Ray tracheids have not been found and traumatic resin ducts are not developed in the wood of the sample examined.

The fossil material described here agrees closely with its recent analogue *Sequoia sempervirens* on the following characters: the structure of the growth rings found in the stem or branch wood, the distribution of resiniferous parenchyma, the pitting of the radial walls of the tracheids, the types of rays (the very high and the bi- and triseriate rays intermingled with relatively low ones), the pitting of the cross-field, the smooth or slightly bead-like pitting of the horizontal walls of the xylem parenchyma and lastly the occurrence of "Strand Tracheids".

Our fossil also anatomically agrees very well with the sample af *Sequoia gypsaceum* (Göppert) described and figured by P. Greguss (1967, no. 9). As will appear from the generic name chosen by Greguss he considers the fossil wood to correspond so closely anatomically with the wood of the recent *S. sempervirens* that he has taken the decisive step of establishing a still closer connection of the fossil with its extant analogue by adopting the generic name *Sequoia*. This is supported by the fact that foliage twigs as well as cones of *S. langsdorffii*, which is evidently closely related to *S. sempervirens*, occur in the same Tertiary lignite layers as the wood referable in *Sequoia sempervirens*. The two species might be mutually interdependent but, of course, this is not strictly demonstrable even if it is very probable.

It must be kept in mind that *Sequoiadendron giganteum* (J. Lindley) J. T. Buchholz 1939 possesses wood of another anatomical structure and has been classed as a *Cupressinoxylon* due to its type of cross-field pitting. The organo-genus *Taxodioxylon* Gothan is mainly based on the shape of the blind pits of the radial ray walls and not on the pitted structure of the horizontal walls of the xylem parenchyma which certainly is most strongly and most typically developed in *Taxodium*, but occasionally also occurs in *S. sempervirens* (I. W, Bailey and A. F. Faull 1934, Plate 106, Fig. 52 and 55) and so it might possibly also be found in the fossil. I have considered it safest to retain, at least provisionally, the generic name *Taxodioxylon* given by W. Gothan (1905) comprising fossil wood of the *Taxodium* and *S. sempervirens* type.

Taxodium dubium (K. von Sternberg 1838) O. Heer 1855

(*Taxodium distichum miocenum* O. Heer 1869)

The lignitic clays at Moselund, Fasterholt and Silkeborg Vesterskov are particularly rich in deciduous, foliage twigs, cone scales and seeds referable to *Taxodium*. The material from Moselund and Silkeborg Vesterskov, especially, is partly in an excellent state of preservation thus facilitating the anatomical study of the remains. Foliage twigs of *Taxodium* are sometimes also found in the brown coal itself.

In European, North American and Arctic Tertiary deposits, ranging in age from Eocene to Pliocene, remains of *Taxodium* are locally exceedingly common and consequently described and figured in numerous papers. Besides the very complete lists of relevant literature compiled by P. Friedrich (1883), M. Staub (1887) and P. Menzel (1900) there are the important references in the critical review by R. W. Chaney (1951).

A selection of the most commonly occurring types of deciduous, foliage twigs with distichous leaves referable to *Taxodium dubium* is figured in Plate XIV. All the specimens are from the lignitic clay at Moselund. The leaf substance of the twigs figured in A, D and G of Plate XIV was sufficiently coherent to allow the preparation of the cuticles and partly also of the mesophyll. The distribution of the stomata in two narrow stripes on the upper and two broader on the under side of the leaf, as well as the orientation of the palisade cells agrees very well with that found in the recent *Taxodium* species (R. Florin 1931, Plate 41, Figs. 1 and 2). In the outer wall of the epidermal cells a fine dotted structure is perceptible signifying the former presence of minute crystals of calcium oxalate, and on the upper side of the leaf here and there remains of scattered subepidermal, thin-walled prosenchymatous elements are recognizable.

The mesophyll is mostly collapsed but the arrangement of the elements in transverse lamellae, running from the transfusion tissue enclosing the midrib to the margin of the leaf, is sometimes traceable as well as the structure of the thin-walled tracheids of the transfusion tissue itself.

Cone scales referable to *Taxodium* are rather common in the lignitic clay at Moselund and Silkeborg Vesterskov, whereas entire cones do not occur. Plate XV, A shows a selection of such scales. The sculpture of the abaxial (dorsal) side of the cone scale is conspicuous, though the scales are highly compressed. The adaxial (ventral) side does not show any details, the tissue here being mainly composed of rather thin-walled elements while, as in the extant Taxodia, the dorsal shows an abundant development of subepidermal sclerenchyma as well as scattered brachysclereids throughout the whole of the mesophyll. A transverse cut of the scale shows one or two brownish-yellow stripes, each representing a balsam cyst.

The seeds vary much in size as is also the case in the extant *Taxodium*, those from the base of the cone being larger than those from the apex. They are characterized by their peculiar shape and especially by the sharply salient, longitudinally running ridges which in the larger specimens are developed as low wings (Plate XV, B–J). The brittleness of the material did not allow the preparation of satisfactory sections so the anatomy had to be studied by maceration of the entire seed.

Both the outer and inner sides of the testa have an epidermis of rather large elements with brown, irregularly undulating side walls. In the preparations the epidermis is mostly dissolved so that only the finely dotted cuticle is left. The exotesta as well as the endotesta consists of a few layers of thick-walled, finely pitted, sclerenchyma cells which, according to the shape of the lumen, often have enclosed a crystal (calcium oxalate). The mesotesta is composed of a parenchymatous tissue with rather thin-walled cells which in the fossils have collapsed. Along two opposing stripes running from the seed cavity out to the flanks the parenchymatous tissue grades into a tissue of small, rectangular elements each sculptured by a set of parallel, transverse thickenings.

The anatomical details of the fossil material agree with the recent *Taxodium* spp., and *T. distichum* seems to be especially closely allied. The fossil seeds differ somewhat in shape from the seeds of the recent analogue, the testa here having a far more markedly winged and irregular outline.

O. Heer has figured single scales, entire cones (1869), seeds and even male inflorescens (1870) so very much like those of *T. distichum* (L.) L.-C. Marie Richard that he was unable to distinguish the fossil form from the extant species and thus considered them specifically identical (*Taxodium distichum miocenum* O. Heer). This view seems to be shared by most of the subsequent authors [e.g. W. P. Schimper and A. Schenk (1890), P. Menzel (1900) and Z. Zalewska (1959)] and has remained almost unchallenged. Yet A. C. Seward (1919) has expressed some doubt and probably it would be safer to term the remains simply as *Taxodium miocenum*, but according to R. W. Chaney (1951) the name *Taxodium dubium* (*Taxites dubius* K. von Sternberg 1838) has priority and this name is also used by O. Heer for a fossil species of *Taxodium* considered as allied but differing slightly from his *Taxodium distichum miocenum*.

A rather slight, but as it seems, constant difference occurs between the anatomy of the secondary wood in the recent *T. distichum* and the pieces of fossil wood in our collections, undoubtedly referable to a *Taxodium* sp., as well as in the material described as *Taxodioxylon taxodii* Gothan from other European localities (see below).

The Mexican *Taxodium mucronatum* M. Tenore (*T. mexicanum*) differs from *T. distichum* in its growth form, its partly persistent foliage twigs and mainly by the smaller cones with more prominantly mucronate scales.

In the recent *Taxodium* species the seeds adhere to the cone scale and, as the tissue connecting the scale with the axis is brittle, the scales of the mature cone are easily detached and shed together with the adhering seeds.

Root knees of *Taxodium*, a salient character of the extant *T. distichum*, have not been seen in our lignites and they seem rarely to occur as fossils though they are known in a calcified condition from the Neogene deposits at Parschlug in Steiermark (E. Hofmann 1927).

R. W. Chaney (1951) in his critical and comprehensive memoir has revised the fossil Taxodia. In support of the opinion of F. N. Knowlton he states as a conclusion that the fossil *Taxodium* of North America is not specifically different from *T. dubium* and, making use of the recent discovery of *Metasequoia*, he succeeded in correcting many previous determinations which erroneously had referred foliage twigs of *Metasequoia*, as well as those of *Sequoia langsdorffii*, to *Taxodium*. As remains of *Metasequoia* are also found in European Tertiary deposits (Z. Zalewska 1959, *M. europaea* n.sp.). a correspondingly critical review of the European material is required.

Taxodioxylon taxodii W. Gothan

Pieces of fossil wood referable to this organo-genus are among the most common macrofossils in the lignites of Jutland and in some places form a considerable part of the brown coal itself. Imbedded in the coal matrix they are most often highly altered by compression so that a reliable determination is not always easy. However, it was possible to collect some specimens in a perfect state of preservation from the quarries at Troldhede and the following description is based mainly on the study of this material.

In our collections the determinable specimens appear in several forms, mainly distinguishable by the proportion between early and late wood. The transverse section figured in Plate XVI, A represents the most common type (type I — 15 samples); the thickness of the growth rings is variable but the transgression from early to late wood is always even. A second type (type II — 10 samples) is shown in Plate XVII, A; it exhibits quite narrow growth rings of rather uniform thickness with an abrupt change from early to late wood, the latter only composed of a few layers. The third type (type III — 2 samples) (Plate XVIII, A) is characterized by relatively broad growth rings, mainly composed of uniformly narrow, rather thick-walled tracheids of the late wood type. The first type (type I) might represent the normal stem and branch wood, the second (type II) anatomically agrees with the type commonly developed in the root of gymnosperms, and the third type (type III) might represent a "compressed" state of development, such as is found, e.g. on the underside of horizontal branches, a feature occasionally also seen in the *Taxodium* group. The boundary between the growth rings is always distinct.

Transverse section. Resiniferous parenchyma is common and perceptible as dark brown elements scattered throughout the growth ring or arranged in tangential groups. The side walls are rather thin. Where the cut has touched near a horizontal wall and the resin content disappeared the pitting of this wall is easily perceptible. The Fig. 11, D to G show the common feature; the central part of the wall forms a solid, lenticular disc and the pores are concentrated near the circumference.

The rays are uniseriate and pits are not visible in the horizontal walls. The circumference of the tracheids is, as a rule, regularly hexagonal with here and there the elements of a single radial row tending towards a rounded outline. In the early wood the tracheids sometimes attain a radial diameter of 40 μ.

Radial section. In the early wood the first formed and more thin-walled tracheids commonly show two rows of juxtaposed bordered pits, the pit pairs separated by distinct crassulae. Sometimes the pits are few and scattered but the arrangement in two rows is still traceable. A very regular, two rowed pitting is developed in the relatively broad early wood of the type II ("root wood"), the pitted area covering the greater part of the radial wall. Here the number of bordered pits in the horizontal rows may increase to three. In the narrower tracheids the uniseriate pitting dominates and consequently prevails in type III. The bordered pits attain a diameter of 16 μ.

The ray cells are rather thin-walled in the early wood and somewhat more solid in the late wood, with horizontal walls smooth or appearing sporadically slightly pitted. Interstitia occur but are rare and only feebly developed. The blind pitting of the radial wall is of the well known taxodioidal type, most typically developed in the early wood but are rather variable in size and arrangement. In the type III wood the taxodioidal

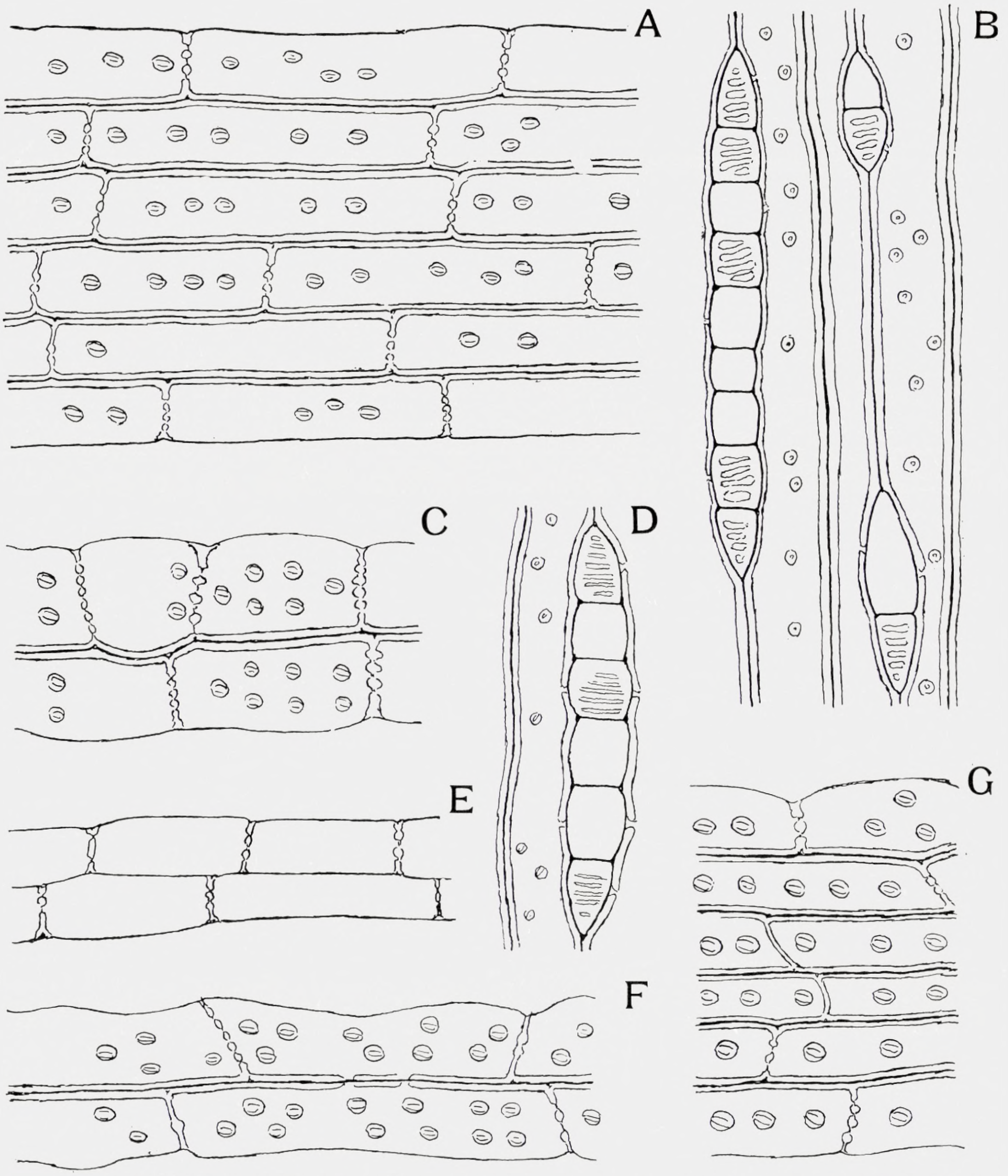


Fig. 10. *Taxodioxylon taxodii* W. Gothan. A, C, E, F and G, selected parts of rays in which the pitting of the tangential walls is prominent. B and D, tangential view of rays of the same type. (×400). Troldhede.

pits are confined to the first formed early wood. The tangential walls of the ray cells may be smooth and without any sculpture, but most often exhibit a feeble pitting giving the wall a bead-like appearance if strongly accentuated it produces a knotty outline approaching the "Juniperus Tüpfelung" of W. Gothan (1905). The latter appearance is especially developed in the late wood and therefore most common in the wood type III, but a single or a few knots may also appear even in the most thin-walled, marginal ray cells of the early wood. The thickenings are most conspicuously developed in the wood of type II. In type I it is not rare to find areas of the ray tissue in which most of the tangential walls are quite smooth. The various types of tangential ray cell pitting may, however, occur irregularly intermingled (Fig. 11, H).

Tangential section. The tangential section shows small, bordered pits on the walls of the last formed of the late wood tracheids.

The vertical extension of the rays is highly variable. In the samples of type II they rarely exceed a height of 10 cell rows while in types I and III a height of 25 to 30 rows is not rare and this number may occasionally be exceeded to 40 or even more rows. Such rays are, for example, sometimes found in wood of type I where a maximum height of about 60 rows was noted. Where a tangential ray cell wall with bead-like thickening is included in the sectional plane 1 to 5 transverse bars, or bars forming a network, are observed with the more or less fine pitting appearing as fine horizontal stripes (Fig. 10, B and D), the bars and pits corresponding respectively to the bead-like thickenings on the tangential walls, and the intermediate unthickened parts. As a single ray cell may cover 8 to 10 tracheidal rows the tangential walls appear rather rarely in the thin microtome sections.

The details of the horizontal (transverse) walls of the resiniferous parenchyma are much more conspicuous in the tangential sections of the wood than in the radial since the elements often are somewhat broader tangentially. Fig. 11, A and B show the highly projecting middle part of the wall and the pits of the circumference; where the transverse wall is notably thinner the pitting may only cause a bead-like pattern (Fig. 11, C). The vertical walls of the parenchyma are provided with half bordered pits where the walls joins a tracheid; where two parenchymatous elements have a wall in common the pitting is simple.

Affinities

A diagnosis of the organo-genus *Taxodioxylon* is given by R. Kräusel (1949, p. 168) which runs as follows: "Tüpfel im Spätholz mit schräg-spaltenförmigen, im Frühholz mit breitem ± wagerechten Porus (Taxodioide Tüpfelung, W. Gothan). Markstrahlwände meist glatt, Holzparenchym häufig, im Wundholz zuweilen Harztaschen".

Among the extant genera of gymnosperms this diagnosis only covers the types referable to *Taxodium* and *Sequoia sempervirens,* while the wood of *Sequoiadendron* (J. Lindley) *giganteum* J. F. Buchholz anatomically tends towards the *Cupressinoxylon* type (W. Gothan 1905). This also applies to the wood of other recent genera which are commonly referred to the Taxodiaceae (*Athrotaxis*, *Cryptomeria*, *Taiwania*), while *Glyptostrobus* and *Cunninghamia*, through their dominating "glyptostroboidal" cross-field pitting, form a particular type deviating from the rest of the group. *Metasequoia* also forms a special type.

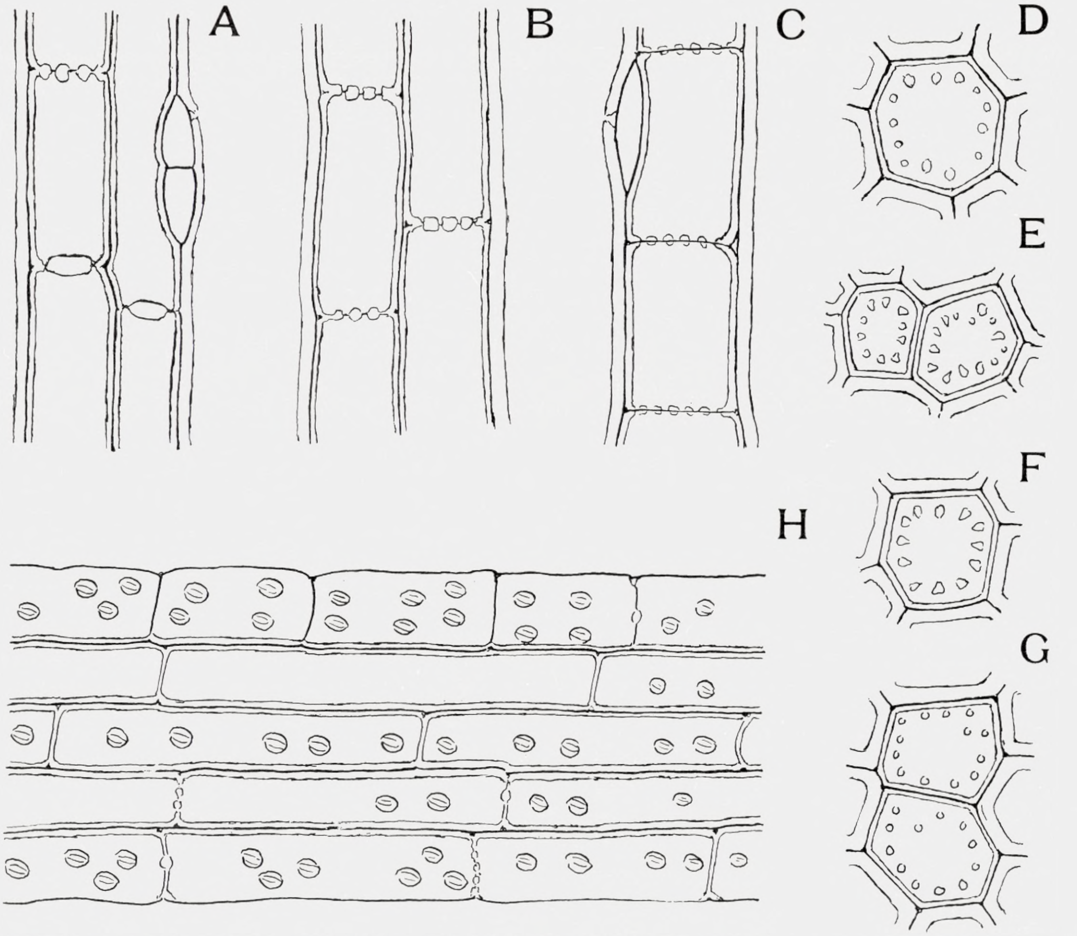


Fig. 11. *Taxodioxylon taxodii* W. Gothan. A, B and C, tangential section of xylem parenchyma; A and B show thick and highly pitted horizontal walls, C represents a type of thinner horizontal walls with a more bead-like pitting. D–G, horizontal walls of xylem parenchyma as they appear in transverse section. H, part of a ray with feebly developed pitting of the tangential walls. (×400). Troldhede.

The fossil genus *Taxodioxylon* was first delimited by W. Gothan (1905, p. 49) whose description adds supplementary information to that of R. Kräusel. According to W. Gothan *Taxodium* has a blind pit type intermediate between the cupressoidal and the glyptostroboidal cross-field pitting as the pit is markedly widened in the early wood but does not take the shape of a real oëopore.

Other details of value for the systematic anatomy of the wood structure of the Taxodiaceae are given in the analytic tables of E. J. Slyper (1933), R. Kräusel (1949, p. 94–95) and P. Greguss (1955) which mainly concerns the wood of extant conifers. A diagnostic table covering the anatomical characters of the groups of the analogue fossils is also given by R. Kräusel (1949, p. 150–151).

According to the definition the anatomical features of all our specimens agree with what is considered as characteristic for the wood of the extant *Taxodium* and for the fossil *Taxodioxylon taxodii*. Yet an important difference, probably in part overlooked, and, at any rate, hitherto not taken sufficiently into consideration, is found which taken alone would change the systematic position of the fossil from the *Taxodioxylon* to the *Juniperoxylon* group.

On a close examination of perfect material from our specimens a distinct pitting of the tangential walls of a good many ray cells could be demonstrated. In the keys cited above for the determination of gymnospermous wood of the *Taxodioxylon* type this character is not mentioned. W. Gothan (1905) has noted that the organo-genera *Taxodioxylon* and *Glyptostroboxylon* are devoid af "Juniperus Tüpfelung" which is correct in that they do not show the often highly conspicuous and mostly uniformly developed knotty thickenings of the tangential ray cell walls found in the recent *Juniperus* spp. (*J. drupacea* (*Arceutos*), it is true, is an exception). In his paper of 1906 W. Gothan amends his remarks on *Taxodioxylon sequoianum* (Mercklin) W. Gothan in the way that: ". . . . man bei ihm sowohl im Radial- wie im Tangentialschnitt eine schwache der Juniperus-Tüpfelung ähnliche Verdickung der Markstrahlzell Tangentialwände sah, die ich jedoch bei ihrer schwachen Ausbildung und ihrem unregelmässigen Auftreten diagnostische Bedeutung nicht beimesse".

Through the liberal kindness of the late Professor R. Kräusel, Frankfurt am Main and the late Professor W. Gothan, Berlin, I have obtained samples of *Taxodioxylon taxodii* and *T. sequoianum* from the lignites at Senftenberg for comparison (for details see Fig. 12). Anatomically they agree with the descriptions, but I found that the knotty character of the tangential ray cell walls in the samples described and figured as *Taxodioxylon sequoianum* agrees closer to *T. taxodii* (probably a misunderstanding has crept in concerning the two species being discussed). W. Prill (1913) states that the bordered pits in the radial walls of the tracheids in the genera *Taxodium, Glyptostrobus* and *Sequoia,* in contrast to those in the Cupressaeeae, are most often arranged in two (or more) rows in the early wood. This observation was considered important by the early authors (R. Kräusel 1919, p. 208) and certainly must be regarded as a character of some value and corresponding to the commonly far larger diameter of early wood tracheids in the Taxodiaceae than in the Cupressaceae.

A fossil wood termed *Juniperoxylon silesiacum* (W. Prill) R. Kräusel has been thoroughly investigated and the salient details of the anatomy figured in the paper of R. Kräusel and G. Schönfeld (1924). In this paper a considerable number of similar specimens (77 samples of wood of the "trunk type" and 34 of the "root type") of the material collected from the same layers of the "Braunkohle" at Süd-Limburg were com-

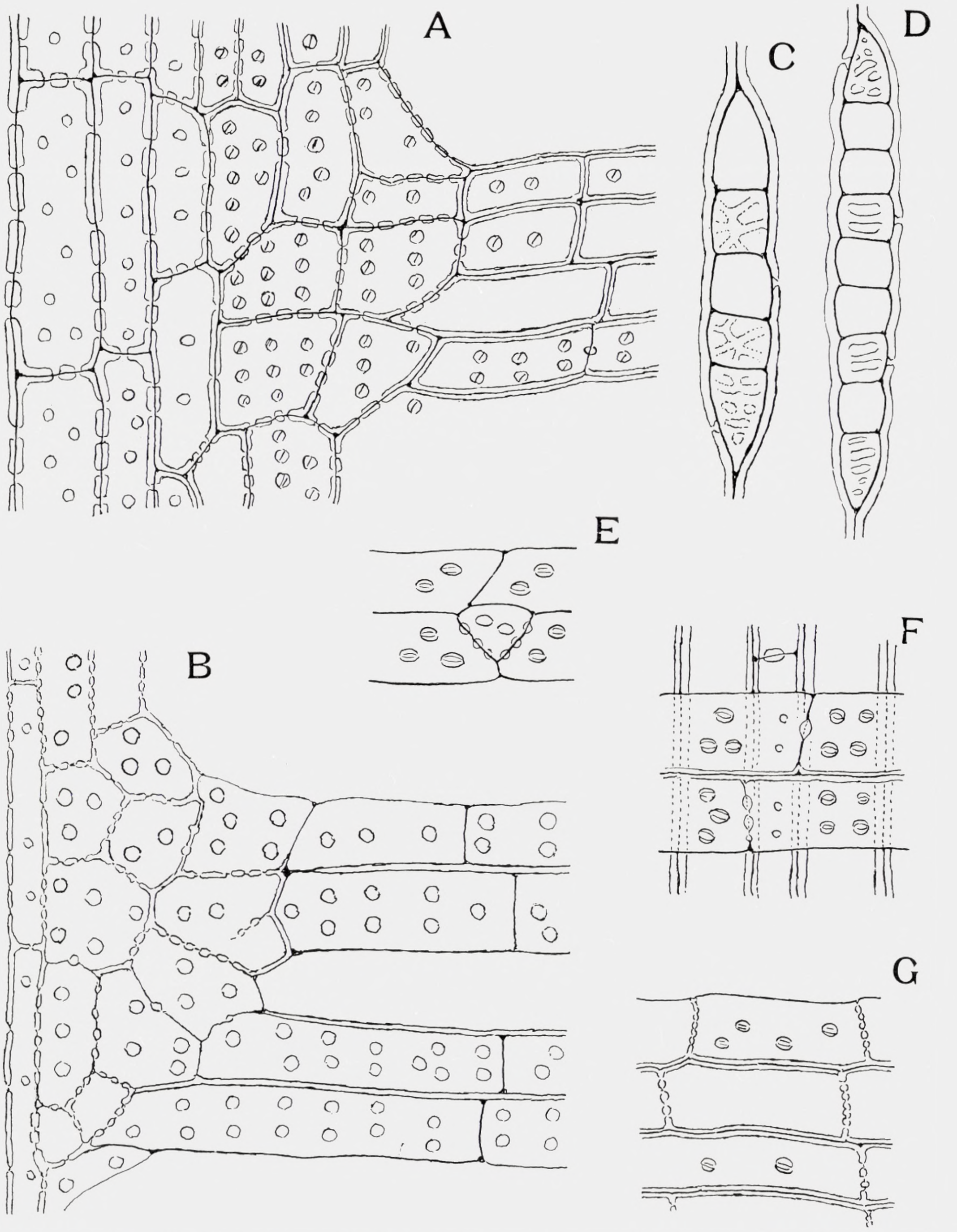


Fig. 12. *Taxodium distichum* (L.) L.–C. Marie Richard. In A is shown the transition of the medullary parenchyma iuto the first fosmed tissure of the rays. B shows similar features in *Glyptostrobus pensilis* A. B. Lambert. (A and B × 400).
Taxodioxylon taxodii W. Gothan. C and D, tangential sections of rays and E–G radial sections; the tangential walls of the ray cells are strongly pitted in the parts selected for drawing. (C to G × 400). Material from the lignitic layers at Senftenberg. Germany.

pared. The state of preservation was satisfactory and partly excellent. The photographs (R. Kräusel and G. Schönfeld 1924, Plate XXII, Figs. 1–4) show transverse sections of wood which agree very well with the sections of the first and second types of our fossils from the Danish lignites. The radial section in their figures exhibits one, or very frequently two, rows of bordered pits, the pit pairs segregated by distinct crassulae, or the pits are alternating. The horizontal walls of the resiniferous parenchyma, according to their description, are either bead-like or provided with prominent knots and consequently more or less distinctly pitted (this character is not figured). Concerning the ray cells it is stated: "Tangentialwände körnig bis schwachknotig — im Tangentialschnitt leiterformig seltener netzartig verdickt" (R. Kräusel and G. Schönfeld 1924, p. 261). The cross-field in the late wood shows 1 to 2 blind pits of the cupressoid type while in the early wood the number of pits increases to six often arranged in two to three horizontal rows and, according to their photographs (Plate XXII, Figs. 8 and 9, and text Fig. 4) tend more towards the taxodioidal type or even approach the glyptostroboidal (i.e. circular in outline and almost without borders). These authors, as mentioned, refer their material to "*Juniperoxylon silesiacum*" (W. Prill) R. Kräusel (1919).

It seems justified to bring together the woods described by R. Kräusel and G. Schönfeld (1924) and W. Gothan (1906) with the material from Denmark. Kräusel and Schönfeld are inclined to unite other specimens from the lignites, formerly described as *Juniperoxyla* (*J. pachyderma* and *J. pauciporosa*), with the *J. silesiacum* but in that case *J. pachyderma* (Göppert), as was pointed out by R. Kräusel (1949), has priority. Z. Zalewska (1953) has described the type under this name.

According to Z. Zalewska (1953) the fossils from Turów on the Lusatian Neisse (Poland) agree anatomically very well with those described by R. Kräusel and G. Schönfeld. The thickenings of the transverse walls of the xylem parenchyma appear markedly developed and so is the structure of the tangential ray cell walls with their peculiar alternation of quite smooth membranes along with those showing knotty thickenings. The bordered pits on the radial tracheidal wall of the early wood are frequently opposite and the pit pairs separated by crassulae. 15 cell rows was the maximum height of the rays noted.

F. Stockmans and Y. Willière (1934) have demonstrated the presence of the type in the Neogene Tertiary layers (Oligocene to Lower Miocene) of Belgium. These authors express doubts on their systematic position citing a remark found in a paper of W. Gothan and T. Sapper (1933 — non vidi) "Gelegentliche Verdickungen der Art, wie sie Kräusels Juniperoxylon zeigt, können auch bei andere Hölzern, z.B. Taxodicen, vorkommen, woraus die Mahnung zur Vorsicht ergibt".

In a recent work P. Greguss (1967) has described *Taxodioxylon taxodii* but without mentioning the sculpture of the tangential ray cell walls. In several places in the accompanying photographs (Table LXXVII, 7 and 8) it seems to me that a structure agreeing with what occurs in the Danish fossils can be traced under a reading glass. The figures cited show a cross-field pitting tending towards the glyptostroboidal type.

When all the details are considered it must be regarded as rather doubtful whether the type in question should be referred to the organo-genus *Juniperoxylon*. According to P. Greguss (1955), for example, the secondary wood of the extant Cupressaceae is mostly far more homogeneous than is usual in the Taxodiaceae; the difference between the width of the tracheids of the early and the late wood being smaller, or insignificant, and consequently the bordered pits on the radial walls are most commonly only uniseriate. In the genera where the tangential walls of the ray cells have locally thickened parts (knots) these are typically of a more uniform development than in the fossils considered here where the walls, which have highly protruding knots, alternate irregularly with walls in which the knots are only slightly protruding, and where the walls having knotty thickenings are intermingled with walls of a bead-like appearance or almost smooth (Z. Zalewska 1953). It should be noted that the fine pitting in sections giving the wall a bead-like appearance is also a common feature among the Cupressaceae. The horizontal walls of the resiniferous elements agree with what is considered as typical for *Taxodioxylon*, but some *Juniperus* species also show a similar development. The pitting of the cross-field is of a type distinctly pointing towards the Taxodiaceae and this is supported by the presence of the occasional very high rays.

The fully grown secondary stem wood of the extant *Taxodium distichum* is devoid of thickenings on the tangential walls of the ray cells, or they are at any rate extremely rare, and they are practically absent also in the wood of the roots and the knees. In the wood of *T. mucronatum* I have sought for them in vane, according to P. Greguss (1955), they may be developed in the wood of *T. adcendens* but seem also here to be rare. As is shown in my drawing (Fig. 12, A) the thickenings are not quite alien to *T. distichum*, the first formed parts of the ray tissue showing a mode of pitting in the horizontal and tangential walls approaching the "Juniperus Tüpfelung" (W. Gothan 1905) and agreeing closely with that found in the mature wood of the fossils. But this pitting rarely reaches the border of the first year's growth and still more rarely is it found outside this. The pitting of the radial walls, connecting the ray cells with the adjacent tracheids, is composed of numerous quite small oculipores which outwards gradually change to the typical taxodioidal type.

Unfortunately I do not possess twigs of the fossil thick enough to show these details. For the exact systematic position of the *Taxodioxylon taxodii* type of wood the characters derived from the structure of the medulla would also be of great interest. It is to be hoped that further finds will throw light on such details.

M. N. Doyle and J. Doyle (1948–50) and B. Kubart (1924) have given valuable notes on the structure of the medulla of the extant Taxodiaceae. It appears from these papers that *Taxodium distichum* differs greatly from its nearest extant relative, *Glyptostrobus*, by possessing a homogeneous medulla (Plate XIX, B and D). The slides figured in Plate XIX were cut from thin (4 to 5 mm thick) branches and agree with those given by M. N. Doyle and J. Doyle, but in the medulla of *Taxodium* from a thick trunk (30 cm diameter) the elements are far more irregular in shape and the tissue tends to be somewhat heterogeneous. In the photographs of Plate XX, A and B there appear to be groups of vertically arranged, thin-walled and feebly pitted elements interspersed with a surrounding tissue composed of thick-walled, distinctly pored cells often divided by secondary transverse walls. I should like to add that the medulla of *T. mucronatum* M. Tenore, in contradiction to the account by M. N. Doyle and J. Doyle, can also be heterogeneous. In my material (*T. mucronatum* M. Tenore, San Diego, Valle de Tehuaean, collected by Liebmann 1841–42, and verified by P. B. Standley 1930), which consists of two samples of about 5 mm thick twigs, some sclereids are present (Plate XX, C and D). They differ from those of *Glyptostrobus* by retaining the shape of the surrounding, regularly arranged elements.

R. Kräusel and G. Schönfeld (1924) have had the opportunity to study the structure of the medulla of "*J. silesiacum*". Their photographs, l.c. Plate XXII, Figs. 7 and 15, represent the view of a radial and transverse section respectively and their text figure is supplementary. The irregular disposition of the elements is conspicuous in the radial section accompanied by a difference in shape and thickness of the wall which gives a heterogeneous aspect to the tissue closely agreeing with what is found in *Taxodium distichum*. The authors cited have called attention to the alternation of the medullary structure in *Taxodium* during the growth, "Eine Schwierigkeit besteht allerdings darin, dass das Mark im Laufe der Jahre nicht unerhebliche Veränderungen erleidet" (loc. cit. p. 266). This alternation is evident in *Taxodium distichum* when Plate XIX, B and D is compared with Plate XX, A and B.

The resemblance of the medullary structure of the mature trunk in *Taxodium* to the medulla of "*J. silesiacum*" figured (e.g. Tab. XXII, Fig. 7 loc. cit.) is rather striking and corraborates the systematic position of this fossil wood that is suggested here.

The anatomical characters of our fossils may be summed up as follows thus forming a diagnosis which may serve as a guidance for the type of the fossil wood *Taxodioxylon taxodii*.

Diagnosis

Growth rings distinct and of various thicknesses, the proportion between early and late wood highly variable. Several types discernable, corresponding to what may be considered as the normal stem type and the root type. The thinwalled tracheids of the early wood hexagonal in transverse section, measuring up to 40 μ in width, the thick-walled tracheids of the late wood here and there tending to a rounded outline.

Xylem parenchyma copious, the elements single or occurring in tangentially extended groups. Rays uniseriate, composed of thin-walled elements often greatly extended radially. The tracheids of the early wood, with numerous bordered pits most often arranged in pairs, separated by distinct crassulae, or more irregularly disposed, but commonly forming two vertical rows. Diameter of the border 16 μ. The ray cells of early wood with typical taxodioidal pitting sometimes even tending towards the glyptostroboidal type. Tangential ray cell walls in some areas smooth, but often bead-like thickened or showing one to five more or less prominent knots which in the late wood often approach the *Juniperous* type of thickening, corresponding to which the wall in tangential view shows a characteristic sculpture of simple pits. The separating bars sometimes form a network. The rays are of very variable extension; in the stem type of wood they sometimes attain 60 cell rows in height.

The transverse walls of the xylem parenchyma in section are exhibiting a more or less lenticular thickened central part with a peripheral circle of easily perceptible pits. Half bordered pits connect tracheids with parenchyma cells whereas simple pits connect adjacent elements of xylem parenchyma.

The commonly occurring thickenings of the tangential ray cell walls form a marked difference between the fossils here termed *Taxodioxylon taxodii* and the wood of the extant *Taxodium* spp. These thickenings might in some cases have been overlooked in the fossils by the investigators (they are often somewhat difficult to ascertain especially in the late wood) but there seems to me, considering the unquestionable variation of the character even in the same sample, to be rather insufficient evidence to admit the existence of two biological types of the Neogene fossil *Taxodium*. It remains to be noted that both R. Kräusel (1919) and Z. Zalewska (1953), besides their *Juniperoxylon pachyderma*, have described and figured a fossil wood of the same type but without the thickenings of the tangential ray cell wall under the name *Taxodioxylon taxodii*. A few samples in our material show the thickenings, but rarely.

That the genus was abundantly represented in the lignitic floras of our continent must be regarded as above all doubt; the common occurrence of foliage twigs, cones (usually isolated cone scales, rarely entire) and seeds form unquestionable evidence. The very resistant wood of the *Taxodium* type should consequently be expected to be of common occurrence in these strata, as in fact is the case when the supplementary characters in the diagnosis are included. Remnants of Cupressaceae showing the true "Juniperus Tüpfelung" (W. Gothan 1905) character of the rays are, on the other hand, rare. The berry-like strobili referred by Z. Zalewska (1960) to *Arceutos* (*A. drupacea*) seems to be the best established remnants of a fossil *Juniperus*.

Glyptostrobus europaeus (A. T. Brongniart) O. Heer

Foliage twigs, cones and seeds referable to this species are common in the lignitic clay of Moselund and Fasterholt and are often so well preserved that an anatomical investigation is possible. In the lignitic layer of Silkeborg Vesterskov such remains were not found, but among the samples of fossil wood from the Troldhede area several specimens could, with certainty, be referred to the type of fossil wood named *Glyptostroboxylon*.

A very complete list of references concerning the fossils referred to this species and covering the literature from 1821 up to the year 1886 has been compiled by M. Staub (1887). It comprises more than a hundred relevant papers and gives an idea of the widespread occurrence of this plant in the European Paleogene and Neogene. P. Menzel has later continued the list up to 1900. The older determinations are not supported by anatomical studies and some of them, where only leaf-bearing twigs are concerned, may be uncertain; where cones are also considered the identification should be reliable. In a paper appearing in 1959 Z. Zalewska has completed the account of the characteristic features of *Glyptostrobus europaeus* with photographs of the epidermis of the leaf.

According to P. Menzel (1900) an adequate diagnosis of fossils included under the name *Glyptostrobus europaeus* may be expressed as follows: Glyptostrobus ramulis strictis; foliis spiraliter insertis, in ramis perennibus squamaeformibus, adpressis, oviformibus, apicem versus latioribus, breviter acuminatis, dorso 2–3-striatis, basi decurrentibus, in senioribus ramis saepius apice patentibus; in ramulis annuis deciduis foliis subdistichis, erectis, linearibus, apice acuminatis, basin versus numquam angustatis, late decurrentibus, nervo medio valido; amentis masculinis apicalibus, rotundatis, multifloris, basi foliis brevibus, ovalis, acutis circumdatis; amentis femineis terminalibus ad ramulos breves laterales foliis squamaeformibus instructos, ovalibus; strobilis obovatis vel subglobosis; squamis lignescentibus, imbricatis, maturis hiantibus, e basi cuneata in discum ovalem, sulcatum incrassatis, disco sub apice mucronato, margine anteriore toro semicirculari 6–9 crenato et longitudinaliter sulcato circumdatis; seminibus sub quavis squama duobus, ovatis, arcuatis, erectis, marginibus alis angustis, basi ala producta instructis.

It is apparent from this diagnosis that the author has considered a certain dimorphy of the leaf-bearing twigs. This is indeed a salient feature and caused O. Heer (1859) to establish two closely related fossil species, *G. europaeus* and *G. ungeri*, the first with only scaly leaves and the second with scale leaves and leaves of the *Taxodium* type but much narrower than in the typically developed *Taxodium*. The recent *Glyptostrobus* is markedly heterophyllous and in 1833 A. T. Brongniart chose this character as the basis of his specific name ("*Taxodium heterophyllum*"), but at that time the plant had already been described by A. B. Lambert (1832) under the name *Thuja pensilis*, and his specific name consequently claims priority.

As is evident, e.g. from the paper by Augustine Henry and Marion McIntyre (1926), the leaves of the recent *Glyptostrobus* are extremely variable in size and shape and it might be useful to cite their very clear and thorough statements as far as they are relevant to the fossil material dealt with here. "The foliage of Glyptostrobus is heterophyllous, two or three kinds of leaves being born on an individual tree at the same time; and the foliage also varies in character with the age of the tree, being different in the seedling, young and adult stages".

"Three quite distinct types of leaves occur in Glyptostrobus in addition to the cotyledons, which may be looked upon as a fourth type. As a rule only one kind of leaf occurs on any one branchlet, but occasionally the leaves towards the base of an axis may differ from the rest in shape. It is interesting to note that these three types simulate the leaves which are characteristic of the three allied genera, Taxodium, Cryptomeria, and Cupressus [the latter in shape only as they are not oppositely arranged]; and in the following description they will be named accordingly Taxodioid, Cryptomeroid and Cupressoid". (p. 94–95).

The accompanying figures illustrate these facts very clearly. Their figures (Plate III, 9 and IV, 1) show branchlets in which the leaves from the base upwards to the middle part are "cupressoid" while the foliage of the upper half is taxodioid or cryptomeroid. Z. Zalewska (1959) Plate IV, Fig. 1 and 2 has given excellent photographs of twigs of *Glyptostrobus pensilis* with markedly cryptomeroid leaves as well as photographs of young cones.

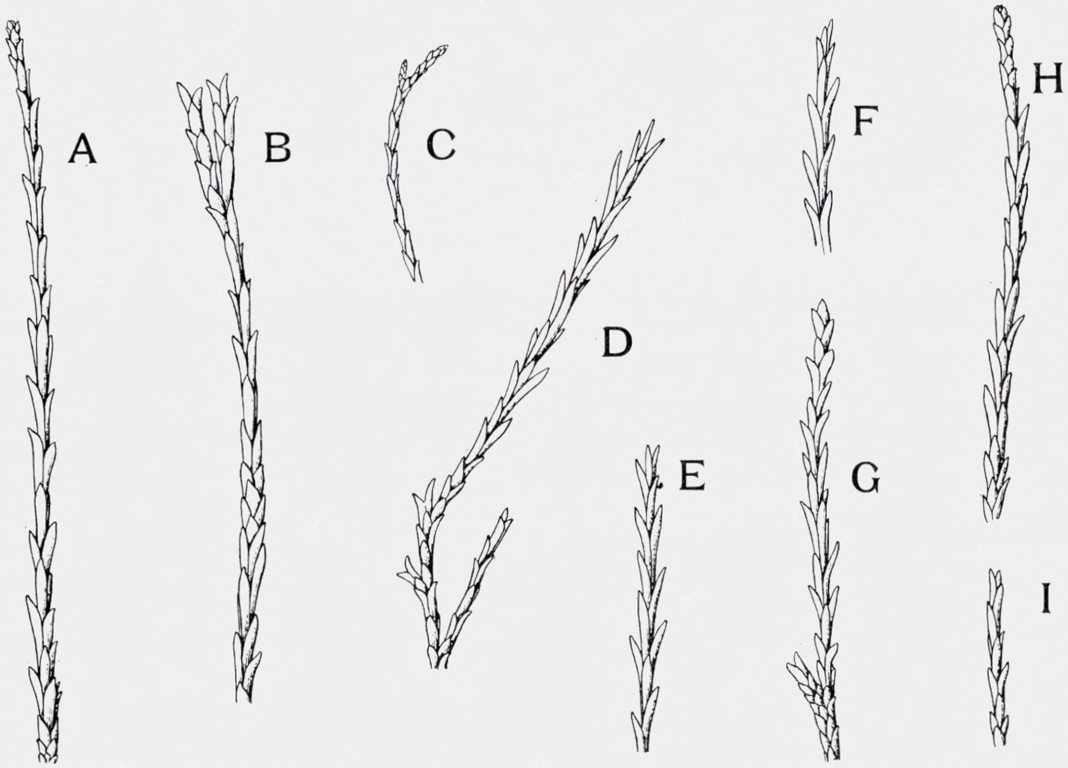


Fig. 13. *Glyptostrobus europaeus* (A. T. Brongniart) O. Heer. A–I, foliage twigs (×2). Moselund.

A. Henry and Marion McIntyre in summing up their results concerning the fossil *Glyptostrobus* have written as follows — "The Tertiary specimens are referable to one species, correctly named *G. europaeus* Heer. The material, however, can be sorted into two kinds. In one set, to which Heer at first limited his species *G. europaeus*, the branchlets often bear flowers and ripe cones, but have only Cupressoid foliage, thus corresponding to the winter stage of the living species in China. In another set of specimens the branches bear both Cupressoid and Cryptomeroid foliage, and must have been blown off in the summer, when the trees were carrying their annual branchlets. They constitute *G. Ungeri,* Heer; but this name must be abandoned, as it indicates merely a stage of growth, and not a distinct species". (p. 100).

The leaves of the taxodioid type of the extant *Glyptostrobus* are commonly much narrower than the normal *Taxodium* leaf, scarcely more than 1 mm broad, and almost rhomboidal in transverse section. The *Glyptostrobus ungeri* O. Heer is characterised by similar narrow leaves and agrees with material from taxodioid branchlets obtained from the Botanical Museum of Copenhagen University, but according to R. Florin (1931, Taf. 10, Fig. A) similar foliage also occurs on *Taxodium*

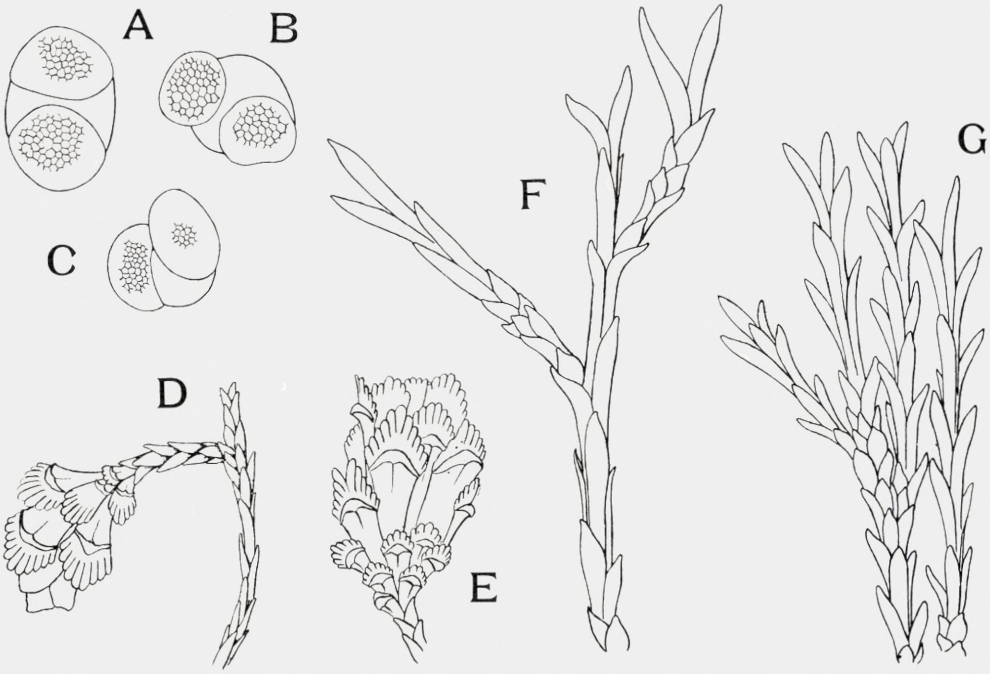


Fig. 14. A–C, pollen grains of the *Pityosporites* type (× 250). Moselund. *Glyptostrobus europaeus* (A. T. Brongniart) O. Heer. D and E, cones drawn from casts, F and G, foliage twigs. (D–G × 3). Moselund.

In our fossil material branchlets with "cupressoid" leaves predominate. The Fig. 13, A to I show such branchlets while Fig. 14, F and G show other specimens with leaves of a slender form and more patent. Heterophyllous branchlets are rare; some specimens representing this type are illustrated in Fig. 15, A to C; but anatomical ve rification could not be obtained as the branchlets were found as imprints in the yellow part of the "gyttja" at Moselund and most of the leaf substance has been reduced to powder. The determination as *Glyptostrobus* might have remained doubtful if it had not been for the marked heterophylly on the same branchlet.

The ample supply of subepidermal prosenchyma is a very salient character of the leaf and has probably contributed to the commonly excellent state of preservation.

These elements have originally been rather thick-walled but the thickening layers have mostly dissolved, so that tracing them in the fossil material is often difficult. The prosenchyma is mostly developed on the under (abaxial) side of the leaf where it forms an almost continuous layer only interrupted by two rather broad, longitudinally stretched gaps under which the covering epidermis has stomata of the same type as those of the upper (adaxial) side.

The stomata on the upper side of the leaf are especially numerous just inside the margin where they form a broad band on either side from the base of the leaf to the apex as in the leaf of the *Glyptostrobus pensilis* figured by R. Florin (1931, Taf. 15).

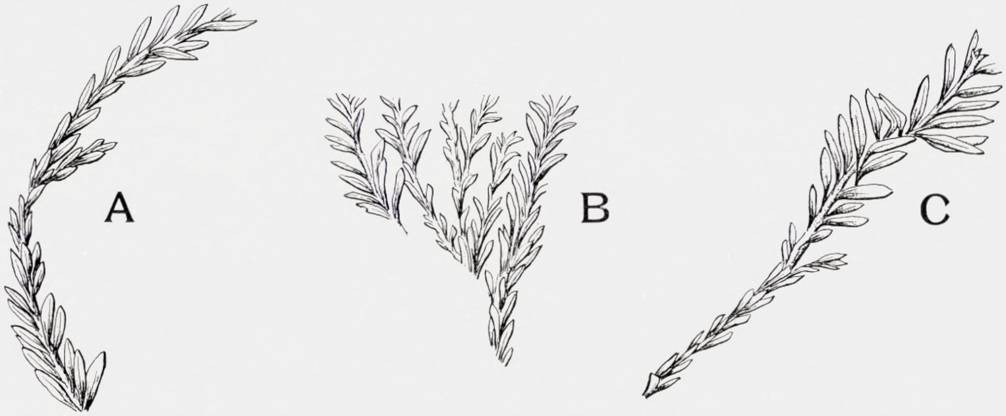


Fig. 15. *Glyptostrobus europaeus* (A. T. Brongniart) O. Heer. Foliage twigs showing dimorphous leaves (×2). Moselund. Mrs. E. Nordmann: del.

The type of the stomatal apparatus agrees completely with that of the recent *Glyptostrobus* (cf. R. Florin 1931, Taf. 14 and 15); the transfusion tissue also agrees. Intermingled with the small crystal cavities (the contents of which are dissolved) there occur markedly larger crystal cavities (R. Florin 1931, p. 362, Taf. 14, Fig. 7) especially in the epidermis of the abaxial side of the leaf in the recent as well as in the fossil *Glyptostrobus*. The tissue of the leaves is remarkably well preserved and by clearing the leaf substance with a dilute solution of sodium hypochlorite satisfactory preparations were obtained so that most of the branchlets drawn could be anatomically verified.

Cones of *Glyptostrobus* are found in the hardened lignitic clay at Moselund and in the state quarry at Fasterholt and occur also in the brown coals themselves (Fasterholt, Torvig and Gammel Ry). Even though damaged by compression and partly dissolved the cones are usually easily recognisable.

The photograph of Plate XV, K shows an exceptionally fine specimen from Fasterholt. The three partly split up cones each proceed from a short twig and the common axis is mostly preserved. The drawings of Fig. 14 D and E (Moselund) were executed from casts produced by filling out the cavity left in the matrix after the carbonized substance of the cones had been removed. This is the only way of studying the surface

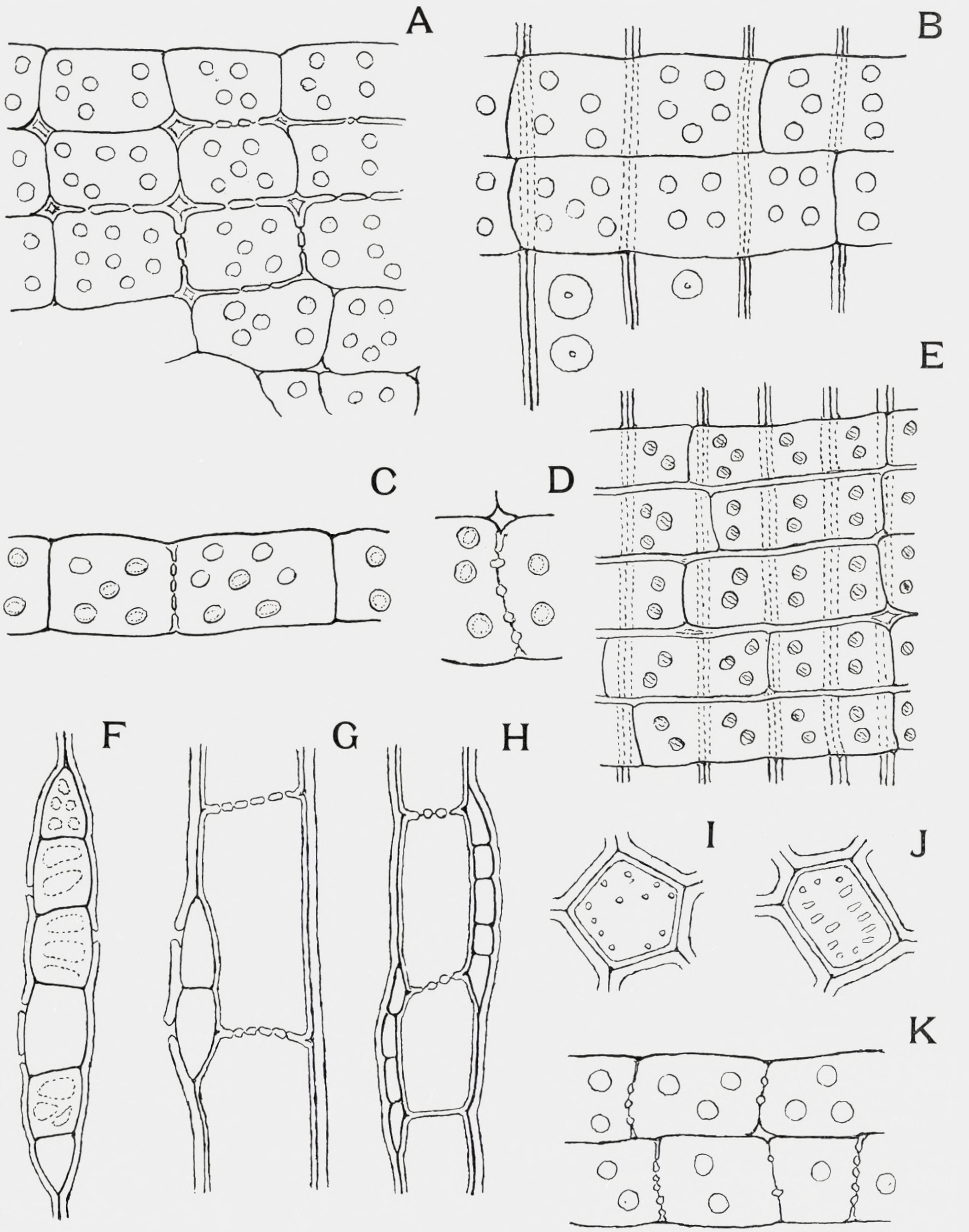


Fig. 16. *Glyptostroboxylon tenerum*. N. Conwentz (G. Kraus). A–E and K, radial sections of rays (E, cross-fields from the late wood type). F. tangential section of ray. G and H, xylem parenchyma in tangential section. I and J, transverse sections of xylem parenchyma, showing the pitting of the horizontal walls. (×400). Troldhede.

of the cone scales of our material since the cones always split when the matrix is removed as the bracts are distended and the clay penetrates between them thus preventing the intact cone from coming loose from the enclosing clay.

The cones are obovate to almost globular with somewhat outstanding scales when ripe. The scales have a cuneate basal part and in their upper portion they widen out in a rhomboidal semicircular part with a crenate margin and on the front there are furrows in continuation of the incisions of the margin. An upturned, transverse ridge on the escutcheon, extending in a small mucro, separates the upper part of the scale from the lower cuneate part.

Good figures of entire cones have been given by O. Heer (1855, Plates XIX and XX) and J. Velenovsky (1881, Plate I).

I refer the winged seeds shown in Plate VII, H and I to *Glyptostrobus*. As mentioned in the diagnosis given by P. Menzel (1900) the seeds of *Glyptostrobus* are unilaterally winged. The size and shape of the fossil corresponds well to his description, and finally I must mention that on the back side of an isolated cone scale there were impressions that correspond perfectly in shape and size with the fossil seeds. According to P. Menzel (1900) C. v. Ettingshausen gives figures of seeds of the fossil *Glyptostrobus* in his Fossile Flora von Schoenegg (Plate I, Fig. 40–68). This paper has not been accessible to me. P. Menzel states that C. v. Ettingshausen regards the fossil described and figure by O. Heer (1859, Plate IX, Fig. 1–6) as seeds of *Glyptostrobus*, and they correspond in shape to our seeds, but are somewhat larger. Anatomically our fossils agree very well with the seeds of the recent *Glyptostrobus*

Glyptostrobus europaeus (A. T. Brogniart) O. Heer extends throughout the whole of the Tertiary, including the Pliocene, in Europe and the Arctic (M. Staub 1887, A. Henry and M. McIntyre 1926).

Glyptostroboxylon tenerum (G. Kraus,) N. Conwentz 1882 (*Glyptostrobus tener* G. Kraus 1866).

Material referable to this species occurs as four samples from the Torvig quarry, Troldhede. The detailed structure is tolerably well preserved and the samples agree anatomically.

In the transverse section the growth rings are distinctly defined. The transition between the thin-walled tracheids of the early wood and the few cells thick late wood is rather abrupt. Resiniferous parenchyma occurs frequently, especially in the late wood and, as the early wood is not compressed, the thin-walled rays appear straight.

Radial sections show one to two rows of bordered pits; crassulae are frequent. The pitting of the cross-fields in the early wood appears to be of a rather mixed type differing somewhat from that commonly regarded as normal for the species: purely oëoporous throughout the whole of the early wood. This mode of pitting is only distinct in the cross-field of the first formed tracheids where it is typically developed with circular blind pits in the thin corresponding wall of the tracheid. (Fig. 16, A to D and K).

The rest of the crossfield pits are of a more or less elliptical shape, typically oculiporous in the late wood but most often showing a narrow margin. The tangential walls of the ray cells are thin, smooth, sometimes with a bead-like sculpture, or exhibiting 1 to 3 prominent thickenings. The horizontal walls are rather diffusely pored with the smooth bordering walls of the marginal cell rows quite thin. The resiniferous parenchyma has horizontal walls which commonly are smooth and finely pored, bead-like, and rarely with more prominent thickenings, in the latter case they approach the prevailing type in the wood of *Taxodium*.

Tangential section. Numerous, small, bordered pits form a rather characteristic feature on the tangential walls of the late wood tracheids, especially in the last developed tracheidal layer where the pits are of uniform size and only 8 to 11 μ in diameter. The photograph 9(?) of Plate 22 of R. Kräusel (1919) illustrates this character very well. The rays were found to attain a height of up to 25 rows of cells. The small bordered pits on the tangential walls are often confluent (Plate XXII, A).

The structure of the ray cells and the resiniferous parenchyma is in accord with recent *Glyptostrobus* material. A difference occurs in the frequency and distribution of the oëopores (blind pits) on the radial walls of the ray cells; most commonly the oëoporous type is stated to dominate in the whole of the early wood and most published figures show this, but the Fig. 3, Plate 186 given by P. Greguss (1955) shows an example in which the oculiporous pitting dominates throughout the growth ring. The material is stated to be derived from "a fair-sized piece of a stem (Shanghai)". Whether this structural detail is the most common in the older axes is still an open question. There seems to be a certain relation between the type of the cross-field pitting and the thickness of the tracheidal wall as well as the diameter of the tracheids. A sample of wood of the recent *Glyptostrobus* from the Forest Department of Yale University, which according to the curve of the growth rings must have been taken from an axis of considerable thickness, shows the relations hitherto considered as normal.

B. Kubart (1924) and K. Rudolph (1935) have drawn attention to several difficulties in distingushing the wood of *Taxodium* and *Glyptostrobus*. In all the *Glyptostrobus* material examined the transverse wall of the resiniferous parenchyma, which is normally smooth, is often found intermingled with walls that show a bead-like thickening. But they admit that the thickenings in *Glyptostrobus* are commonly far less pronounced than in *Taxodium*, to which I would add also far more rare: "Da wären wohl noch zum Beispiel die Kreuzungsfeldtüpfel zu berücksichtigen gewesen, nach meinen Beobachtungen an rezentem Materiale erscheint mir aber die Unterscheidung der beiden Gattungen auf Grund der Kreuzungsfeldtüpfel gerade nicht immer gar so leicht" (K. Rudolph 1935). I would support this opinion. Z. Zalewska (1953, Figs. 8, 10 and 12) has figured transverse walls of resiniferous parenchyma with well pronounced thickenings, a character also found in my material (Fig. 16, G and H; I and J).

Axial parts with well preserved medulla and the first growth rings are unfortunately not represented in our fossil material. This part of the stem would probably exhibit several anatomical details of systematic value.

In the recent *G. pensilis* the first growth ring shows the radial and horizontal walls of the ray cells highly pitted (Fig. 12, B), the radial walls with pits (6 to 8 μ) of the oëoporous type. The marked pitting of the walls rapidly gives way to the normal structure of the mature wood. The medulla is composed of large, rather thin-walled and only slightly pored elements, intermingled with groups of the thick-walled scleroides pre-eminently developed in the persisting twigs (Plate XIX, A and C).

Glyptostroboxylon tenerum (G. Kraus) N. Conwentz is noted, according to R. Kräusel (1949), from several European deposits of Miocene to Pliocene age. The sediments from Turów (Poland) probably range from the Middle Oligocene to the Middle Miocene (Z. Zalewska 1953).

A sample of lignitic wood referable to *Glyptostroboxylon*, but showing a somewhat curious state of preservation, was collected by the late Mr. V. Milthers at Fiskbæk by Herning in 1936. While most of the early wood has collapsed sporadic patches are almost unaltered (Plate XXII, C). The change from early to late wood is abrupt. In the tracheidal elements of the early wood there are 2 to 3 rows of bordered pits in the radial walls discernable under a reading glass in the photograph. In the late wood most of the tracheids show bordered tangential pits. Resiniferous parenchyma cells are common and often form tangential groups. The transition from well preserved early wood to the collapsed and pressed state can be followed at the tips of the tangentially stretched and unaltered groups of early wood elements.

In the radial section, cleared in a weak solution of sodium hypochlorite, the collapsed parts appear as composed of extremely altered, thin-walled elements, while in the unaltered parts the pit rows are found separated by distinct crassulae. The poring of the cross-field is distinctly glyptostroboid. The tangential section of the late wood is characterized by the numerous, quite small, bordered pits, and the transverse walls of the resiniferous parenchyma vary from smooth to beaded or occasionally knotted. The rays attain a height up to 35 rows of cells, most common are rays of 5 to 15 rows.

In these details the wood in question agrees very well with what is regarded as characteristic for *Glyptostroboxylon*, and I do not hesitate to refer it to this organo-genus.

Cupressinoxylon callitroides n. sp.

Under this heading are described a few samples of fossil wood from the quarries at Troldhede. They differ somewhat in transverse section (Plate XXIII, B and C) but histologically they agree very well with each other, individual differences not being more accentuated than what occurs among other gymnospermous woods. The type which is figured in Plate XXIII, C is a transverse section which might represent the "root type" while that figured in Plate XXIII, B might be accepted as the corresponding "stem type" of the organo-species.

The "root type" is conspicuous for its well delimited growth rings, some rather broad but most of them narrow, consisting of only a few layers of both early and late wood with an abrupt transition.

In the "stem type", figured as B, there is a gradual transgression from the innermost part of the growth ring to its outer border. The tracheids of the early wood are somewhat more thick walled and their walls have undergone a more advanced disintegration of the thickening layers than the tracheids of the "root type".

In the transverse section the outline of the tracheids is roundish, most markedly in the "stem type". Resin containing elements appear thinner walled than the surrounding tracheids and are conspicuous by their dark contents. The rays are always uniseriate.

Plate XXIV, A represents a radial section through the "stem wood type" while Plate XXIV, B shows a radial section through the "root wood type".

In the longitudinal sections the resiniferous parenchyma with its thin and smooth transverse walls and brown resin drops is very conspicuous. The radial tracheidal walls show one, very rarely two, rows of bordered pits. As it appears from the radial section figured in the photograph Plate XXIV, A there is a marked difference between the bordered pits of the size which may be termed as normal (8 to 10 μ in diameter) and those occurring here and there in the tracheids of the early wood, where they only attain a diameter of 4 to 5 μ. The last type appears mainly in the areas where the normal pitting is lacking. Especially in the tracheids of the early wood thin transverse septa are of common occurrence. They are provided with one, or a few, quite small bordered pits, visible in the transverse sections (Plate XXIII) under a reading glass.

The central black spot in most of the pits figured in Plate XXIV, A and B probably represents the outline of the torus; the aperture is quite small, scarcely exceeding 2 μ in diameter. Crassulae are not visible. The rays are composed of thin-walled elements 20 to 24 μ high in which the horizontal walls may or may not have a few scattered, unthickened parts forming slightly marked pits, and smooth tangential walls. Indentures are few and narrow. The pitting of the radial wall is very characteristic. It most commonly shows two to four blind pits only 4 to 6 μ in diameter, but their number increase, especially in the early wood, to 6 or 7 and even more (8 or 9 are sometimes found). If there are 6 or 8 they are very regularly arranged in 3 or 4 horizontal rows. In the last case the cross-field is almost totally occupied by the borders of the blind pits; sometimes two neighbouring pits are confluent and show two extremely small apertures (Plate XXIV, C) a character also occurring in the small pits of the tracheidal wall (see above). The borders of the pits and their apertures are discernable with a reading glass in the plates. Frequently there are found ray cells in which the inner surface is entirely covered with small, densely set excrescences and thus attain a papillose appearance (Plate XXIV, C and Plate XXVI, C); sometimes these excrescences attain an almost thread-like shape filling up the lumen. Small papillae are also commonly developed on the inner surface of the tracheidal wall giving it a very marked appearance (Plate XXVI, B). Most of the tracheids exhibit what looks like a fine granulation of the tertiary lamella. The separate granules are only perceptible under high magnification; in Plate XXVI, B and C they can be traced under a reading glass. Under low magnification this structure appears as a soft lustre of the inner surface, not unlike that of mother of pearl. Here and there the tracheidal wall shows a distinct structure of rather broad but only slightly accentuated spiral bands (Plate XXIV A and C, XXV, A).

The tangential section shows the generally rather low (1 to 6 storied) rays (Plate XXVI, A) but higher rays (12 to 18 stories) occur. Tangential bordered pits, somewhat smaller than those of normal size on the radial walls and here and there confluent, are locally numerous in the late wood.

Diagnosis

Wood of a cupressoid gymnosperm representing both "root type" and "stem type". The two types show the usual anatomical differences in the structure of the growth rings but are otherwise quite similar. The outline of the tracheids is more or less markedly rounded in transverse section and resiniferous parenchyma is abundant. The tracheids are commonly devided by thin transverse septa, provided with one or a few, quite small bordered pits. Tracheidal walls of the early wood have one or rarely two rows of bordered pits differing greatly in size. The pits of the smaller type (4 to 6 μ) are confined to areas of the early wood where pits of the normal size are lacking on the radial walls. Bordered pits are numerous on the tangential walls of tracheids of the late wood. Rays uniseriate, 1 to 12, most commonly 3 to 6, cells high, elements thin walled with 4 to 6, or up to 7 to 9, minute blind pits on the radial walls; when numerous the pits are regularly arranged in 3 to 4 superposed rows, sometimes two neighbouring pits are confluent and show two extremely minute apertures. Horizontal walls are indistinctly pitted with indentures not very pronounced. The inner surface of ray cells and tracheids are often markedly verrucous, the tracheidal inner surface commonly exhibiting a more or less conspicuous, fine granulation of the terminal lamella, producing a soft nacreous lustre on the wall.

Affinities

According to the relevant literature these fossils show a marked anatomical parallelism to the wood of some species of the recent genus *Callitris* constituting a genus comprising about 20 species. At the present time *Callitris* is only indigenous in Australia, Tasmania and New Caledonia. Besides the specific differences concerning foliage and shape and size of the cones there are also histological details in the xylotomy which are of systematic value.

E. J. Slyper (1933), on the basis of xylotomy, has divided the 17 *Callitris* species considered in his keys, into several groups, primarily based on the presence or absence of transverse bars on the inner surface of the tracheidal wall running over the bordered pits (pp. 406–408, "Bars of Kleeberg").

The first group is subdivided in two divisions, 41 a "Auf den Kreuzungsfeldern stehen zusammengesetzte Hoftüpfel mit zwei Poren" and 41 b "Keine zusammengesetzte Hoftüpfel mit zwei Poren". 41 a contains 7 species including the widespread *C. robusta* R. Brown and *C. glauca* R. Brown, and 41 b includes *C. arnosa* A. Gunn. and *C. intertropica*, Bentham.

The second group, (42, no "Bars of Kleeberg" running over the bordered pits) includes, besides species of *Cupressus* and *Libocedrus* also *Widdringtonia, Actinostrobus* and several (5) *Callitris* sp. The three last named genera are further characterized by the rare occurrence of bordered pits on the tangential walls of the tracheids.

No details are mentioned concerning the occurrence of the "zusammensetzte Hoftüpfel mit zwei Poren" (confluent pits) in the subdivisions of 42; 43 a and b. According to my experience they occur also in *Widdringtonia* but are rare. In the group of the five *Callitris* species mentioned I could not demonstrate them in the investigated woods of *C. oblonga* L.-C. Marie Richard and *C. rhomboidea* R. Brown, so the basis of the division is probably applicable to the purpose.

According to these statements confluent pits with two apertures commonly occur in the group 41 a and are lacking or very rare in the subdivisions 41 b, 43 a and b. There seems to be a contradiction between the characters set out in the paragraphs of E. J. Slyper, which cover the combinations found in the extant *Callitris* sp., and those found in our fossil: the absence of "Bars of Kleeberg" combined with the common presence of confluent pits.

The wide gap of time as well as the space of geographical distribution might have called for a development of types in which another combination of these details was made possible. Fossil remains (foliage twigs and cones) referable to the *Callitris* type have not been demonstrated in the European or North American Tertiary. In English Eocene layers cones are found which may be referred to the related genus *Tetraclinis*.

The pittings of the cross-field closely resembles that of *C. glauca*, but it has been impossible to draw a parallel to extant species since material for a closer comparison was not at hand; only 3 to 4 mm thick twigs were available for investigation.

A spiral structure of the tracheidal wall, composed of rather broad bands, is present in several extant *Callitris* sp. P. Greguss (1967, Plate XLVI, Figs. 18 and 19) has figured this character, the presence of which in our fossil might support the validity of our referring this type to the genus. The structure described here of the inner lamella of the tracheids and ray cells is not unfamiliar in species of *Callitris*, but is notably more pronounced in the wood of some *Widdringtonia* sp.

P. Greguss (1967 p. 55) describes a sample of fossil wood under the name of(?) *Callitroxylon*. The very poor material has unforlunately not allowed a closer study, but the crowded and occasionally paired pittings, and also the presence of trace able spirals might point towards the said author's *Platyspiroxylon* (Permian and Lower Liassic). As the locality is mentioned as Gant (Hungary) the geological age is recorded as Lower Eocene. This find claims some interest as the *Platyspiroxylon* type of fossil wood probably might be considered as related to the extant *Callitris* type (P. GREGUSS loc. cit.) and its presence in the Paleogene Tertiary would demonstrate the existence of such a type of gymnosperm at past times in the Northern Hemisphere. In fact details in the anatomical structure of our still younger fossil show certain characters pointing towards such ancestors, details which are only faintly present in the extant *Callitris* spp.

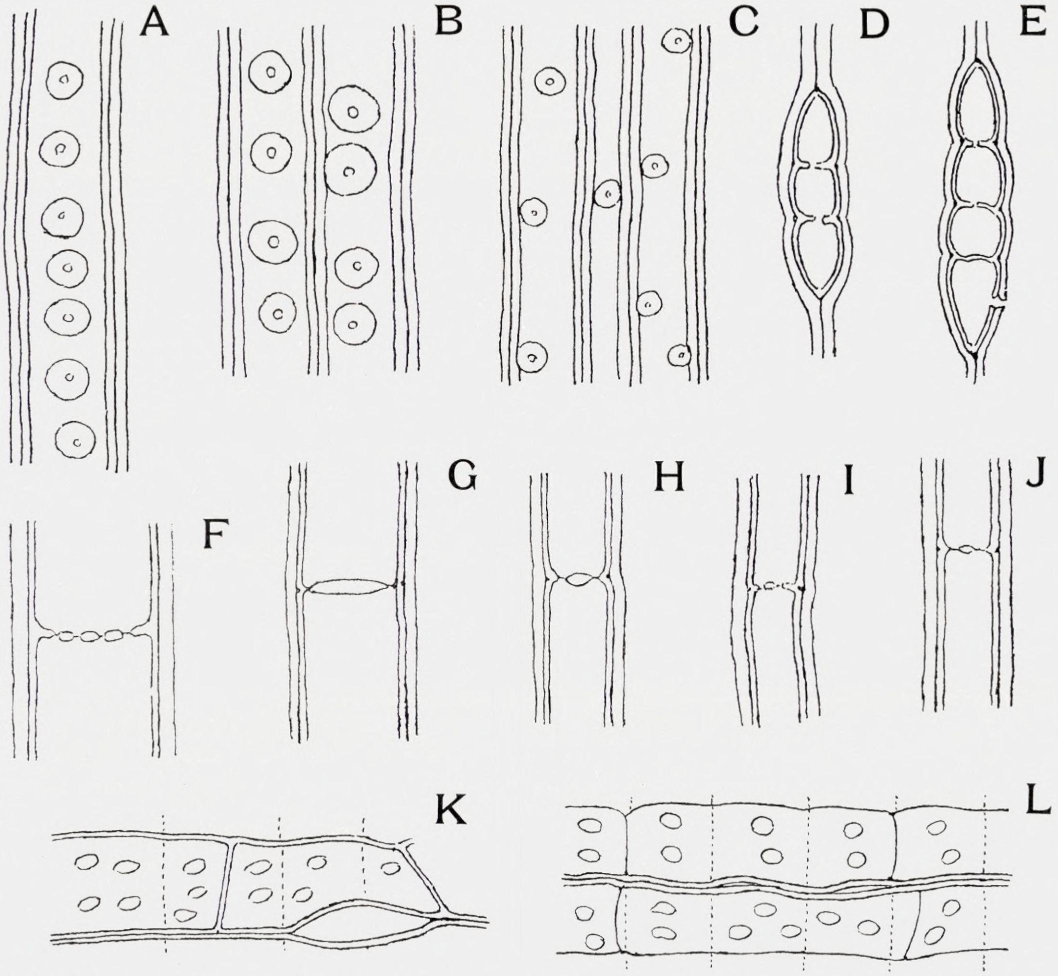


Fig. 17. *Cupressinoxylon thujoides* n.sp. A and B, parts of tracheids in radial, and C, in tangential section. D and E, rays in tangential view. F–J, transverse wall of xylem parenchyma showing variations in the mode of pitting. K and L cross-field pitting in the early wood. (×600). Troldhede State Quarry.

Cupressinoxylon thujoides n. sp.

Only one sample referable to this type has been found (the State quarry, Troldhede). The condition of preservation is fairly good but the structural details of the tracheidal walls are somewhat obscured by the disintegration of the fibrillae of the thickening layers.

The transverse section exhibits a series of growth rings (Plate XXVII, A) with the early wood gradually transcending into the late wood. The texture is "fine grained" yet somewhat coarser than in *C. biotoides* (p. 59). Minute intercellular spaces are common, corresponding to the rounded outline of the tracheids. The radial and tangential walls of the elements composing the uniseriate rays are thin; the horizontal walls show here and there a row of simple pits.

Resin cells are rather rare and are evenly distributed in the growth ring.

A part of a radial section is reproduced as Plate XXVII, C. The bordered pits are arranged in only one row and attain a diameter of 12 to 13 μ, with a minute aperture. In the photograph the fine spiral pattern of the inner part of the tracheidal wall has obscured the bordered pits so that they are hardly recognisable. The Fig. 17, A and B show the proportions between the outline and aperture.

In the early wood especially the cross-field shows a type of pitting characteristically different from the common *Cupressinoxyton* type and approaching the taxodioidal type. Fig. 17, K and L show such cross-fields. The blind pits of the radial ray cell wall of the late wood are from almost circular to somewhat elliptical in outline and the border of the pit is rather narrow. The radial as well as the tangential walls of the ray cells are thin and without any sculpture; the horizontal walls are considerably thicker, scarcely pitted and provided with numerous and partly highly developed indentures.

Some rays, as they appear in the tangential section, are shown in Plate XXVII, B. They are usually low (1 to 4 cell rows) but they may attain a somewhat greater height, up to 8 stories of cells.

The Fig. 17, D and E figure some rays in which the horizontal cell wall is broken; the rupture occurring in the middle part of the wall indicating a marked difference compared with what is commonly found in the ray cells of *Biota* (compare the figures of rays of *Thuja* with those of *Biota* and *C, biotoides* in Figs. 18 and 19).

Fig. 17, C shows some bordered pits on the tangential walls of the tracheids; they measure 5 to 9 μ in diameter and are consequently far smaller than those on the radial walls.

The transverse walls of the resiniferous parenchyma cells are locally thickened in a rather characteristic way (Fig. 17, F to J), a feature mentioned by A. S. Pierce (1937) for the recent *Thuja* spp. and here, as well as in our fossil, easily discernable under a high power objective.

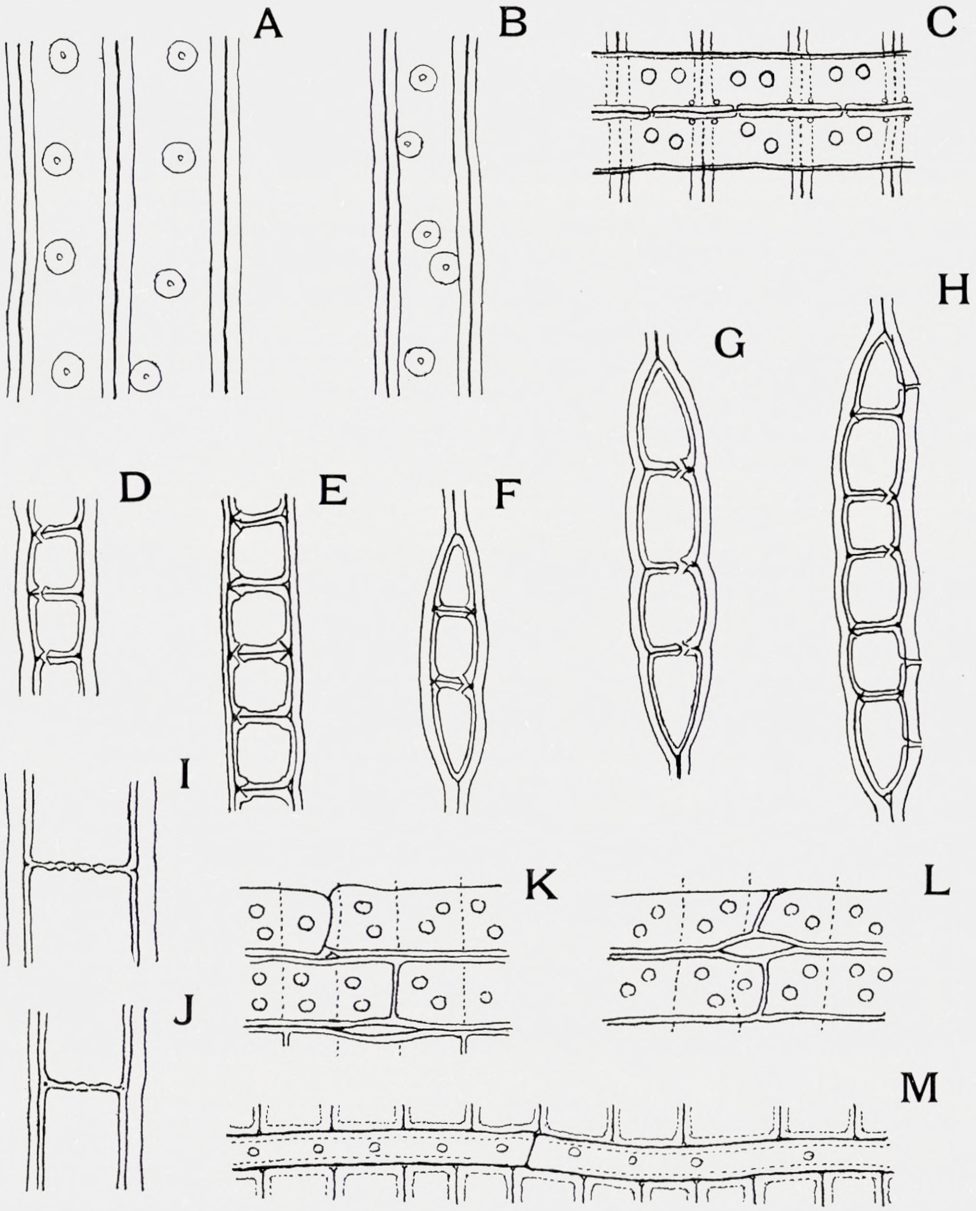


Fig. 18. *Cupressinoxylon biotoides* nov. comb. A and B, parts of tracheids in radial and tangential section. D–H, view of rays in tangential section; in all the figures the ruptures in the horizontal walls fo the ray cells are conspicuous. C, K and L, cross-field pitting; K and L also show indentures. I and J, transverse walls of xylem parenchyma. M, transverse view of ray showing the fairly even distribution of simple pits in the horizontal wall. (×600). Lystrupsminde.

Diagnosis

A gymnospermous wood of the *Cupressinoxylon* type. Growth rings distinct with a gradual transition of the tracheidal elements from early to late wood. The tracheids in transverse section show a rounded outline and between them there are commonly occurring small intercellular spaces. Rays uniserial with the horizontal walls irregularly pitted. Interstitia numerous and well developed. Resiniferous parenchyma rather common with the horizontal walls distinctly, but irregularly, pitted. Bordered pits on the radial wall of the tracheids always in one row, 12 to 18 μ in diameter, aperture small. The tangential wall of the late wood tracheids with scattered bordered pits, measuring 5 to 9 μ in diameter. Rays 1 to 5 (8) cell rows high. In the cross-field of the early wood there are 1 to 4 elliptical, almost taxodioidal blind pits while the pitting of the late wood cross-field is normally cupressoidal. Radial and tangential walls of ray cells thin and the latter without sculpture.

Affinities

According to the anatomical details our fossil may be referred to the genus *Thuja* and agrees especially well with *T. occidentalis* L. A specific correspondence to this species is, of course, impossible to demonstrate on the material available, so the name *Cupressinoxylon thujoides* is proposed as a suitable name for the fossil material. It seems that twigs referable to *Thuja* and *Biota* have not yet been anatomically confirmed.

Z. Zalewska records the presence of a *Thuja* sp. *(T.* cf. *occidentalis* L.) in the lignites of Turów (Aquitanian) and figures a cone and a supposed twig (Z. Zalewska 1960, Plate XV). In Table 11 (l.c.) the same author lists the occurrence of supposed fossil Thuja (and Biota) spp. in Poland and the adjacent territories.

Cupressinoxylon biotoides nov. comb.

(*Biota orientalis* (L.) St. Endlicher var. *miocenica* W. Prill 1913)

Among the samples of fossil wood gathered from the lignite of the Lystrupsminde quarry a small piece (about 5×3×2 cm) was conspicuous by its almost black colour and hardness. The anatomical details proved to be, for the greater part, perfectly preserved.

Plate XXVIII, A shows a photograph of a transverse section exhibiting tree growth rings. The elements of the early wood are collapsed, sometimes in such a way that the lumen forms a sand-glass shaped figure so that the apparently small lumina consequently only represent less than half the original size of the lumen of a tracheid. The transgression from early to late wood seems rather abrupt but, in fact, the elements do not differ much in thickness of the wall; evidently the wall material of the late wood tracheids has also here been more resistant. Outwards the elements of the late wood gradually diminish only slightly in size. As a whole the wood shows an uncommonly even and densely fine texture. In transverse section all the tracheids show a decidedly rounded outline. The rays are uniseriate. Small intercellular spaces between the elements are not uncommon and are especially often found between the very thin radial walls of the ray cells and the bordering tracheids. The rather thick, horizontal wall of the ray cell shows a low, radial furrow, most often extending the length of the cell, in which simple pits are common and evenly distributed (Fig. 18, M). Resin cells occur especially in the outer part of the growth ring where they are discernible by their black contents.

A part of a radial section is reproduced in Plate XXVIII, B. A very conspicuous feature is the regular spiral pattern of the innermost part of the tracheidal wall in the larger part of the section and is especially well developed in the middle and outer part of the late wood. The dark coloured spirals probably represent a special structure of the innermost part of the thickening lamella of the tracheidal wall. This structure is made more conspicuous through partial destruction of the terminal lamellae on fossilization and is also locally seen in the wood of recent Cupressaceae (e.g. *Biota*). It is not to be confused with the more steeply inclined spirals so commonly observed in all types of gymnospermous wood where it represents a texture produced by disintegration of the thickening layers. The tiny spirals in *Biota* show double refraction and under polarized light and crossed nicols appear as sharply discernible light greyish bands.

The bordered pits on the radial walls of the tracheids are always arranged in one row. Their diameter attains a value of 10 to 12 μ with an extremely minute aperture measuring only 1.5 to 2 μ. In the photograph Plate XXVIII, B the pits are mostly hidden by the spirals. Fig. 18, A shows the proportions between porus and the outline. The "tailed" appearance of the blind pits of the rays is due to intervening spaces in the first formed thickening lamellae of the bordering tracheids. The pits of the cross-fields are typically cupressoid. They are in fact circular or almost so with a diameter of 5 to 6 μ. Interstitia in the horizontal walls of the ray cells are rather common (Fig. 18, K and L). In places where the horizontal wall crosses the vertical intercellular spaces between the tracheids bordering a ray four minute dots forming a small rhombic figure are sometimes perceptible (Fig. 18, C). The horizontal walls of the rays appear distinctly pored (Fig. 18, C and M) and also the transverse walls of the resiniferous parenchyma show a fine and irregular poring (Fig. 18, I and J).

In tangential section the spiral pattern of the inner surface of the tracheids is of a very striking appearance (Plate XXVIII, C). On the tangential walls of the tracheids bordered pits of the same type and almost the same size as those of the radial walls are rather common (Fig. 18, B). The proportions between the aperture and the diameter of the pits in the photograph (Plate XXVIII, C) is more conspicuous than in that of the radial section. The rays attain a height of 7 rows of cells. The form of the ray cells is somewhat variable, most often, especially in those of only a few cell rows, axially elongated. Some important peculiarities are not discernible in the photograph but the drawings make up for this disadvantage. In the Fig. 18, D to H some rays are shown in tangential view. In the middle part of the ray cell, where it communicates with the adjacent tracheids through the blind pits, the wall is rather thin, increasing in thickness towards the upper and lower parts of the cell where it passes into the thick horizontal walls. A rupture of the wall is very common and is always effected in such a manner that the connection between the horizontal and the radial walls is broken in the coterminous parts in such a way that the horizontal wall shows

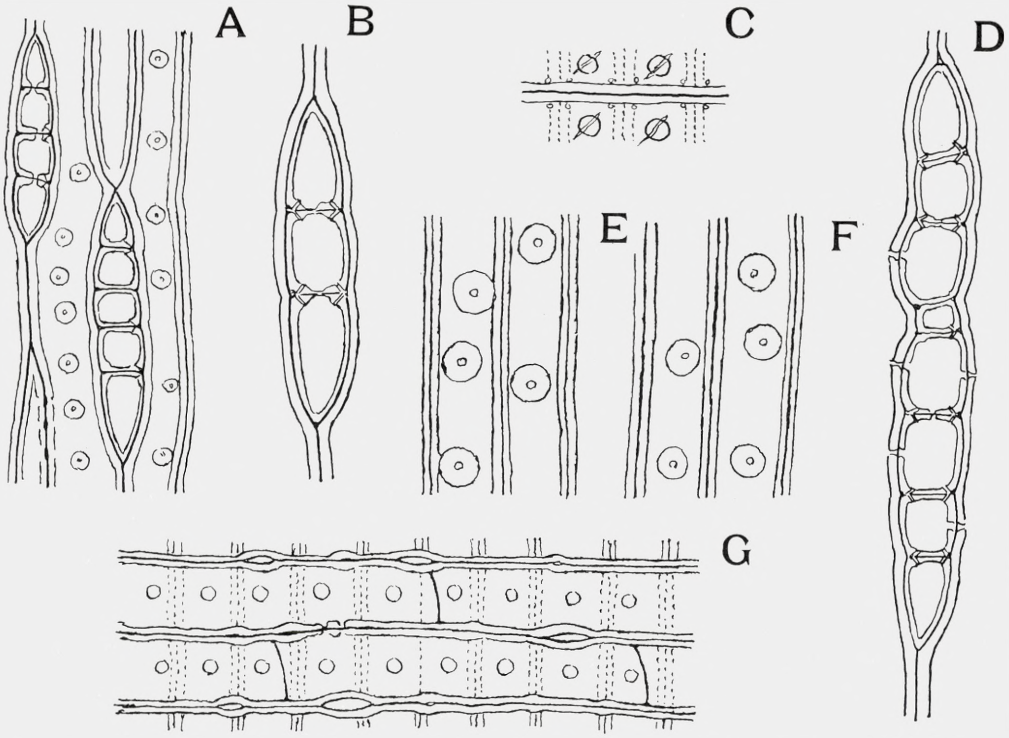


Fig. 19. *Biota orientalis* (L.) St. Endlicher. A, B and D, rays in tangential section. C and G, radial section of rays showing the cross-field pitting and in G indentures. E, radial and F, tangential sections of tracheides. (× 600). Materiel from the Botanical Garden of the University, Copenhagen.

a blunt, regular wedge while part of the radial wall has a corresponding triangular cavity (Fig. 18, D to H). The wall at his place is obviously liable to fracture due to the presence of the two (or two pairs) of divergent pits departing from the very small intercellular space between the corresponding ray cell walls and the bordering tracheids; one (or one pair) is pointing upward and the other downward, crossing, but not perforating, the thickened part of the adjacent ray cells. The pits are also sometimes discernible in the radial sections where they form the small, diaphanous points mentioned above (Fig. 18, C), but owing to the darkness of the medium they were often difficult to ascertain.

Diagnosis

A gymnospermous wood of the *Cupressinoxylon* type. Growth rings distinct. In transverse section the tracheids show a rounded outline with small intercellular spaces notably common between rays and the bordering tracheids. Rays uniseriate with the horizontal walls distinctly pitted. Interstitia numerous and well developed. Resiniferous parenchyma rather common with transverse walls thin and faintly and irregularly pitted. In the tracheids the bordered pits on the radial walls are always in one row, 10 to 12 μ in diameter with a very small aperture, while on the tangential walls the bordered pits are scattered but are almost of the same size and type as those on the radial walls. Rays 1 to 7 cell rows high with 1 to 2 circular blind pits in each cross-field. In the ray cells the transition between the thin radial walls and the horizontal wall is formed by a markedly thickened part which is often traversed by minute pits running from the triangular intercellular space between ray and tracheid through the thickened layers of the ray cell as far as the terminal lamella.

Affinities

According to PILGER (1926) the genus *Thuja* is subdivided into two sections: a) *Euthuja*, comprising three species including *Thuja occidentalis*, and b) *Biota*, only represented by a single species, *Thuja orientalis* L., which is most conveniently considered as a separate genus (*Biota orientalis* (L.) St. Endlicher). According to the keys for the determination of recent and fossil gymnospermous woods by W. GOTHAN (1905), W. PRILL (1913), E. J. SLYPER (1933), A. S. PEIRCE 1937) and P. GREGUSS (1955) only *Biota* can be considered as offering a recent analogue to the fossil described here. In fact, W. PRILL has established (l.c. p. 52) a species of fossil wood under the name of *Biota orientalis* (L.) St. Endlicher var. *miocenica* based mainly on the curious mode of poring in the thickened part of the wall of the ray cell. He recognized the same character ("umgewendete Markstrahlintercellularen") in the fossil as in the living *Biota orientalis* while it is lacking in the other species of cupressoid wood which he examined, including *Thuja occidentalis*. His description of the fossil wood is short and incomplete, without figures, and is insufficient for the foundation of a variety of a recent species which is not otherwise known as a fossil. Yet, probably, he is right to refer his Tertiary fossil wood from Friendorf near Bonn to the *Biota* subdivision of *Thuja*.

While the pits of the radial walls of the ray cells in *Biota orientalis* remain almost circular throughout the growth ring, in the early wood of *T. occidentalis* they appear more or less elliptical in outline. This character is accepted as diagnostic by all the authors. A character which is very characteristic for *Biota* is the close agreement in size of the bordered pits on the radial and tangential walls of the tracheids while in *Thuja* they follow what is usual in gymnospermous wood, viz. they are notably smaller on the tangential than on the radial walls.

A paper published by F. HOLLENDONNER (1912) with the special aim of giving an exact anatomical distinction between the wood of *Thuja orientalis (Biota)* and *Thuja* *occidentalis* is rich in details and is accompanied by excellent figures. According to this paper the main differences may be summed up thus: in *Biota* the outline of the blind pits is circular and extremely small (1.5 to 2 μ), while in *Thuja occidentalis* it is elliptical with the longer axis extended horizontally and notably larger (3 to 5 μ). On the special mode of pitting of the ray he states: "Es gibt ausserdem noch einen Unterschied in den zwischen Markstrahlzellen und Längstracheiden auftretenden Intercellularräumen, welche im Tangentialschnitt bei Thuja dreieckig sind — bei Biota aber gehen aus dem Intercellularraum zwei gabelig verläufende Kanälchen gegen den Hohlraum der übereinander stehenden parenchymatischen Markstrahlenzellen und erstrecken sich, die mächtige sekundäre Lamelle (hier) durchstreckend, bis zur tertiären Lamelle". In our Fig. 19, B and D this structure is demonstrated for *Biota orientalis*. In *Thuja occidentalis*, where the ray cells are almost uniformly thin walled, no such canals are found. The character is mentioned by P. GREGUSS (1955) but is not claimed as being strictly confined to *Biota orientalis*. In fact it also occurs, but more rarely, in the wood of *Thuja standischii*. As W. Prill has already pointed out, this special feature causes a certain weak point in the structure of the horizontal wall within the ray cells and thus often gives rise to ruptures in fossil material during the preparation of slides for microscopy. My experiences confirm the statements made by him.

The fossil described here seems to agree very well with the wood of the living *Biota orientalis*. Specific agreement with the recent analogue is, of course, impossible to demonstrate so the name *Cupressinoxylon biotoides* is suggested. The anatomical peculiarities of the recent genus *Biota* seem to be so well differentiated that the establishment of a fossil analogue organo-genus migtet be justifiable.

Fig. 20. *Sequoia couttsiae* O. Heer. H. V. Vestergaard del. $^1/_1$ Moselund, 1919.

Selected Bibliography

Banke Rasmussen, L. (1961): De miocæne Formationer i Danmark. Danmarks geolog. Undersøgelse IV. Række, Bd. 4. No. 5.

Bailey, I. W. and Anna F. Faull (1934): Structural variability in the Redwood, Sequoia sempervirens, and its significance in the identification of fossil woods. (The cambium and its derivative tissues. IX). Journal of the Arnold Arboretum. Harvard University. Vol. XV. 1934.

Bandulska, Helena (1923): A preliminary paper on the cuticular structure of certain Dicotyledonous and Coniferous leaves from the Middle Eocene flora from Bournemouth. Journal of the Linnean Society. Bot. Vol. XLVI. London.

Baumberger, E. und P. Menzel (1914): Beitrag zur Kenntnis der Tertiärflora aus dem Gebiete der Vierwaldstätter Sees. Mémoires de la Société Paléontologique Suisse. Vol. XI. Genève.

Beust, F. (1885): Untersuchung über fossile Hölzer aus Grønland. Dissertation. Zürich. Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft der gesammten Naturwissenschaften. Bd. XXIX.

Buchholz, J. T. (1939): The generic segregation of the Sequoias. American Journal of Botany. Vol. 26. Pag. 535. Baltimore.

Chandler, M. E. J. (1922): Sequoia Couttsiae Heer, at Hordle, Hants: A study of the characters which serve to distinguish Sequoia from Athrotaxis. Annals of Botany. Vol. XXXVI. Pag. 385 London.

Chaney, R. W. (1930): A Sequoia forest of Tertiary age on St. Lawrence Island. Science. New Series. Vol. LXXII. New York.

Chaney, R. W. (1951): A Revision of fossil Sequoia and Taxodium in Western North America based on the recent discovery of Metasequoia. Transactions of the American Philosophical Society. New Series. Vol. 40. Part 3. Philadelphia.

Committee on Nomenclature, International Association of Wood Anatomists 1933: Glossary of terms used in describing woods. Tropical Woods. 36.

Conwentz, H. (1882): Fossile Hölzer aus der Sammlung der Königl. geologischen Landesanstalt zu Berlin. Jahrbuch der Königl. Preussischen geologischen Landesanstalt XIV. und Bergakademi für 1881.

Dallimore, W. and A. Bruce Jackson (1948): A Handbook of Coniferae including Ginkgoacea. 4. Ed. Revised by S. G. Harrison 1966. London.

Dotzler, Auguste (1938): Zur Kenntnis der Oligozänflora des Bayerischen Alpenvorlandes. Palaeontographica, Abt. B. Bd. LXXXIII. Stuttgart.

Doyle, Mary N. and J. Doyle (1948–50): Pith structure in Conifers. I. Taxodiaceae. Proceedings of the Royal Irish Academy of Science. Sect. B. Vol. 52. Dublin.

Endô, S. (1933): A Neogene species of Sequoia from Japan. Botanical Gazette. Vol. 94. Chicago.

Endô, S. (1936): Note on new fossil Species of Sequoia from the Far East. Proceedings of the Imperial Academy of Japan. Vol. XII. Tokyo.

Ettingshausen, C. v. (1855): Die tertiäre Flora von Häring in Tirol. Abhandl. der Kaiserl. Königl. geologischen Reichsanstalt Wien. Bd. II. Abt. 2. No. 2. Wien.

Florin, R. (1922): Über das Vorkommen von Sciadopitys im Deutschen Tertiär. Senckenbergiana. Bd. 4. Heft 1/2.

Florin, R. (1922): On the geological history of the Sciadopitineae – A preliminary note. Svensk Botanisk Tidskrift. Bd. 16. Hefte 2.

Florin, R. (1926): Waren Eupodecarpeen (Koniferen) in der alttertiären Flora Europas vertreten oder nicht. Senckenbergiana. Bd. VIII. Heft. 2. Frankfurt am Main.

Florin, R. (1931): Untersuchungen zur Stammesgeschichte der Coniferales und Gentales. I. Morphologie der Epidermisstructur der Assimilationsorgane bei den rezenten Coniferen. Kungl. Svenska Vetenskapsakademiens Handlingar. Tredie Serien. Bd. 10. Nr. 1.

Florin, R. (1940): Notes on the past geographical distribution of the genus Amentotaxus Pilger (Coniferales). Svensk Botanisk Tidskrift. Bd. 34. Hefte 2.

Florin, R. (1963): The Distribution of Conifer and Taxad Genera in Time and Space. Acta Horti Bergiani. Bd. 20. Nr. 4. Uppsala.

Friedrich, P. (1883): Beiträge zur Kenntnis der Tertiärflora der Provinz Sachsen. Abhandlungen zur geologischen Spezialkarte von Preussen und den Thüringischen Staaten. Bd. IV. Heft. 3. Königl. Preuss. geolog. Landesanstalt. Berlin. Text and Atlas.

Gardner, J. S. (1883–1886): A Monograph of the British Eocene Flora. Vol. II. Gymnospermae. Palaeontographical Society Publications. London.

Gothan, W. (1905): Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. Königl. Preuss. geolog. Landesanstalt u. Bergakademie. Neue Folge. Heft XLIV. Berlin.

Gothan, W. (1906): Die fossilen Coniferenhölzer v. Senftenberg. Abhandlungen der Königl. Preuss. geolog. Landesanstalt (Neue Folge) Heft XLVI. Berlin.

Gothan, W. (1909): Über Braunkohlenhölzer des rheinischen Tertiärs. Jahrbuch der Königl. Preuss. geolog. Landesanstalt. Bd. XXX. Teil I. Heft. 3. Berlin.

Gothan, W. (1936): Nochmals die "Graskohle": Nadeln der Schirmtanne (Sciadopitys). Braunkohle 1936. Heft. 40. Düsseldorf.

Greguss, P. (1950): Xylotomischer Bestimmungsschlüssel der heute lebender Konifern-Gattungen. Acta Biologica Acad. Scient. Hungarica. I. Budapest.

Greguss, P. (1955): Identification of living Gymnosperms on the basis of xylotomy. Budapest.

Greguss, P. (1967): Fossil Gymnosperm Woods in Hungary from the Permian to the Pliocene. Budapest.

Göppert, N. R. (1842): Über die fossile Flora der Gypsformation zur Derschel in Oberschlesien. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher. Tom. XIX. Part II. Breslau und Bonn.

Göppert, N. R. (1850): Monographie der fossilen Coniferen. Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem. II. Versameling. 6. Deel. Leiden.

Hartz, N. (1909): Bidrag til Danmarks tertiære og diluviale Flora. Danmarks geol. Undersøgelse. II. Række. Nr. 20. København.

Herr, O. (1855–61): Flora Tertiaria Helvetica. I. 1855. II. 1856. III. 1859. Winterthur.

Heer, O. (1863): On the Fossil Flora of Bovey-Tracy. Philosophical Transactions of the Royal Society of London for the Year 1862. Vol. 152. London.

Heer, O. (1868): Flora fossilia arctica I. Zürich.

Heer, O. (1869): Miocene baltische Flora. Beiträge zur Naturkunde Preussens. 2. Herausgegeben von der Königl. physikalisch-ökonomischen Gesellschaft zu Königsberg. Königsberg.

Heer, O. (1870): Über die Braunkohlenpflanzen von Bornstedt. Abhandlungen der Naturforschenden Gesellschaft zu Halle. Bd. XI. Halle.

Heer, O. (1883): Flora fossilis Grønlandica I-II. Zürich.

Henry, A. and Marion McIntyre (1926): The swamp cypresses, Glyptostrobus of China and Taxodium of America with notes on allied genera. Proceedings of the Royal Irish Academy. Vol. 37. Sect. B. No. 13. Dublin.

Hofmann, E. (1927): Vergleichende anatomische Untersuchungen an rezenten Pneumatophoren von Taxodium distichum sowie an fossilen Pneumatophoren aus Parschlug in Steiermark. Berg- und Hüttenmännisches Jahrbuch. Bd. 75. Nr. 3.

Hollendonner, F. (1912): Über die histologische Unterscheidung des Holzes von Biota orientalis Endl. und Thuja occidentalis L. Zeitschrift der Botanischen Section der Königl. Ungarischen Naturwissenschaft. Gesellschaft. Bd. XI. Nr. 2.

Hui-Lin Li (1952): The genus Amentotaxus. Journal of the Arnold Arboretum. Vol. 33. Pag. 192–198. Cambridge, Mass., U.S.A.

Ingwersen, Peter (1954): Some Microfossils from the Danish Late-Tertiary Lignites. Danmarks geol. Undersøgelse. Skrifter II. Række. Nr. 80. København.

Jeffrey, E. C. (1903): The comparative anatomy and phylogeny of the Coniferales. Part I. The Genus Sequoia. Memoirs of the Boston Society of Natural History. Vol. V. Boston.

Jurasky, K. A. (1928): Paläobotanische Braunkohlen Studien. III. Ein neuer Fund von Sciadopitys in der Braunkohle (Sciadopityoxylon Wettsteinii n.sp.) Senckenbergiana. Bd. 10. Nr. 6. Frankfurt a.M.

Kirchheimer, F. (1950): Das Vorkommen von Sciadopitys im mitteleuropäischen Tertiär und die Bedeutung ihres Pollens für die Stratigraphie der Braunkohlenschichten. Neues Jahrbuch für Geologie und Paläontologie. Heft 2. Stuttgart.

Kobbe, F. (1887): Über die foss. Hölzer der Mecklenburger Braunkohle. Dissertation. Rostock.

Kräusel, R. (1913): Beiträge zur Kenntnis der Hölzer aus den Schlesischen Braunkohlen. Teil I. (Dissertation) Botanisches Centralblatt. Bd. CXXIII. Jena.

Kräusel. R. (H. Reimann, E. Reichenbach, P. Meyer und W. Prill) (1919): Die Pflanzen des Schlesischens Tertiärs (Braunkohlenhölzer. Pag. 191). Jahrbuch der Preussischen geol. Landesanstalt für 1917. Bd. XXXVIII. Teil. II. Heft 1-2. Berlin.

Kräusel, R. (1919): Die fossilen Koniferen hölzer, (unter Ausschluss von Araucarioxylon Kraus). Palaeontographica. Abt. B. Bd. LXII. Stuttgart. Nachtrag: Senckenbergiana. Bd. 2. 1920. Frankfurt a.M.

Kräusel, R. (1920): Nachträge zur Tertiärflora Schlesiens. II. Braunkohlenhölzer. Jahrbuch der Preussischen geolog. Landesanstalt für 1918. Bd. XXXIX. Teil I. Heft. 3. Berlin.

Kräusel, R. und G. Schönfeld (1924): Fossile Hölzer aus der Braunkohle von Süd-Limburg. Abh. der Senckenbergischen Naturforsch. Gesellschaft. Bd. 38. Heft 3. Frankfurt a.M.

Kräusel, R. (1935): Palaeobot. Notizen. XX. Die Koniferengattung Amentotaxus Pilg. im Tertiär der Wetterau. Senckenbergiana. Bd. 17. Nr. 3/4. Frankfurt a.M.

Kräusel, R. (1949): Die fossilen Koniferen-Hölzer (unter Ausschluss von Araucarioxylon Kraus). II. Teil. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferenhölzer. Palaeontographica. Abt. B. Bd. LXXXIX. Stuttgart.

Kraus, A. (1866): Mikroskopische Untersuchungen über den Bau lebender und vorweltlicher Nadelhölzer. Würzburger Naturwissenschaftliche Zeitschrift. Bd. VI. Würzburg.

Krystofovich, A. (1929): Evolution of the Tertiary Flora of Asia. New Phytologist. Vol. 28. London.

Kubart, B. (1924): Einige Bemerkungen über den diagnostischen Wert des Markkörpers bei Koniferenhölzern. Berichte der Deutschen Botanischen Gesellschaft. Bd. 42. Berlin.

Lesquereux, L. (1878): Contributions to the Fossil Flora of the Western Territories. Part II. Report of the U.S.A. Geological Survey of the Territories. Botany VII. Washington.

Lingelsheim, A. (1908): Über die Braunkohlenhölzer von Saarau. 85. Jahresbericht der Schlesischen Gesellschaft für Vaterländische Cultur. Bd. LXXXV. Abt. II. Naturwissenschaften. Zoolog. Bot. Section. Pag. 24–36. Breslau.

LINNELL, T. (1938): Om tertiära vedrester av Sequoia typ i nordöstra Skånes Kvartärformation. Sveriges Geologiska Undersökning. Ser. C. Nr. 406. Årbok 31. Stockholm.

LOTSY, J. P. (1911): Vorträge über Botanische Stammesgeschichte etc. Bd. III. Cormophyta Siphonogamia I. Jena.

MATHIESEN, F. J. (1965): Palaeobotanical Investigations into some Cormophytic Macrofossils from the Neogene Tertiary Lignites of Central Jutland. Kgl. Danske Videnskabernes Selskab. Biolog. Skrifter. Bd. 17 no. 3. Copenhagen.

MENZEL, P. (1900): Die Gymnospermen der nordböhmischen Braunkohlenformation. Abhandlungen der naturwissenschaftlichen Gesellschaft Isis in Dresden. 1900. Theil I-II.

MENZEL, P. (1913): Beiträge zur Flora der Niederrheinischen Braunkohlenformation. Jahrbuch der Königl. Preussischen geolog. Landesanstalt. 34. Teil 1. Berlin.

PHILLIPS, E. W. J. (1941) The Indentification of Coniferous Woods by their Microscopic structure. Journal of the Linnean Scoiety, Botany. Vol. 52. London.

PIERCE, A. S. (1935): Anatomy of the xylem of Sciadopitys. American Journal of Botany. Vol. 22. Baltimore.

PEIRCE, A. S. (1936): Anatomical interrelationships of the Taxodiaceae. Tropical Woods. No. 46. Yale University. School of Forestry.

PEIRCE, A. S. (1937): Systematic Anatomy of the woods of the Cupressaceae. Tropical Woods. No. 49. Yale University. School of Forestry.

PILGER, R. (1903): Taxaceae. A. Engler: Das Pflanzenreich. IV. 5. Leipzig.

PILGER, R. (1926): Gymnospermae. A. Engler und K. Prantl: Die natürlichen Pflanzenfamilien Bd. 13.

PRILL, W. (1913): Beiträge zur Kenntnis schlesischer Braunkohlenhölzer. II. Teil. Dissertation. Breslau.

RADAIS, M. (1894): Contribution à l'étude de l'anatomie comparée du fruit des conifères. Annales des Sciences Naturelles, Botanique. Sér. 7. Tom. 19. Pag. 165–368. Paris.

REGNÉLL, GERHARD (1940): Et nytt fynd av tertiär ved i Södra Skåne. Kgl. Fysiographiska Sällskapets i Lund Förhandlingar. Bd. 10. Nr. 11. 1939–1940. Pag. 123–127. Lund.

REID, CLEMENT and ELEANOR M. REID (1910): The lignites of Bovey Tracey. Philosophical Transactions of the Royal Society of London. Series B. Vol. 201. London.

ROBERTSON, AGNES (1907): The Taxodieae; a phylogenetic study. New Phytologist. Vol. VI. London.

RUDOLPH, KARL (1935): Microfloristische Untersuchungen tertiärer Ablagerungen im nördlichen Böhmen. Beihefte zum Botanischen Centralblatt. Bd. LIV. Abt. B. Dresden.

SAPORTA, G. DE (1862–73): Études sur les végétaux du Sud-Est de la France à l'époque tertiaire. Annales des Sciences Naturelles. Botanique IV. Sér. Tome XVI. 1862. IV. Sér. Tome XVII. 1862. V. Sér. Tome III. 1865. V. Sér. Tome IV. 1865. V. Sér. Tome IX. V. Sér. 1867. Tome XVII. 1873. Paris. In the V. Sér. Tome III. 1865 are described and figured foliag twigs and cones of *Taxodium* and *Sequoia* from Armissan.

SAXTON, W. T. (1910): Notes on the anatomy of Widdringtonia and Callitris. South African Journal of Science. Pag. 282. Cape Town.

SCHENK, A. (1869): Über einige in der Braunkohle Sachsens vorkommende Pflanzenreste. Botanische Zeitung. 27. Jahrgang. Leipzig.

SCHIMPER, W. PH. (1869–1874): Traité de Paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel. Vol. II. 1870. Conifères. Pag. 227–385. Paris. + Atlas.

SCHIMPER, W. PH. und A. SCHENK (1890): Abt. II. Paläophytologie: K. A. Zittel: Handbuch der Paläontologie. München und Leipzig.

SCHNARF, K. (1937): Anatomie der Gymnospermen-Samen. K. Linsbauer: Handbuch der Pflanzenanatomie. II. Abt. Bd. X. 1. Berlin.

Schröter, C. (1880): Untersuchung über fossile Hölzer aus der arctischen Zone. (O. Heer: Flora fossilis arctica VI. 1 and 2. Zürich 1880). Dissertation.

Schwartz, O. and Heinz Weide (1962): Systematische Revision der Gattung Sequoia. Feddes Repertorium. Vol. 66. Berlin.

Schönfeld, G. (1955): Metasequoia in der westdeutschen Braunkohle. Senckenbergiana. Bd. 36. Heft 5–6. Pag. 389–399. Frankfurt a.M.

Seward, A. C. (1919): Fossil Plants, Vol. IV. Ginkgoales, Coniferales, Gnetales. Cambridge.

Shaw, W. R. (1896): Contribution to the life-history of Sequoia sempervirens. Botanical Gazette. Vol. XXI. Chicago.

Slyper, E. J. (1933): Bestimmungstabelle für rezente und fossile Coniferenhölzer nach mikroskopischen Merkmalen nach Angaben in der Litteratur zusammengestellt. Recuil des Travaux Botanique Néerlandais. Vol. XXX. Amsterdam.

Staub, M. (1887): Die Aquitanische Flora des Zsilthales im Comitate Hunyad. Mittheilungen aus dem Jahrbuch der Königl. ungarischen geolog. Anstalt. Bd. VII. Heft 6. Budapest.

Steinböck, H. (1926): Über den anatomischen Bau des Markkörpers einiger Coniferen. Österreichische Botanische Zeitschrift. Bd. 75. 1926. Wien.

Sternberg, K. von (1821–1838): Versuch einer geognostisch-botanischen Flora der Vorwelt. I–VI. Leipzig und Praha.

Stockmans, F. et Y. Willière (1934, 1936): Notes sur des bois fossiles récoltées en Belgique. I, II. Bulletin de Musée royale d'Histoire naturelle de Belgique. Tome X. Nr. 11 et 30. Bruxelles.

Takamatsu, M. (1929): Fossile Koniferenhölzer aus Sendai-Tertiär. I. Science Reports Tohoku Imperial University, 4th Series (Biology). 55. p. 333–342. Tokyo.

Thiergart, F. (1940): Die Sciadopityszone und der Sciadopitys. Braunkohle. Jahrg. V. Nr. 153. Düsseldorf.

Unger, Fr. (1847): Chloris protogæa. Beiträge zur Flora der Vorwelt. Leipzig.

Unger, Fr. (1861–1866): Sylloge Plantarum fossilium. Sammlung fossiler Pflanzen, besonders aus der Tertiär-Formation. Pugillus primus, secundus et tertius. Denkschriften der Kaiserl. Akademie der Wissenschaften. Mathem.-Naturwiss. Classe. Bd. XIX (1861). Bd. XXII (1864). Bd. XXV (1866). Wien.

Vaupell, Chr. (1853): En botanisk Undersøgelse af det fossile Træ, der findes i Leer- og Sandlagene i Danmark og af Havet opkastes med Ravet paa de Danske Kyster. Manuscript and Plates in the Library of the Bot. Museum. Copenhagen. Text published by N. Hartz in the Meddelelser fra Dansk geologisk Forening. Nr. 12. Pag. 43–64 1906.

Velenovsky, J. (1881): Die Flora aus den ausgebrannten tertiären Letten von Vršovic bei Laun. Abhandlungen der Königl. Böhmischen Gesellschaft der Wissenschaften. VI. Folge 11. Band. Mathem.-Naturwiss. Classe nr. 1. Praha.

Weyland, H. (1937): Beiträge zur' rheinischen Tertiärflora, II. Palaeontographica Abl. B. Bd. LXXX. Abl. 13. Stuttgart.

Walton, J. (1927): On some fossil woods of Mesozoic and Tertiary age from the Arctic zone. Annals of Botany. Vol. 41. London.

Wieler, A. (1940): Die Bedeutung der Innenhaut für die Zelle und die Structur der secundären Verdickungsschichten. Protoplasma. Bd. 34. Wien.

Witusek, N. (1941): Über fossile Hölzer aus dem Egerer Tertiärbecken mit vergl. Untersuchung zur Erkenntnis der Hölzer lebender Taxodiueen. Lotos. Bd. 87. (1939–40).

Yasui, K. (1917): A fossil wood of Sequoia from the Tertiary of Japan. Annals of Botany. Vol. 31. Pag. 101–104. London.

Zalewska, Zofia (1953): Tertiary remains of fossil wood from Turów on the Lusatian Neisse. Pt. I. Acta Geologica Polonica. Vol. III. Nr. 4. Pag. 481–543. Warszawa.

ZALEWSKA, ZOFIA (1955): Tertiary remains of fossil wood from Turów on the Lusatian Neisse. Pt. II. Acta Geologica Polonica. Vol. V. Nr. 2. Pag. 277–304. Warszawa.

ZALEWSKA, ZOFIA (1959): The fossil Flora of Turów near Bogatynia (II) 1. Coniferae, Taxodiaceae. Warszawa. Museum Ziemi Publications.

ZALEWSKA, ZOFIA (1960): Coniferae. Taxaceae, Podocarpaceae, Pinaceae, Taxodiaceae, Cupressaceae. The fossil Flora of Turów near Bogatynia. II. Pt. 2. Pag. 19–49 and 93–102. Systematic description of plant remains. Warszawa. Museum Ziemi Publications.

ØDUM, H. og WERNER CHRISTENSEN (1936): Danske Grundvandstyper og deres geologiske Optræden. Danmarks Geologiske Undersøgelse. III Række. Nr. 20. København.

Indleveret til Selskabet den 4. november 1969.
Færdig fra trykkeriet den 30. oktober 1970.

CORRIGENDA

Plate II. radial sections. Read: longitudinal sections.
Plate V. *Pinus palaeostrobusoo.* Heer. Read: *Pinus palaeostrobus.* O. Heer.
Plate IX. (A and B × 40, C and D × 175). Read: (A and D × 40, B × 60 and C × 175).
Plate XI. langential. Read: tangential.
Plate XII. langential. Read: tangential.
Plate XIX. thisk. Read: thick.

PLATES

PLATE I

Taxoxylon amentotaxoides n.sp. A and C, transverse sections. B, tangential section. (A ×40, B and C ×175). Salten.

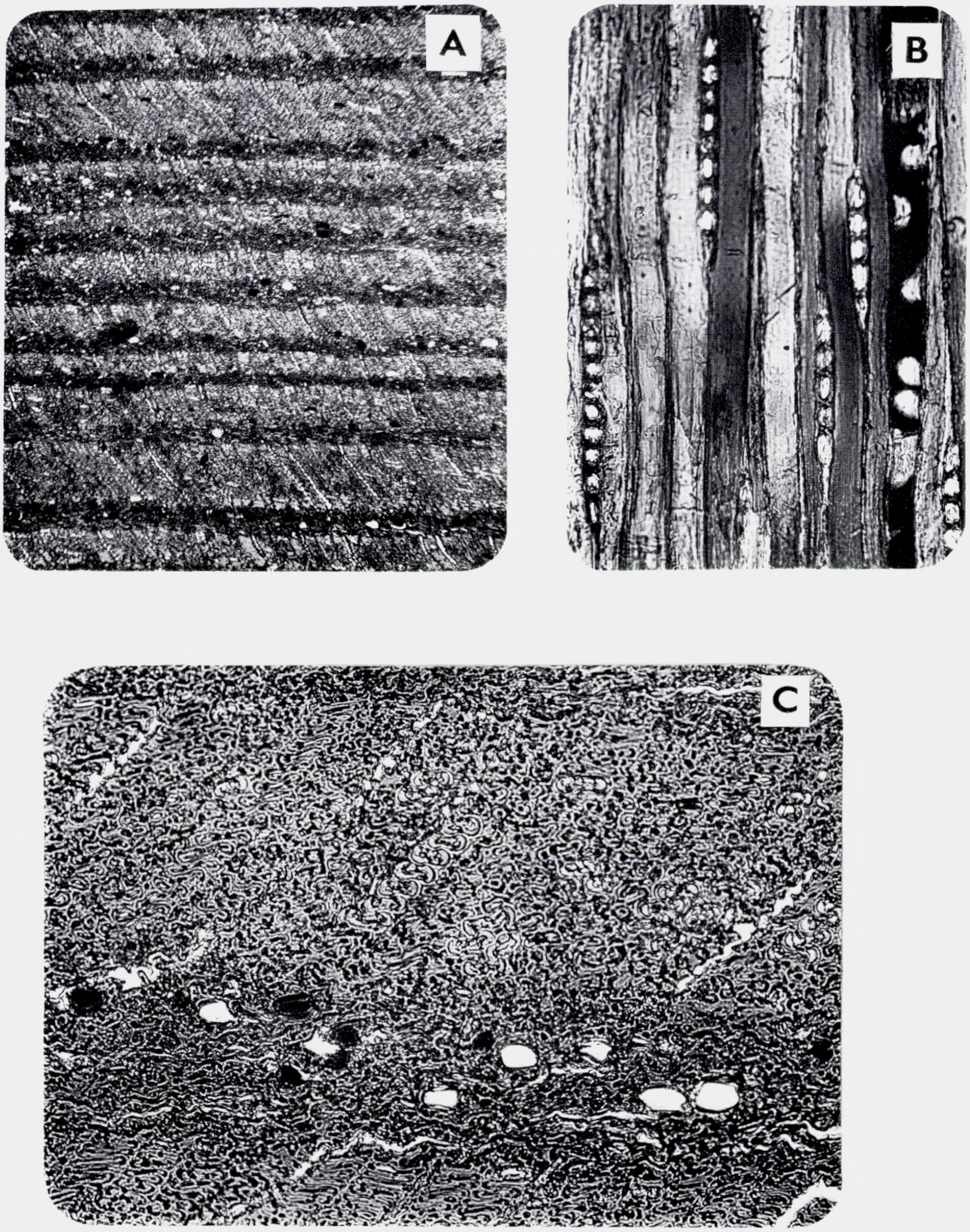

A
B
C

PLATE II

Taxoxylon amentotaxoides n.sp. A and B, radial sections showing the spiral thickenings of the tracheidal wall. (×175). Salten.

Pl. II

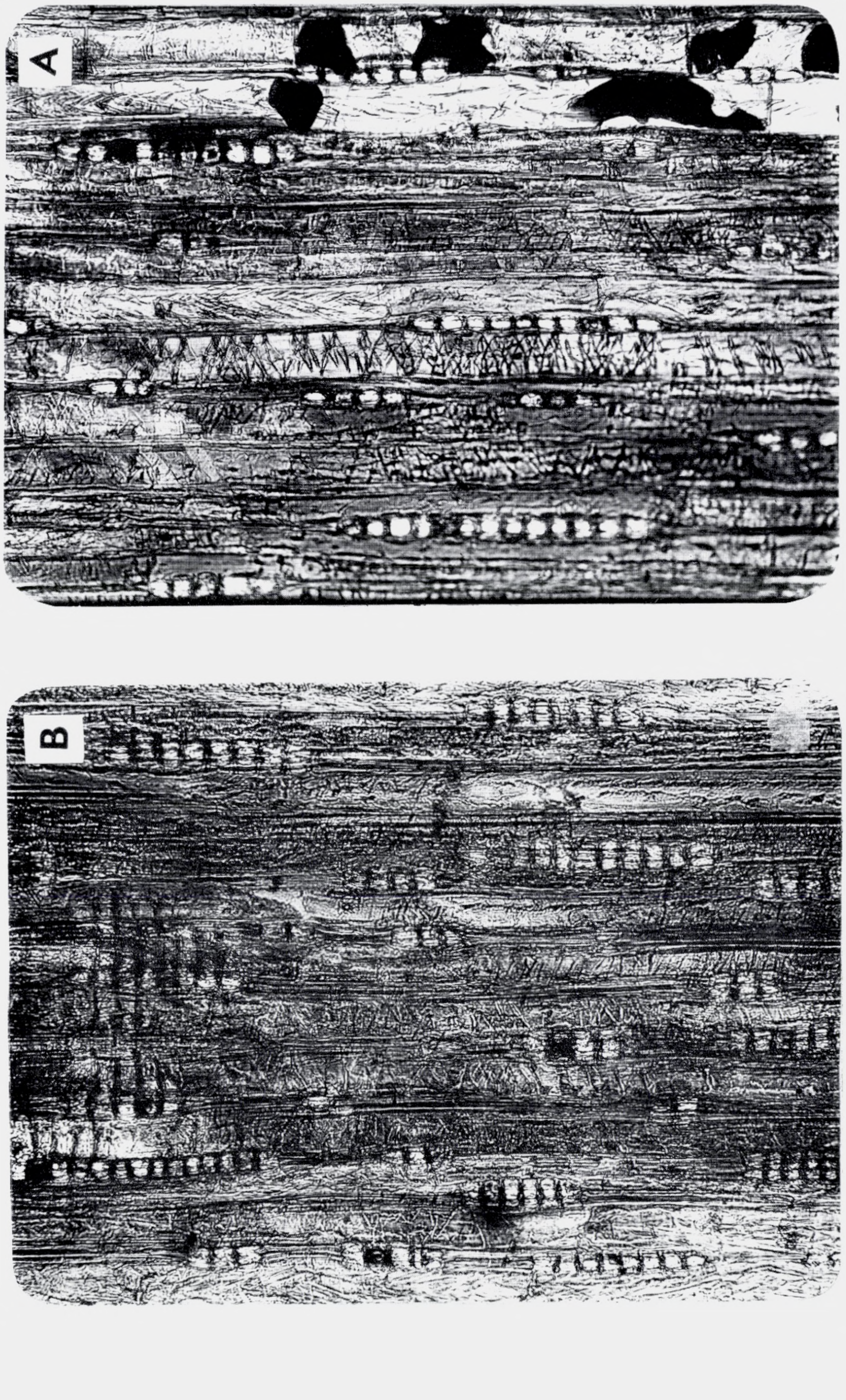


PLATE III

Saxegothaeoxylon miocenicum n. sp. A and B, transverse sections. (A ×40, B ×175). Torvig State Quarry.

Pl. III

PLATE IV

Saxegothaeoxylon miocenicum n.sp. A. transverse section. B, D and E, longitudinal sections of tracheides in various stages of deformation and dissolution of the thickening layers of the wall. C, part of a radial section which shows the cross-field pitting and the pits of the horizontal walls of the ray cells. (×175). Torvig State Quarry.

Pl. IV

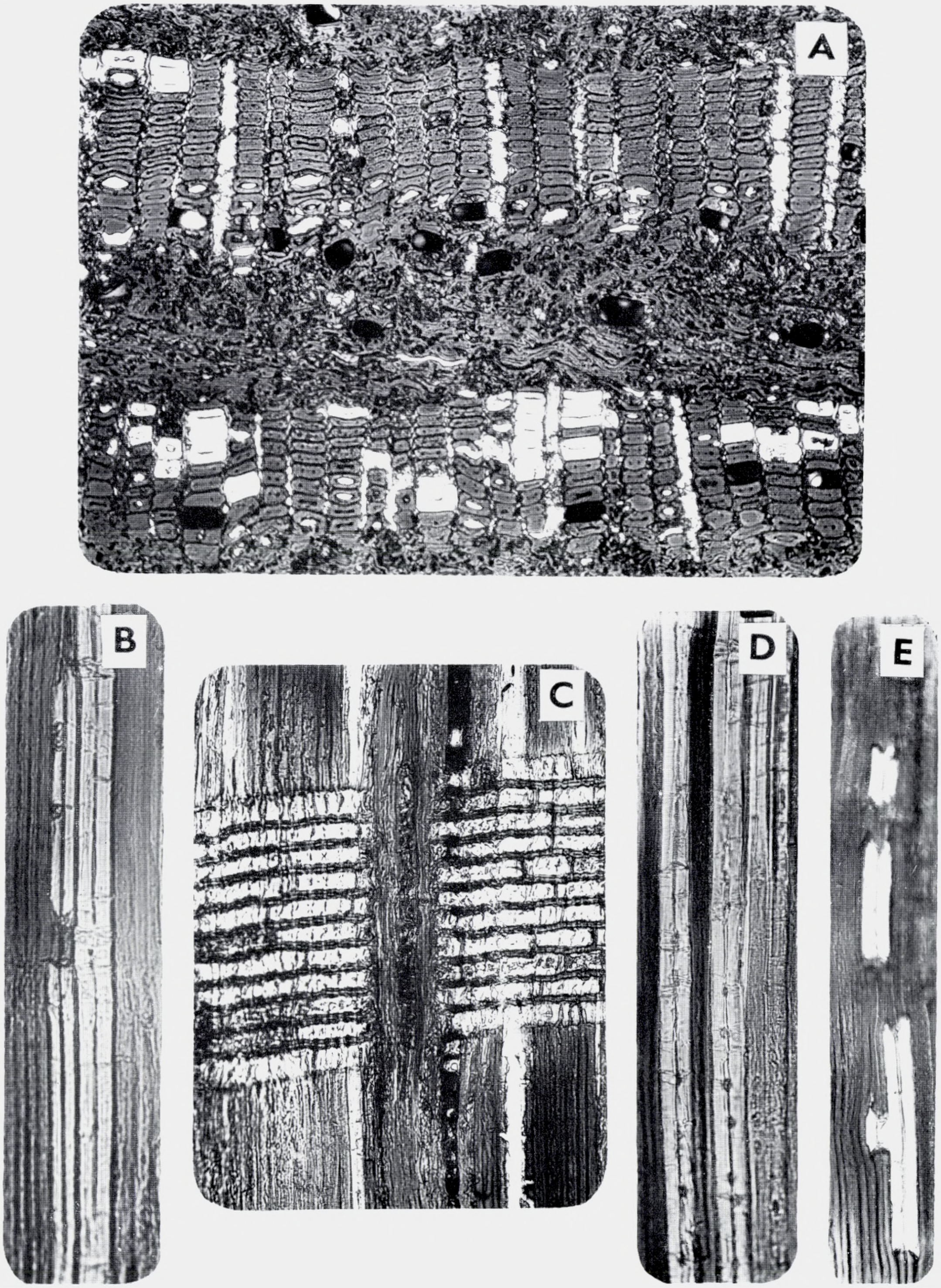


PLATE V

Pinuxylon sp. cf. *P. paxii* R. Kräusel. A, transverse section. B, tangential and C, radial sections. (×175). Torvig State Quarry.

Pinus palaeostrobusoo. Heer. D, a dwarf shoot which has carried five needles (×3). Fasterholt.

Pl. V

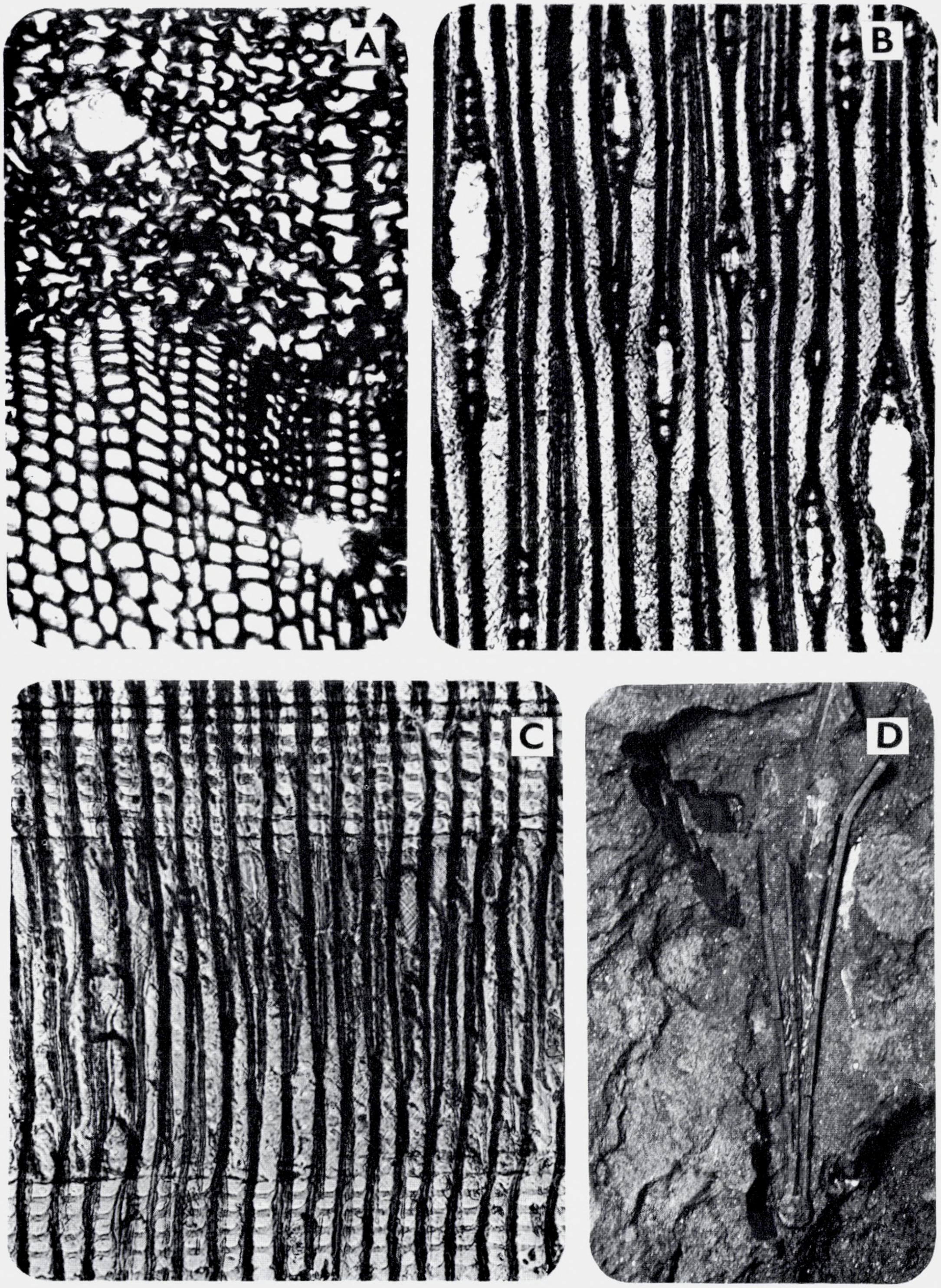


PLATE VI

Sciadopityoxylon wettsteinii. K. A. Jurasky. A, transverse section. B, radial and C, tangential sections. (A ×40, B and C ×175). Lystrupsminde.

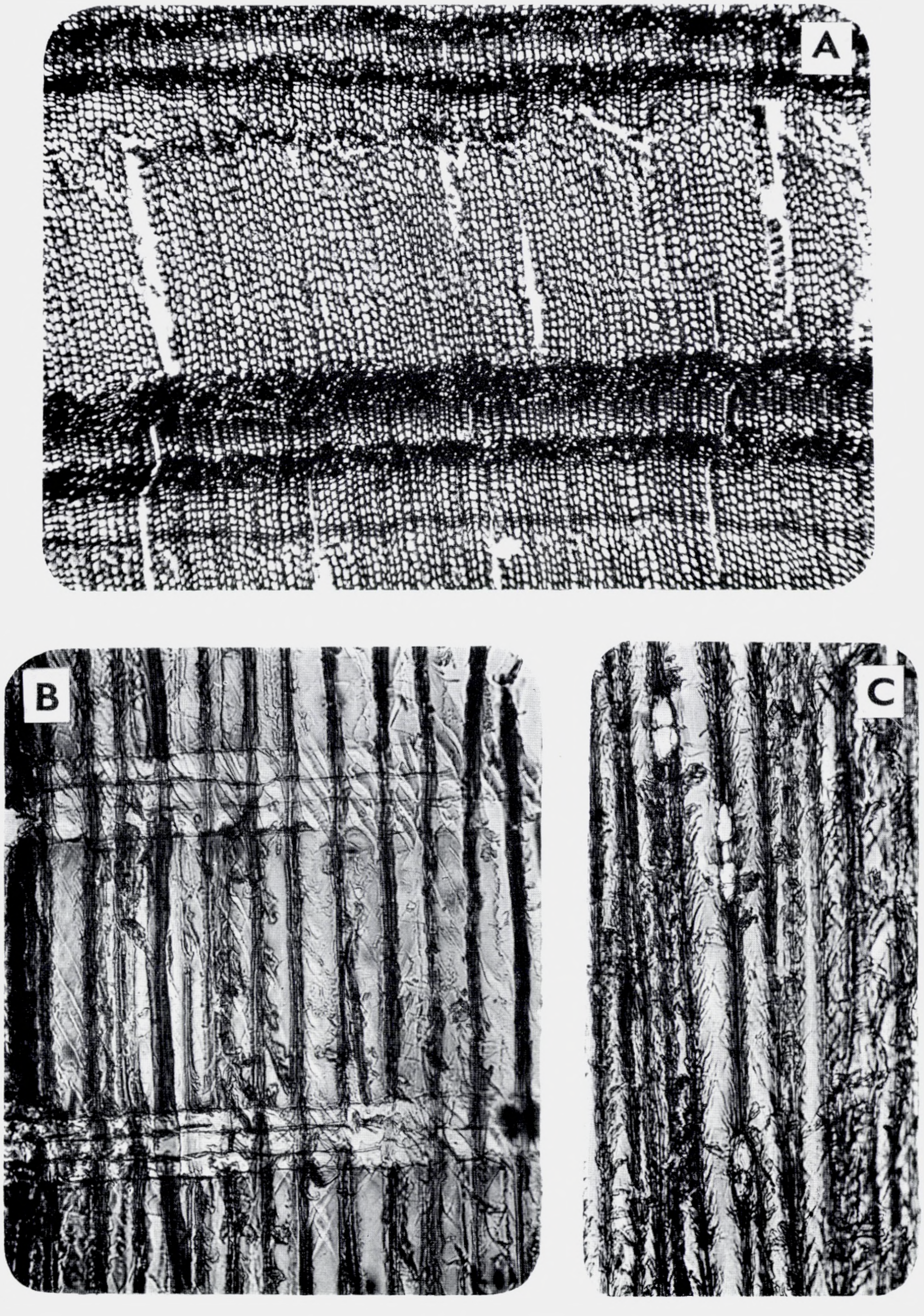

A
B
C

PLATE VII

Sequoia couttsiae. O. Heer. A, bunch of foliage twigs, two terminated by cones. B–D, cones, C, highly compressed. E–G, seeds (A–G × 3). Moselund.

Glyptostrobus europaeus. H and I, seeds (× 3). Moselund.

Pl. VII

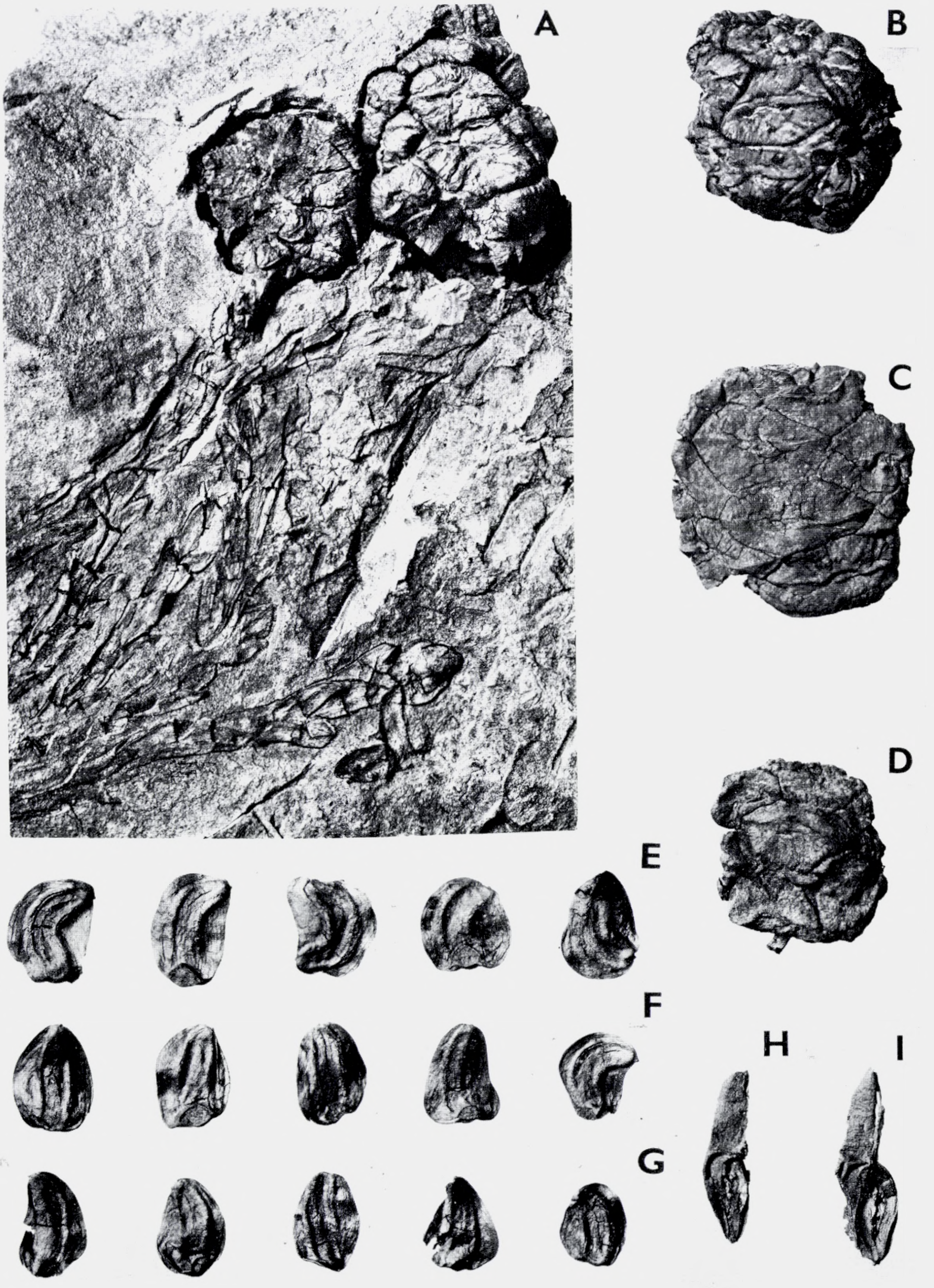


PLATE VIII

Sequoioxylon canadense (C. Schröter) nov. comb. A, transverse section. B, tangential section. C and D, radial sections. (×175). Torvig State Quarry.

Pl. VIII

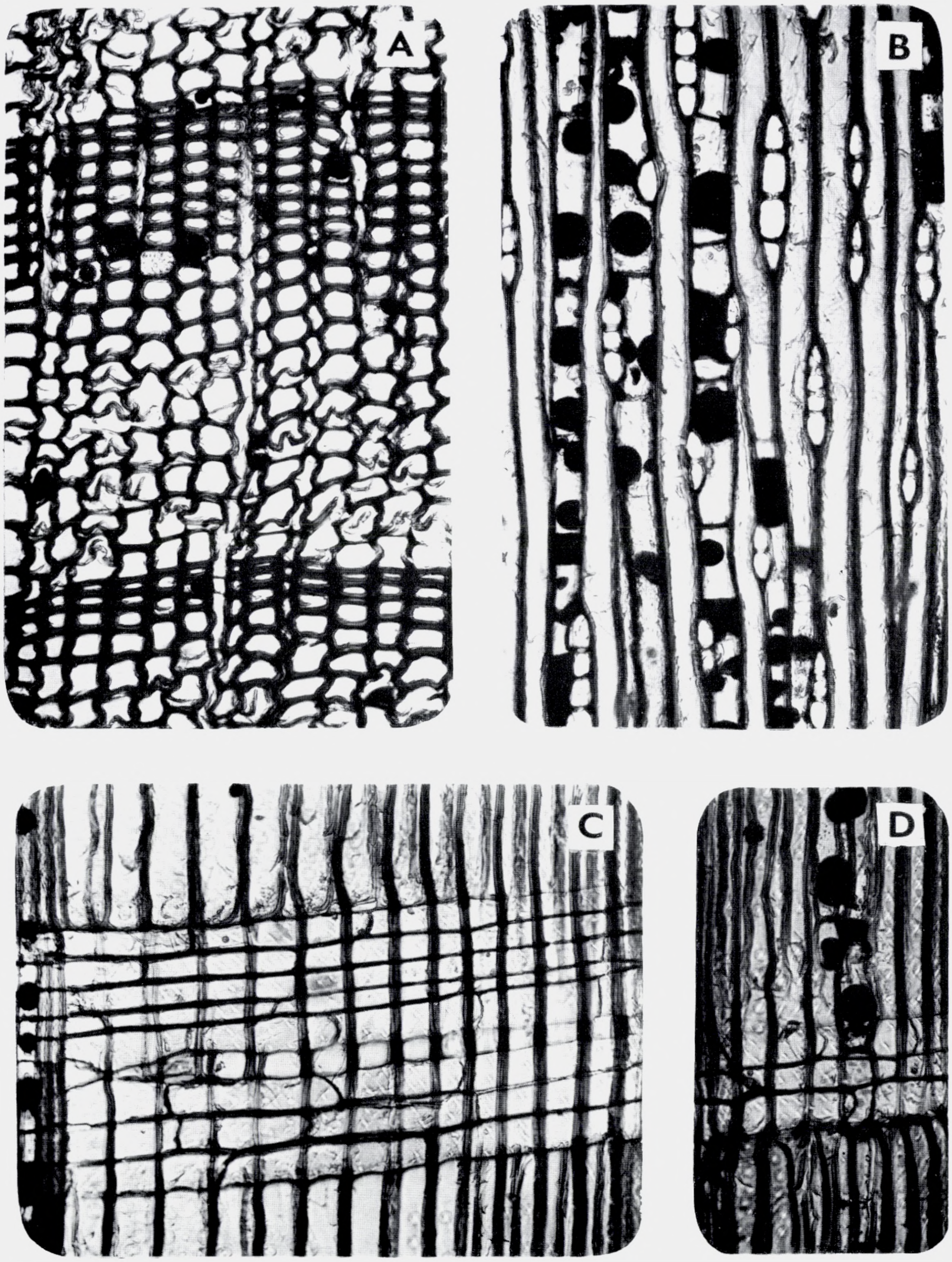


PLATE IX.

Sequoioxylon canadense (C. Schröter) nov. comb. Anomalously developed wood. A, transverse section. B and C, radial sections. D, tangential section. (A and B × 40, C and D × 175). Torvig State Quarry.

Pl. IX

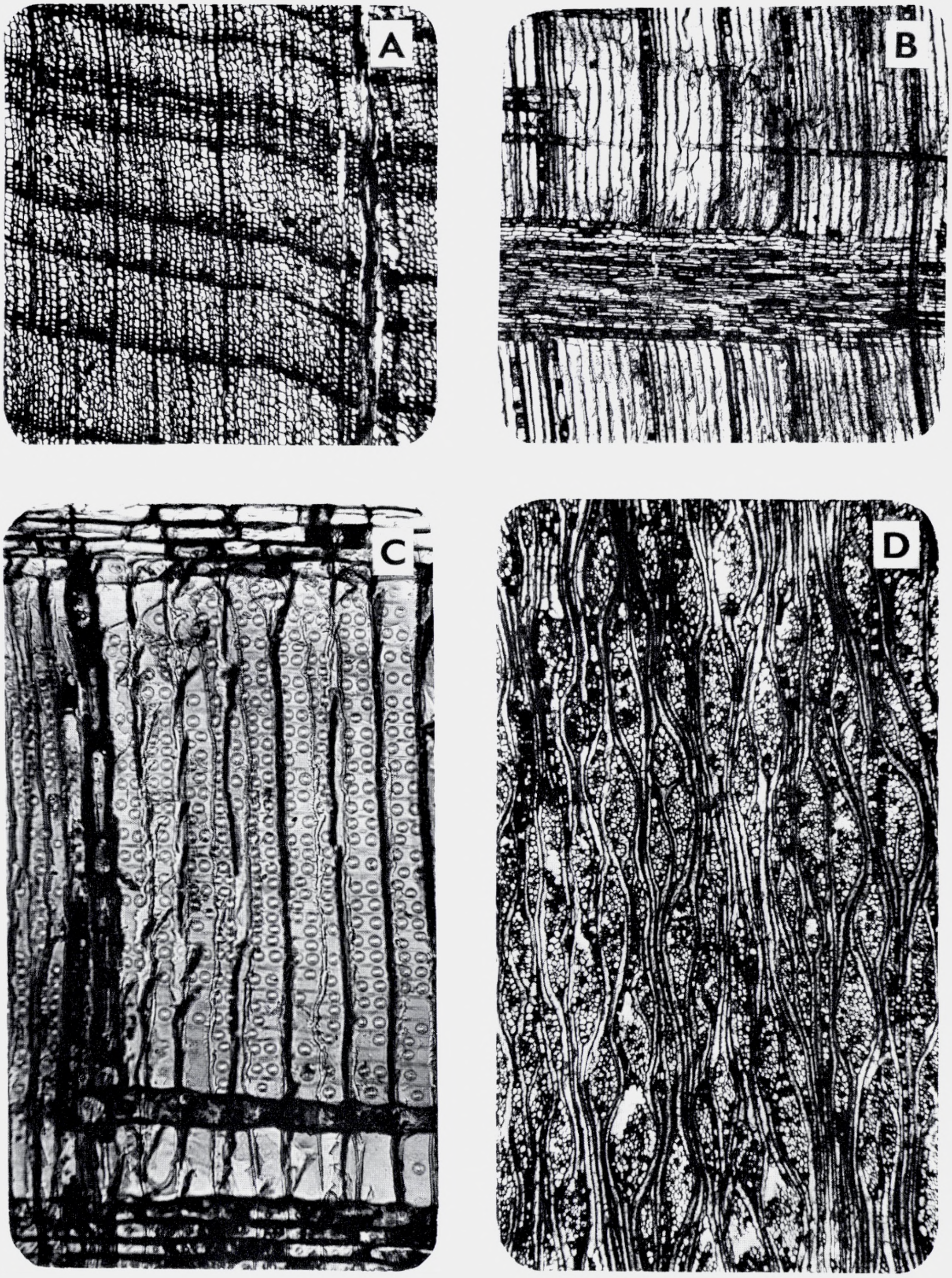


PLATE X

Sequoia langsdorffii. (A. T. Brongniart) O. Heer. A–F, deciduous foliage twigs. G–K cones in transverse and longitudinal planes. (×2). Moselund.

Pl. X

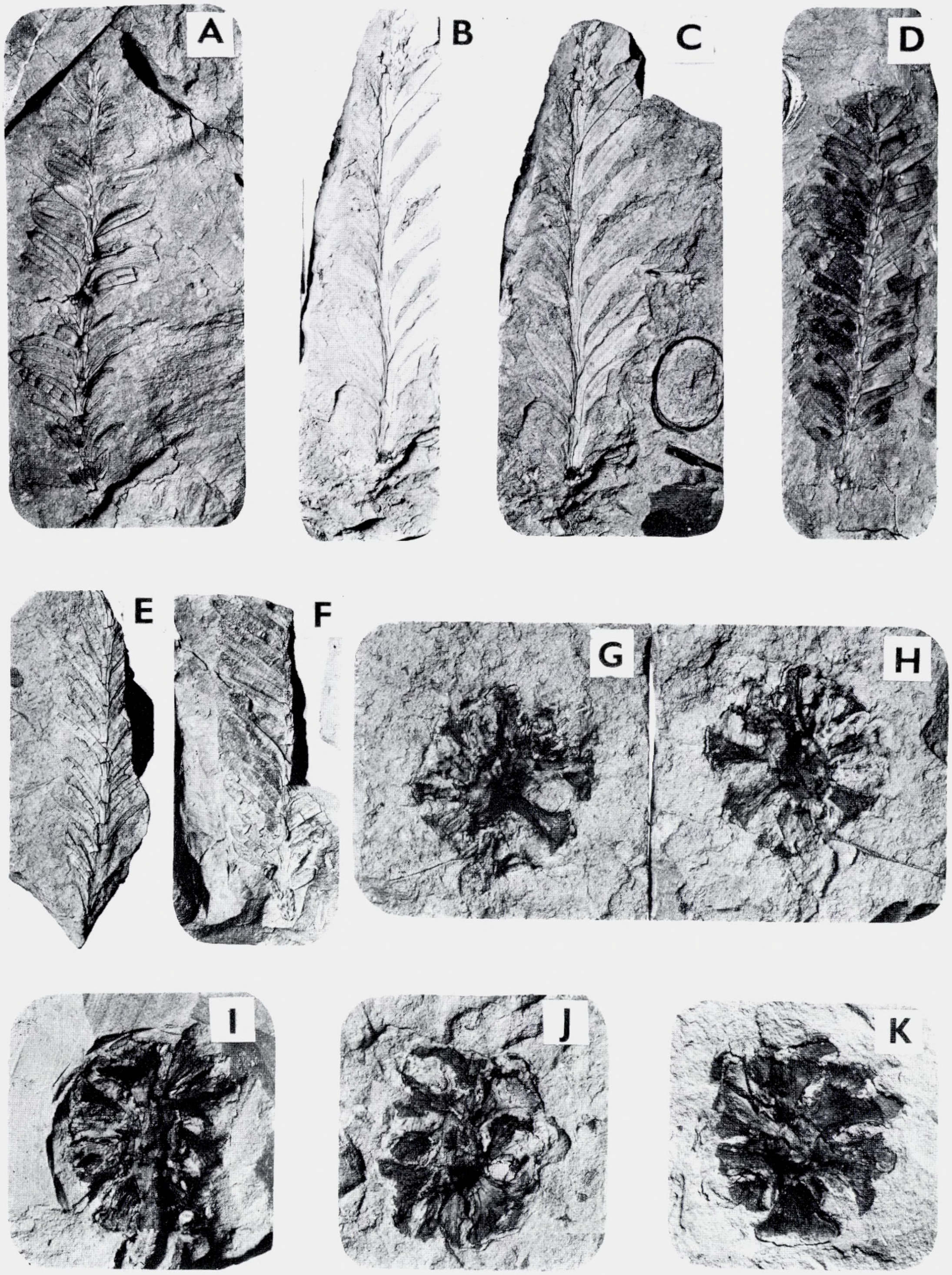


PLATE XI

Taxodioxylon gypsaceum (N. R. Göppert) R. Kräusel. A, transverse and B, langential sections. C and D, radial sections. (×175). Troldhede State Quarry.

Pl. XI

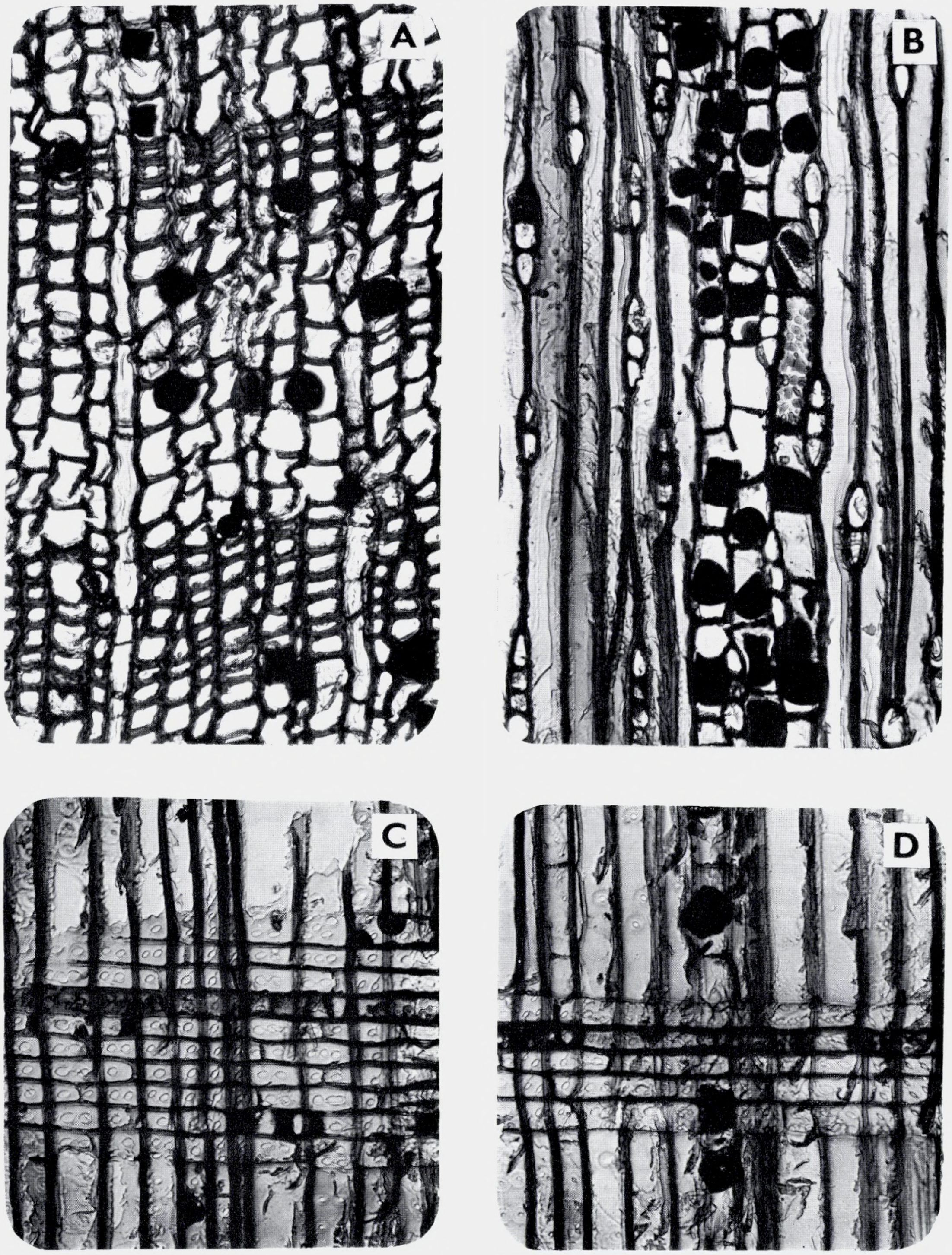


Plate XII

Taxodioxylon gypsaceum (N. R. Göppert) R. Kräusel. A, langential section. B and C, radial sections. (B ×80, A and C, ×175). Troldhede State Quarry.

Pl. XII

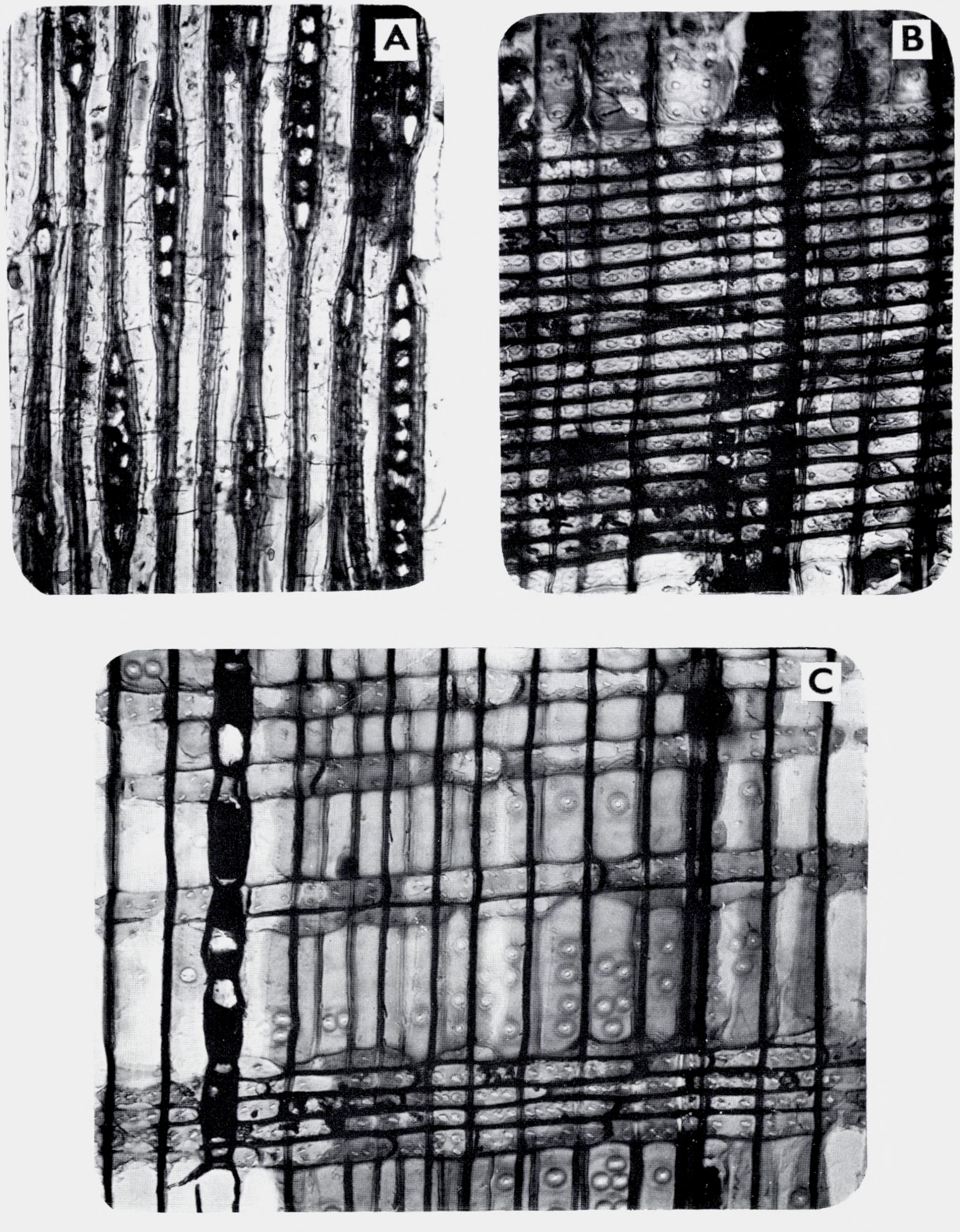


PLATE XIII

Taxodioxylon gypsaceum (N. R. Göppert). R. Kräusel. A–C, tangential sections. D, radial section. (A ×40, B–D ×175). Troldhede State Quarry.

Pl. XIII

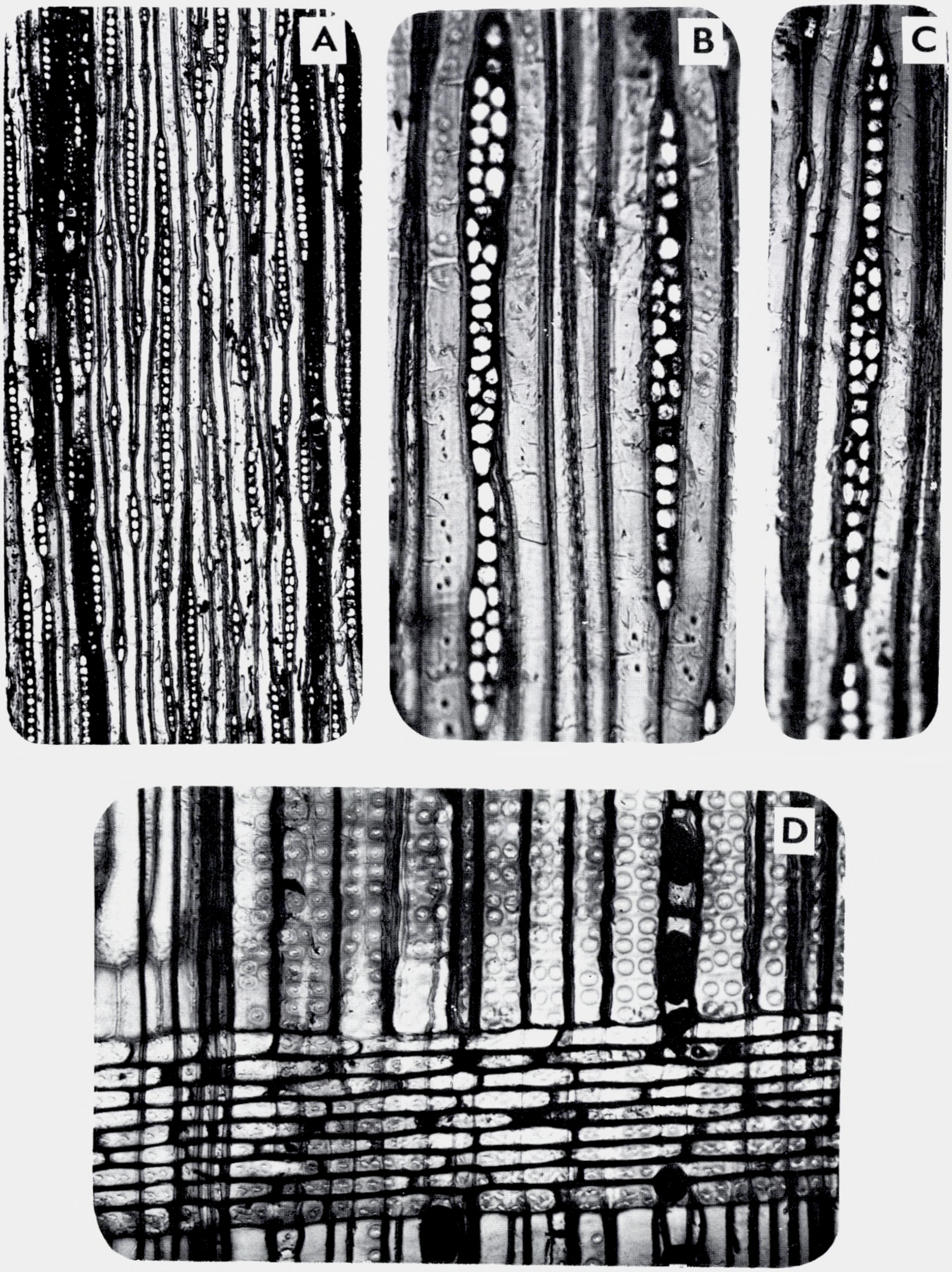


PLATE XIV

Taxodium dubium. (K. v. Sternberg 1838). O. Heer 1855. Deciduous foliage twigs. (×2). Moselund.

Pl. XIV

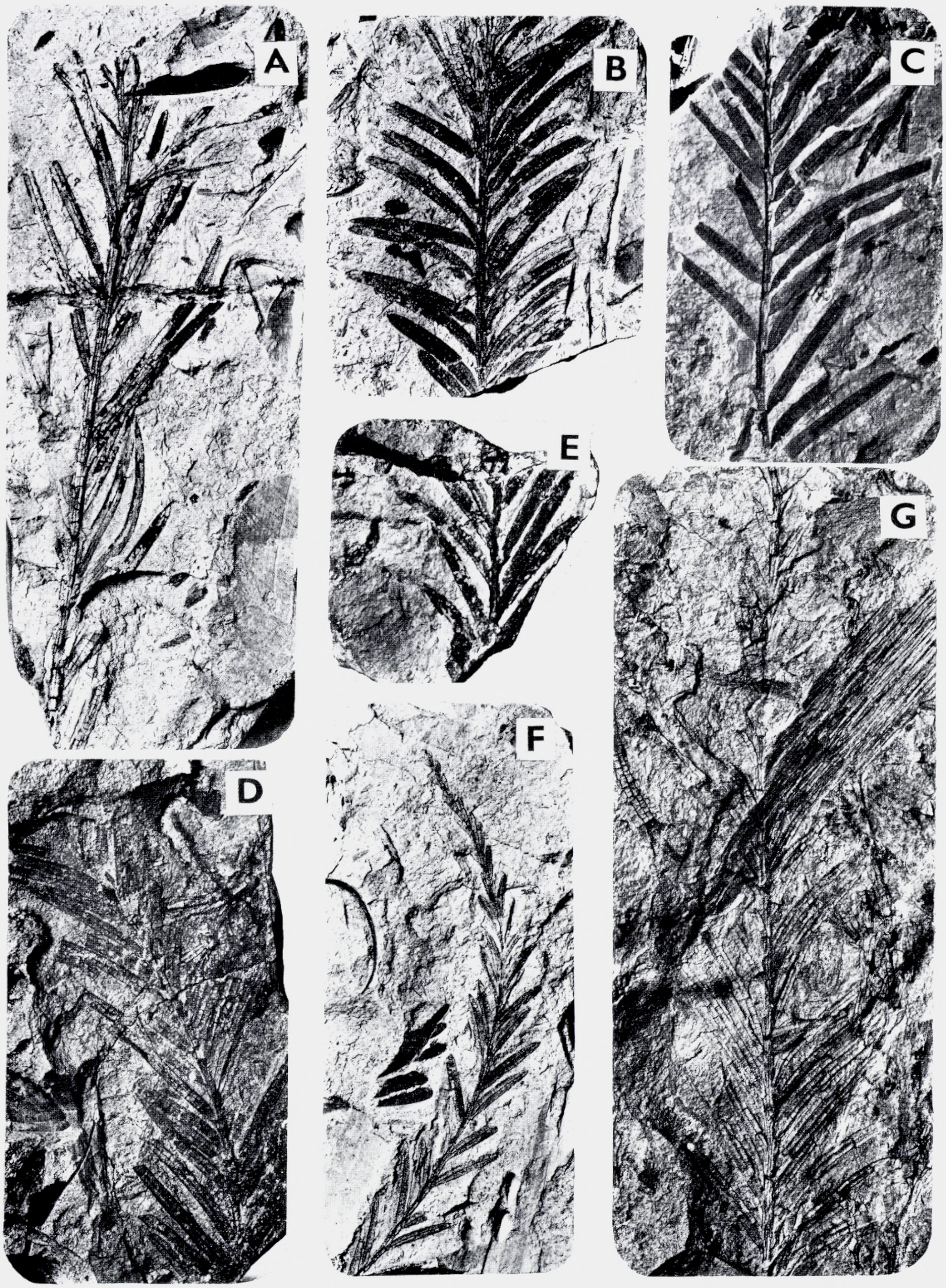


PLATE XV

Taxodium dubium (K. v. Sternberg). O. Heer. A, cone scales. B–J, seeds. (A ×2, B–J ×4). Silkeborg Vesterskov.
K, *Glyptostrobus europaeus* O. Heer. Foliage twigs carrying cones (×2). Fasterholt.

Pl. XV

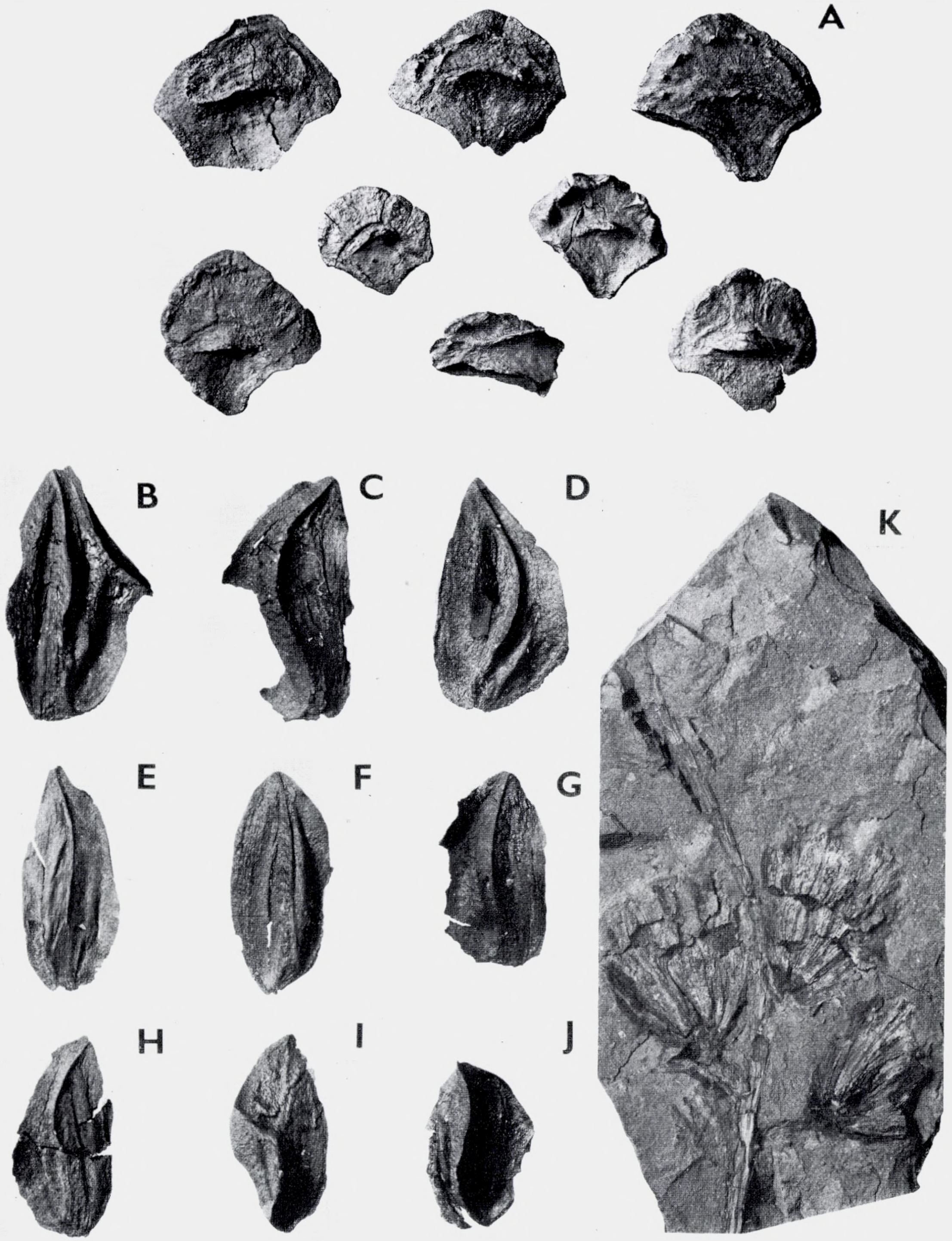


Plate XVI

Taxodioxylon taxodii W. Gothan. Wood of the stem type. A, transverse section. B and D, tangential sections. C, radial section. (A and D ×40, B and C ×175). Troldhede State Quarry.

Pl. XVI

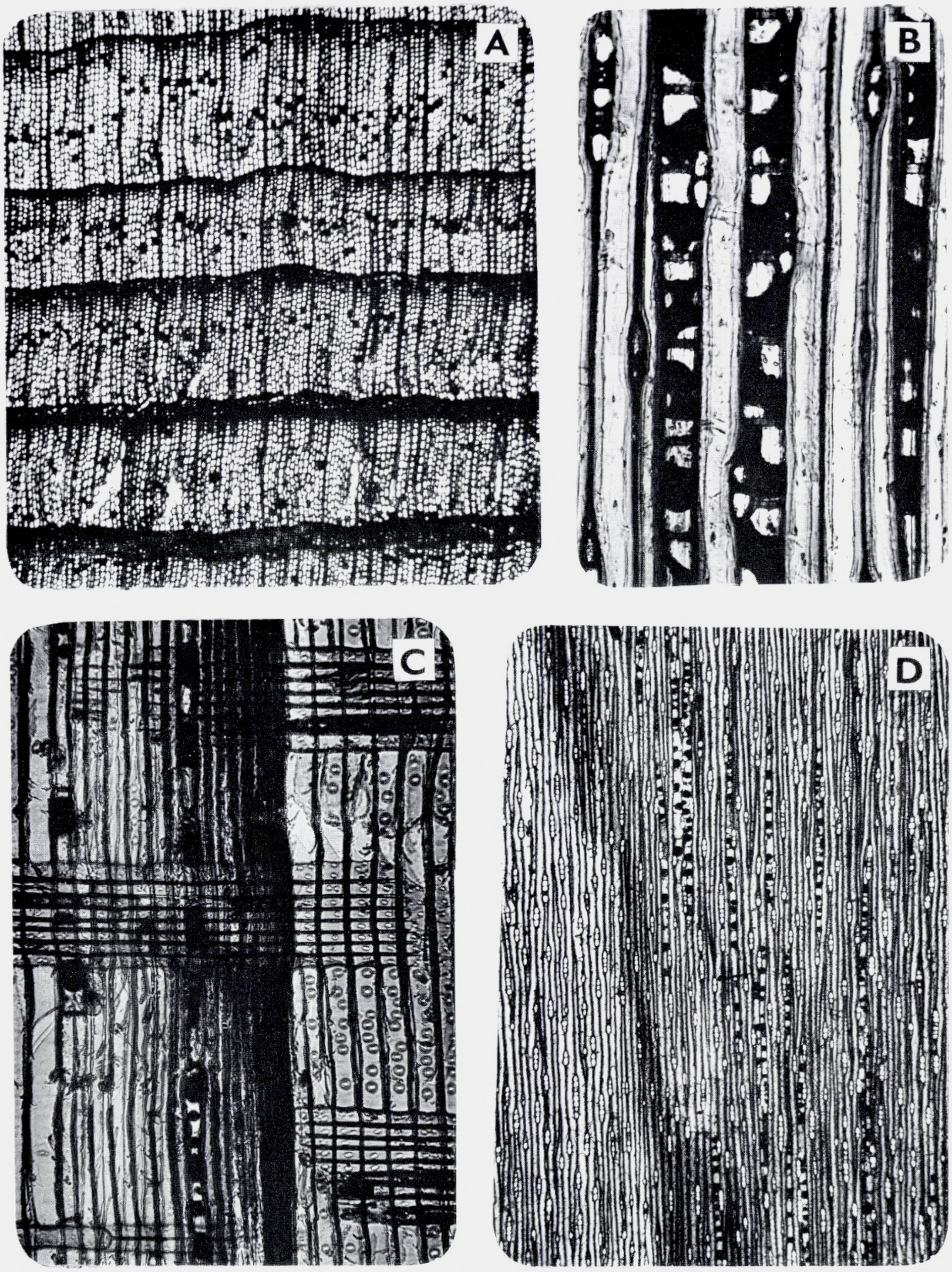


PLATE XVII

Taxodioxylon taxodii W. Gothan. Wood of the root type. A, transverse section. B, tangential section. (A and B ×40). C, radial and D, tangential sections (×175). In C the slide is focused so as to show the schulpturing on the tangential ray cell walls. Troldhede State Quarry.

Pl. XVII

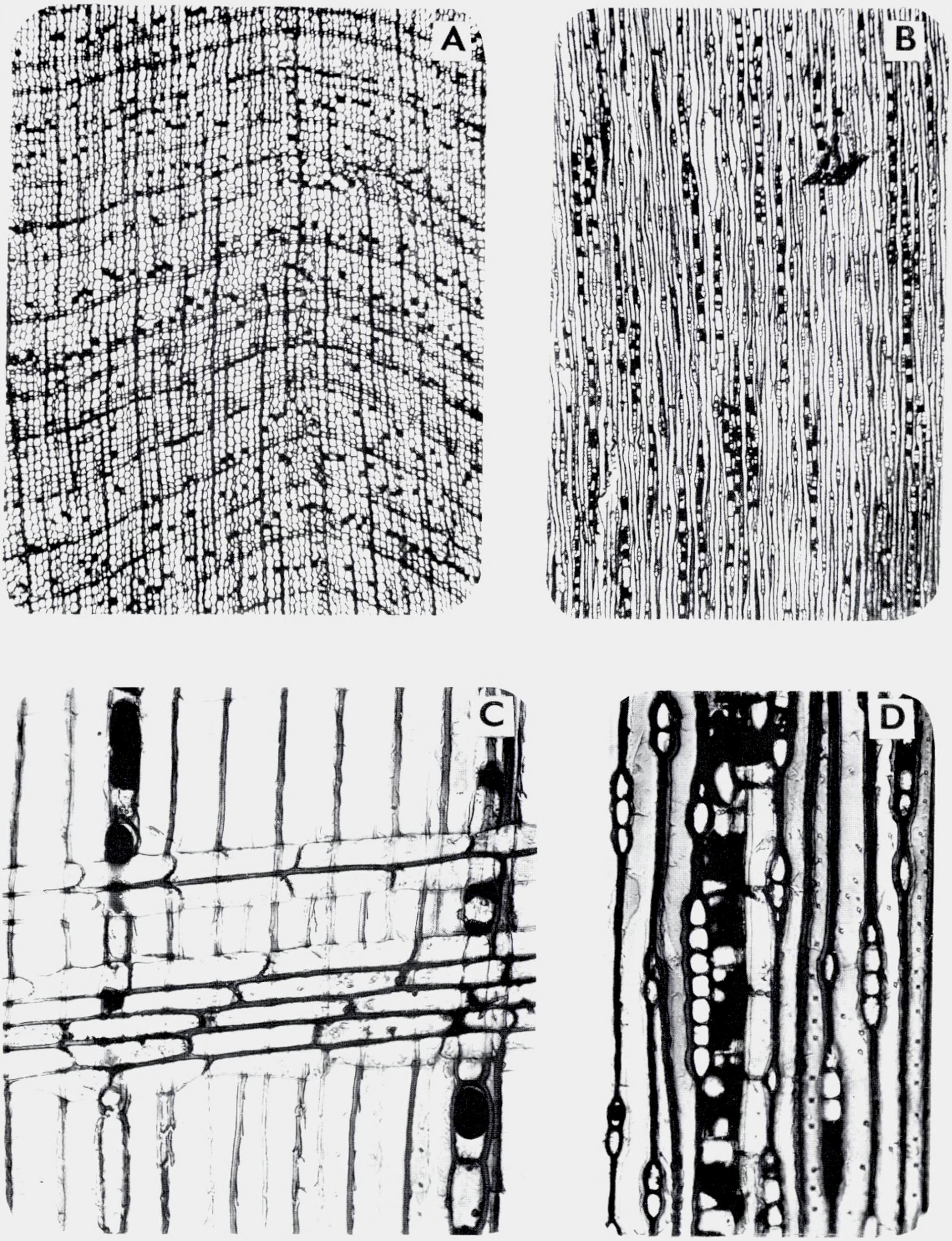


PLATE XVIII

Taxodioxylon taxodii W. Gothan. Wood of the compressed type. A, transverse section. B, tangential and C, radial sections (A ×40, B and C ×175). Troldhede State Quarry.

Pl. XVIII

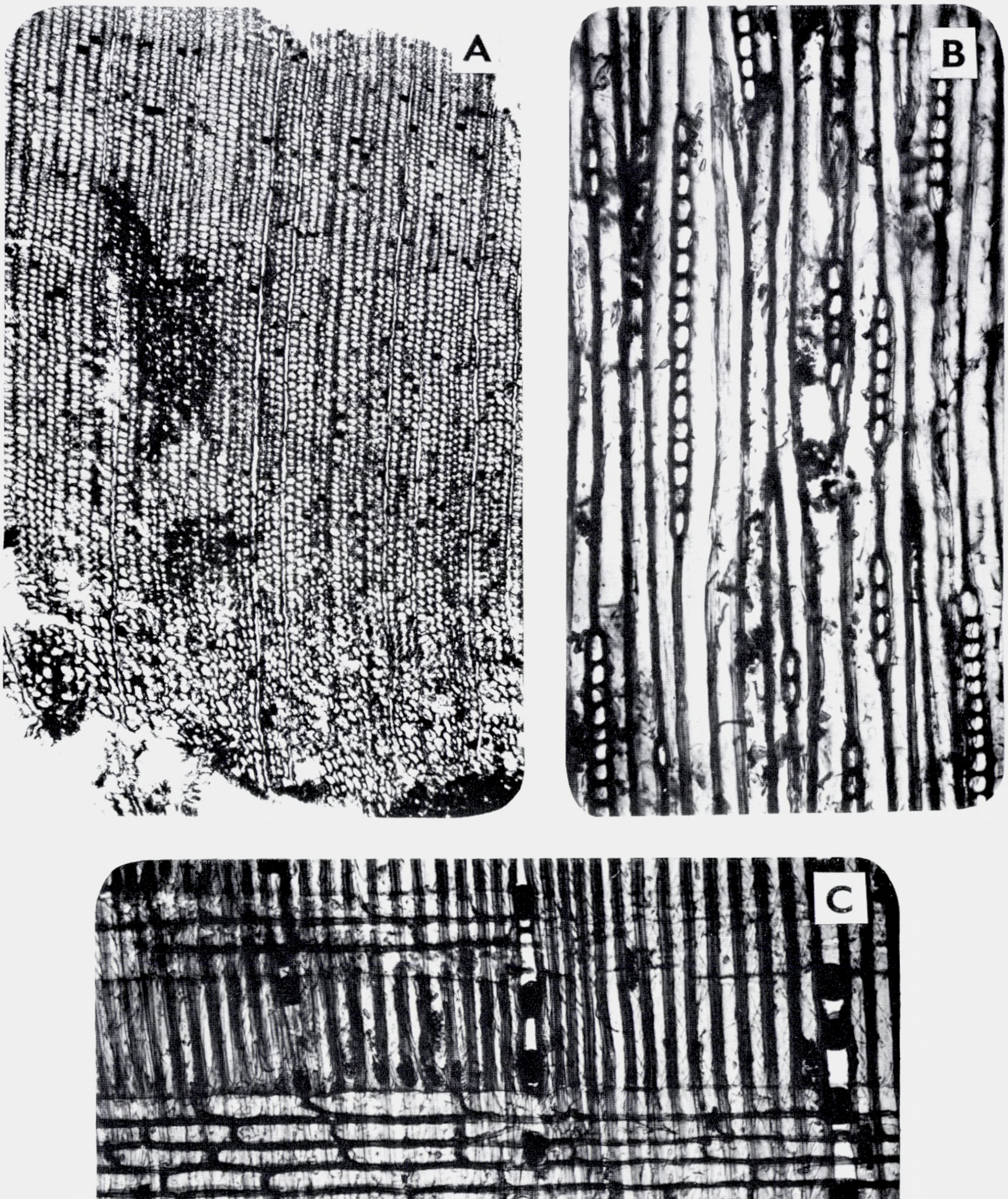


PLATE XIX

Glyptostrobus pensilis (A. B. Lambert). A, transverse and C, radial section of medulla. (×135).
Taxodium distichum (L.) L.-C. Marie Richard. B, transverse and D, radial section of medulla. (×135). From twigs about 5 mm thisk.

PL. XIX

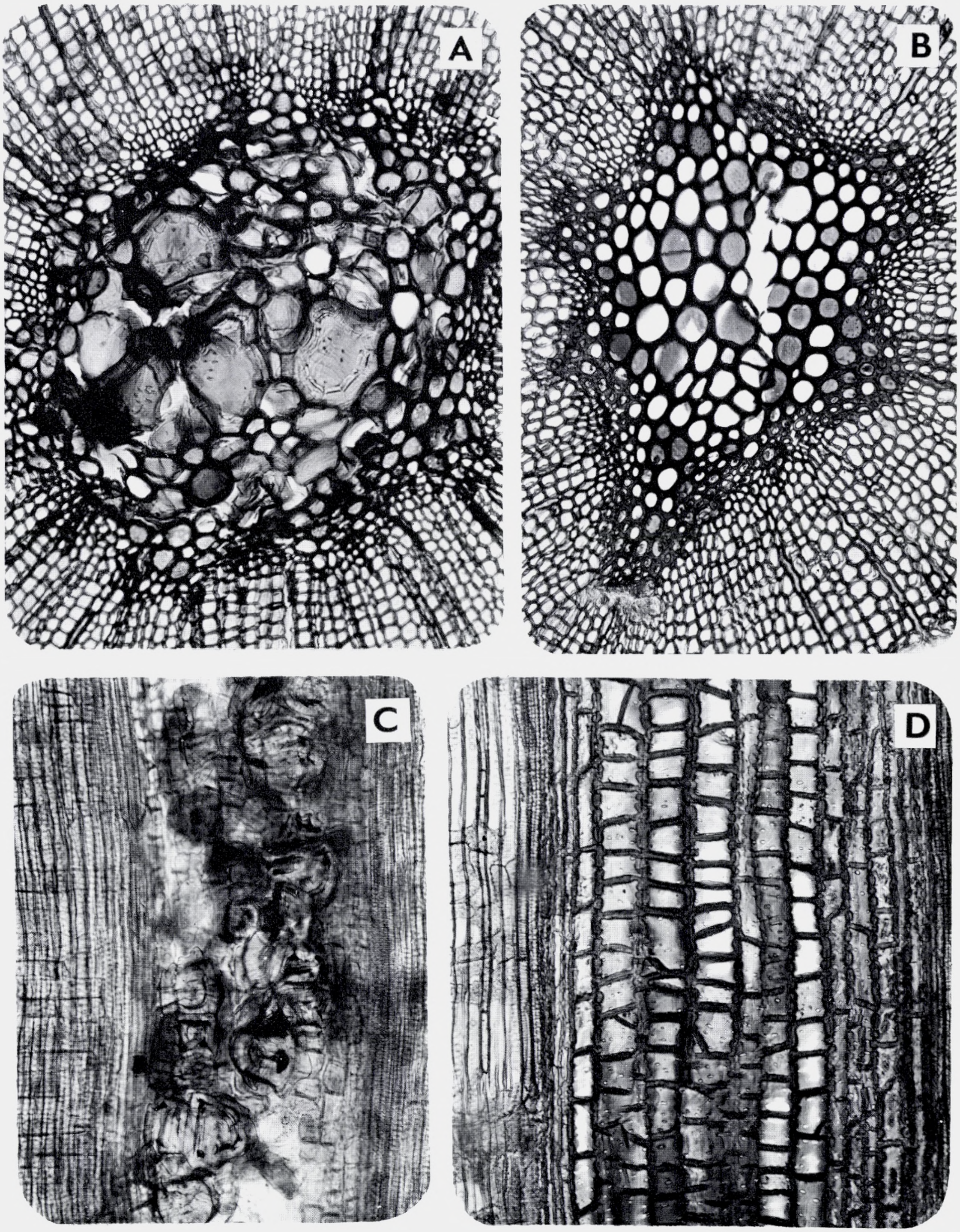


PLATE XX

Taxodium distichum (L.) L.-C. Marie Richard. A, transverse and B, radial section of medulla from a trunk about 60 cm thick. (×135).

Taxodium mucronatum M. Tenore. C, transverse and D, radial section of medulla from a twig about 5 mm thick. (× 135).

Pl. XX

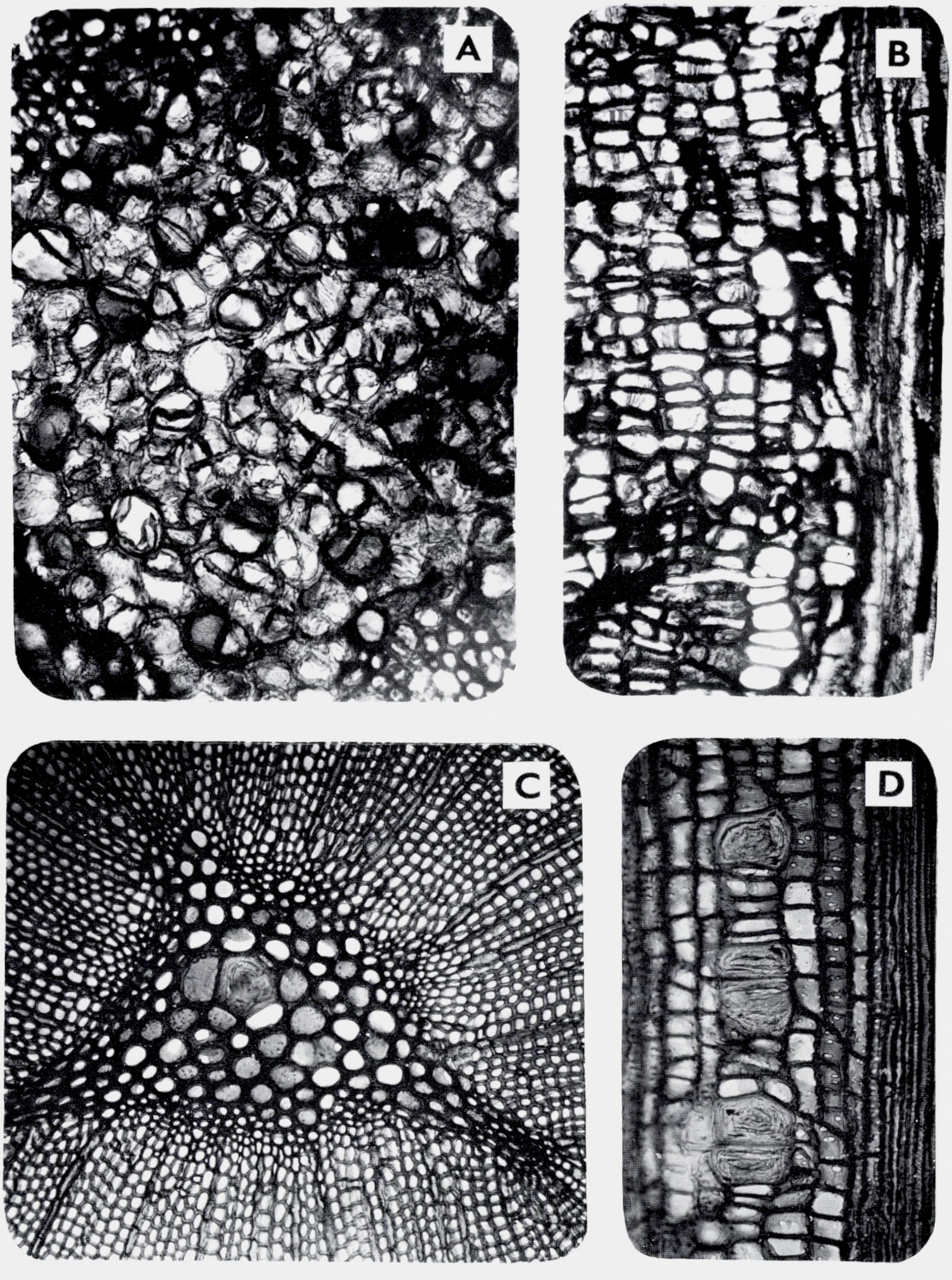


Plate XXI

Glyptostroboxylon tenerum (G. Kraus) N. Conwentz. A, transverse section. (× 40). B and C, radial sections. (×175). Troldhede.

Pl. XXI

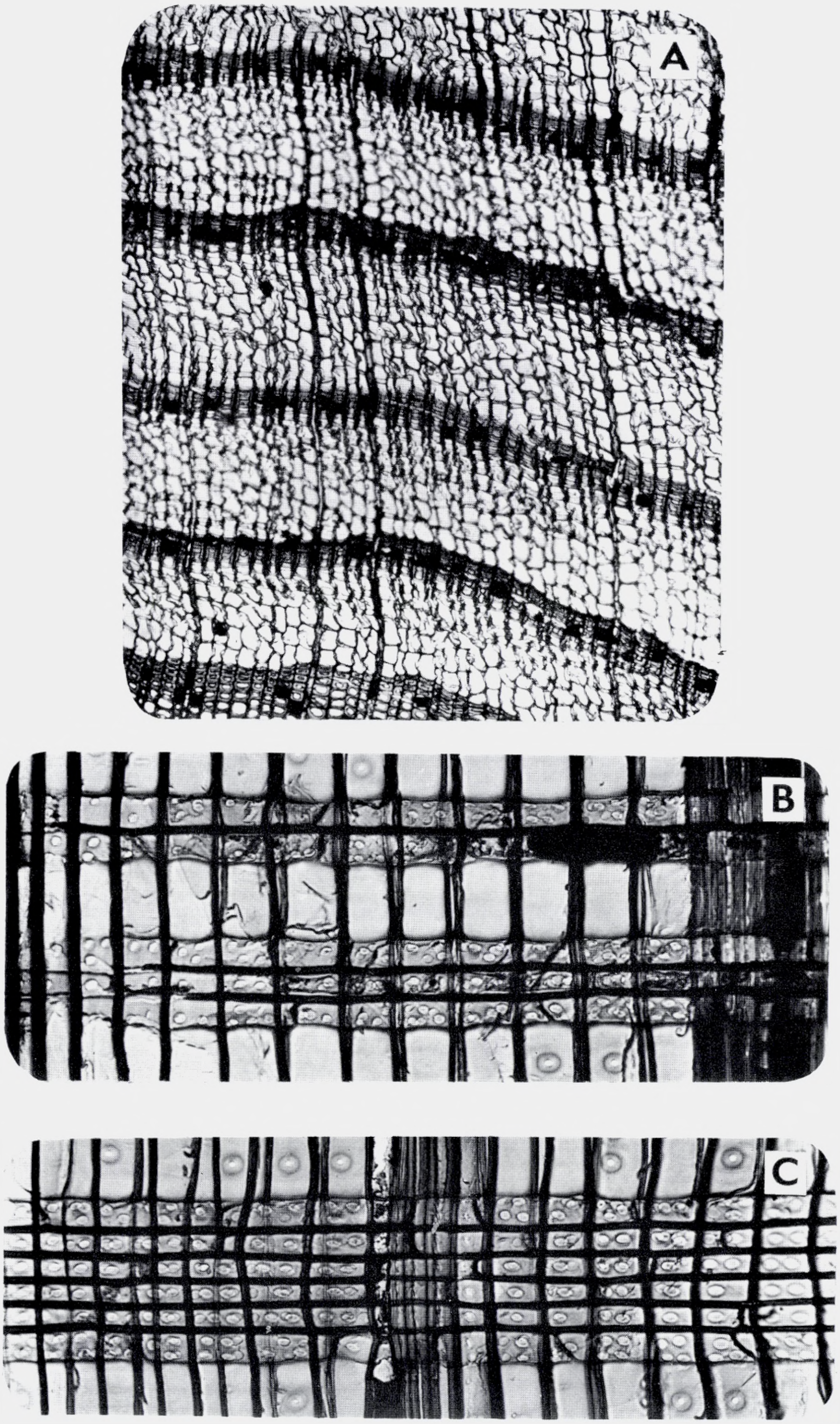
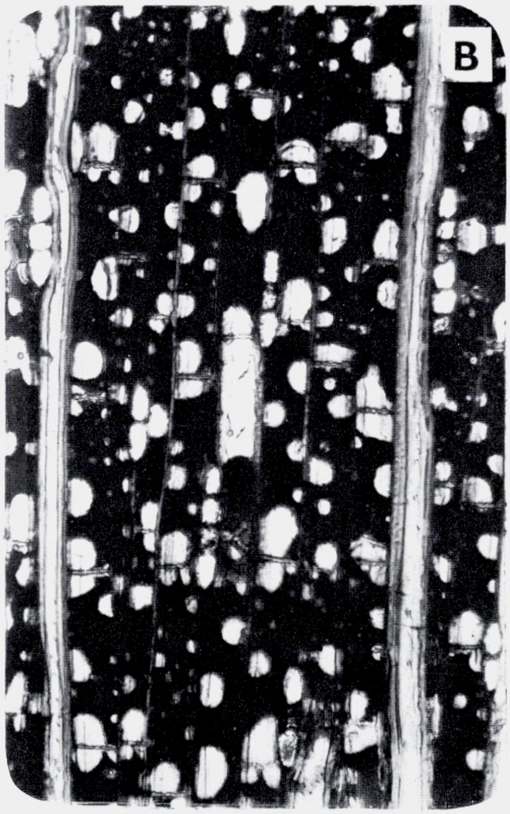


Plate XXII

Glyptostroboxylon tenerum (G. Kraus) N. Conwentz. A and B, tangential sections of late wood (×175). Troldhede. C, transverse section (×40) (from a quarry at Fiskbæk).


A


B

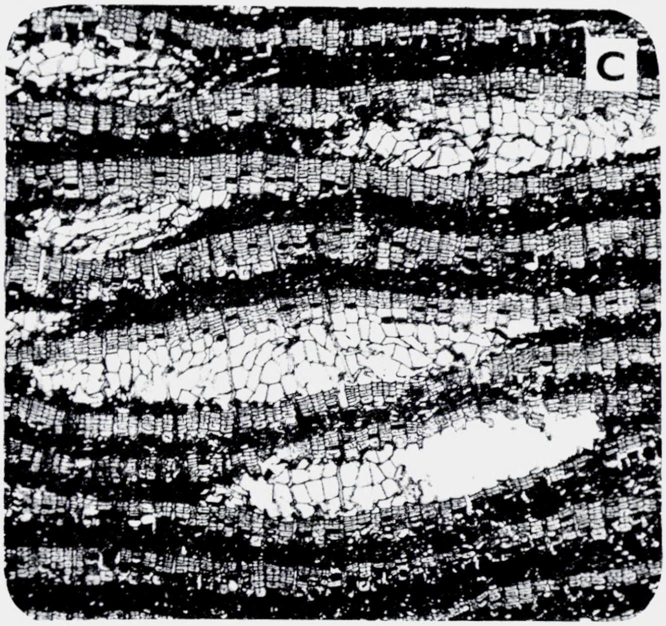

C

Plate XXIII

Cupressinoxylon callitroides n.sp. A, shows the variation in the thickness of the growth rings. (× 40). B, a growth ring in wood of the stem type and C, some growth rings in wood of the root type. Transverse sections (B and C ×175). Troldhede.

Pl. XXIII

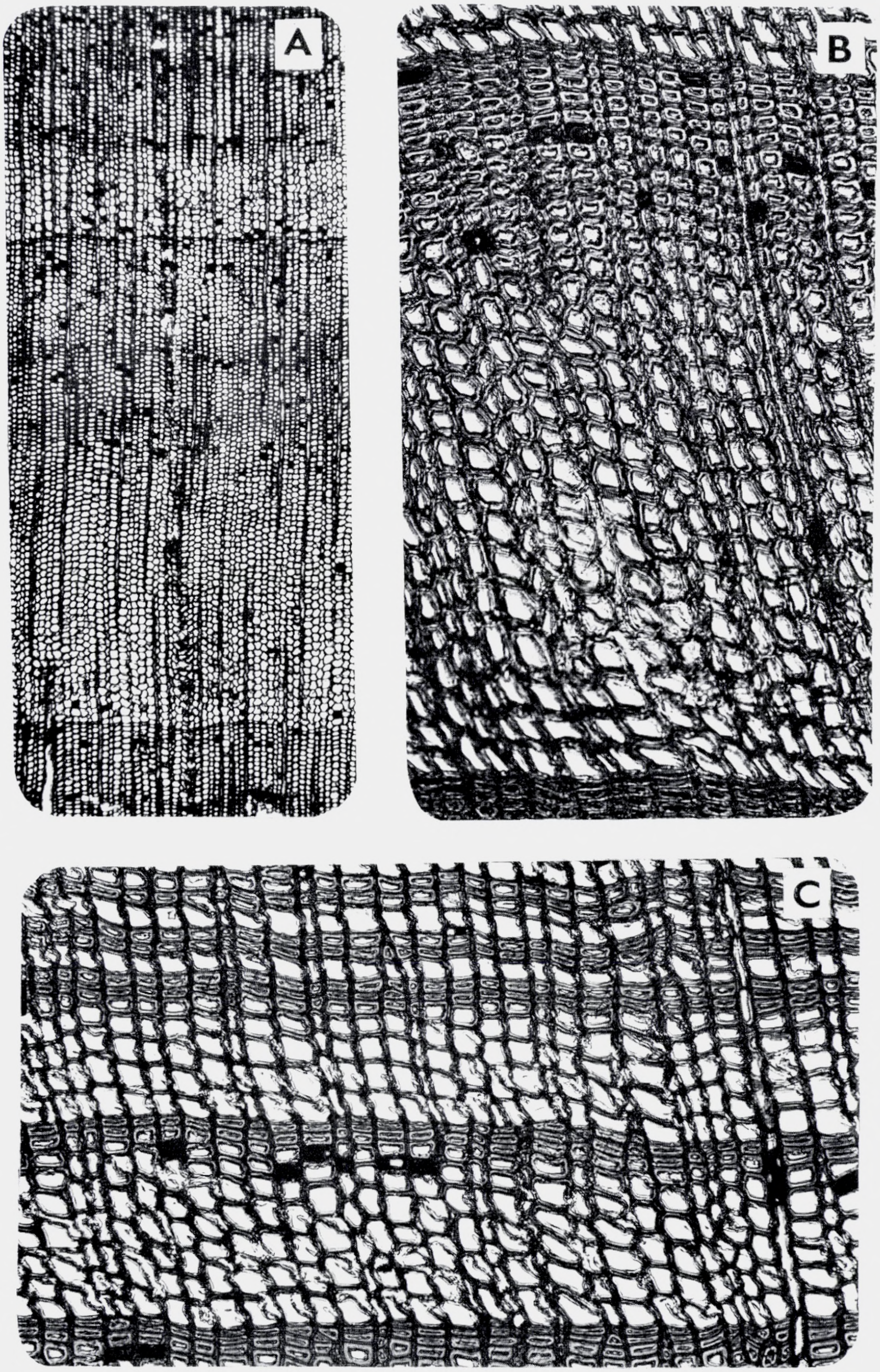


PLATE XXIV

Cupressinoxylon callitroides n.sp. A, radial section of wood of the stem type and B, radial section of wood of the root type. C, radial section of ray cells the inner surface of which shows a papillose appearance; confluent pits with double aperture occur here and there. (A and B ×175, C ×600). Troldhede.

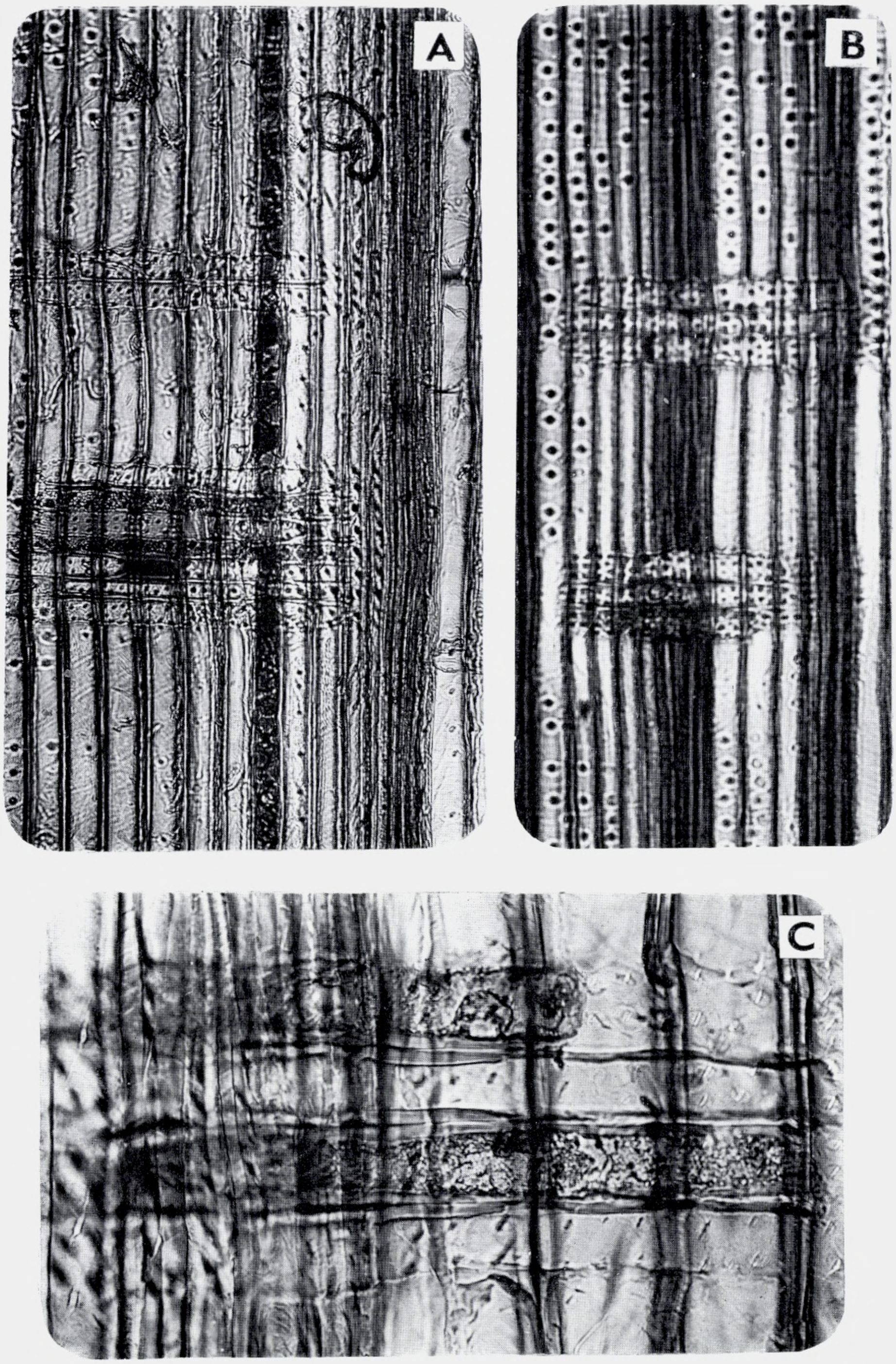

A
B
C

PLATE XXV

Cupressinoxylon callitroides n.sp. Tangential sections of wood of the stem type A, and of the root type B. (×175). In A the spiral structure of the tracheidal wall is distinct, e.g. to the right in the photo. Troldhede.

Pl. XXV

PLATE XXVI

Cupressinoxylon callitroides n.sp. A, tangential section. B, tangential section showing the papillose inner surface of a tracheid. C, radial section, the ray cells are partly papillose (A ×40, B and C ×600). Troldhede.

Pl. XXVI

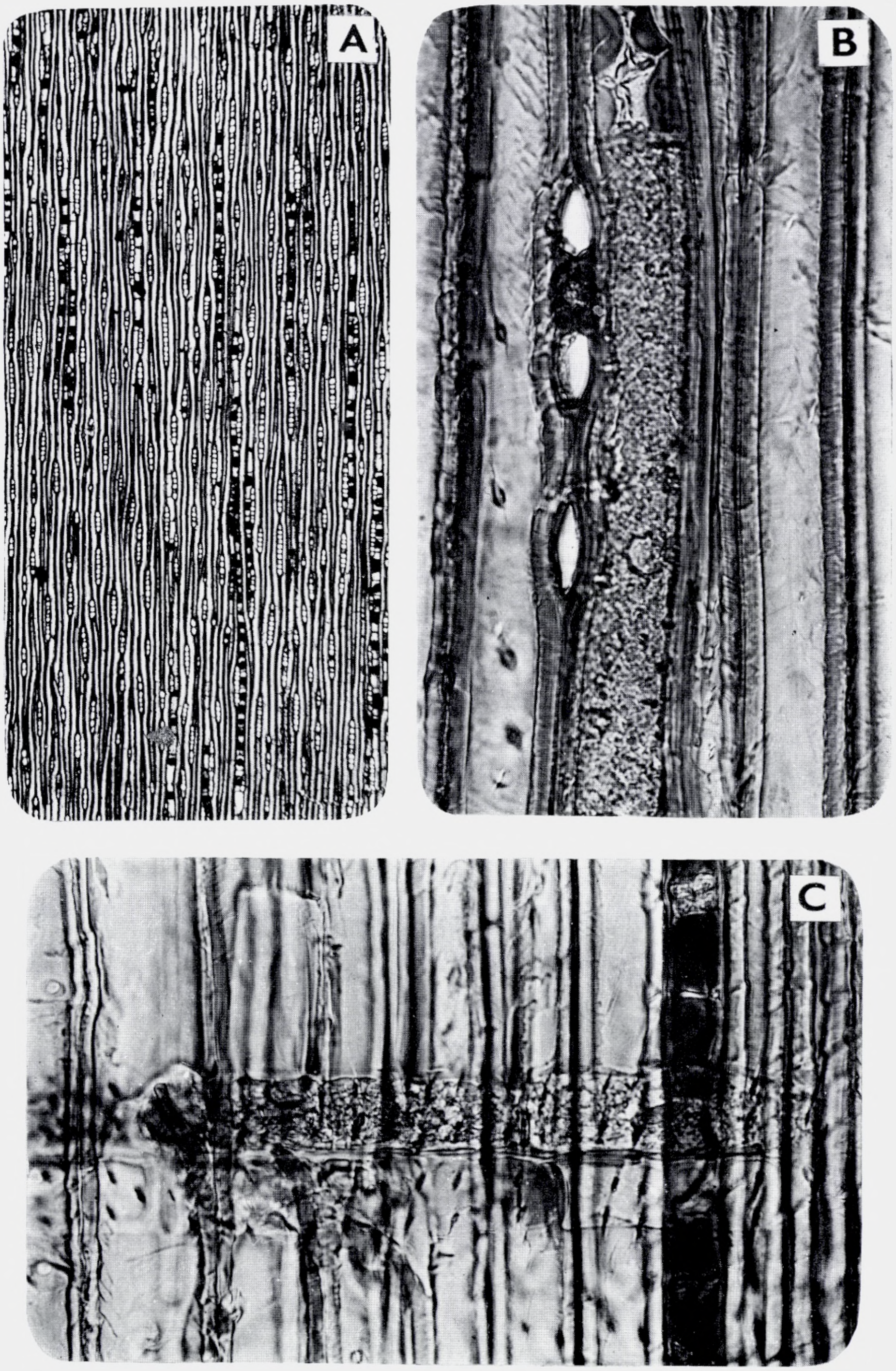
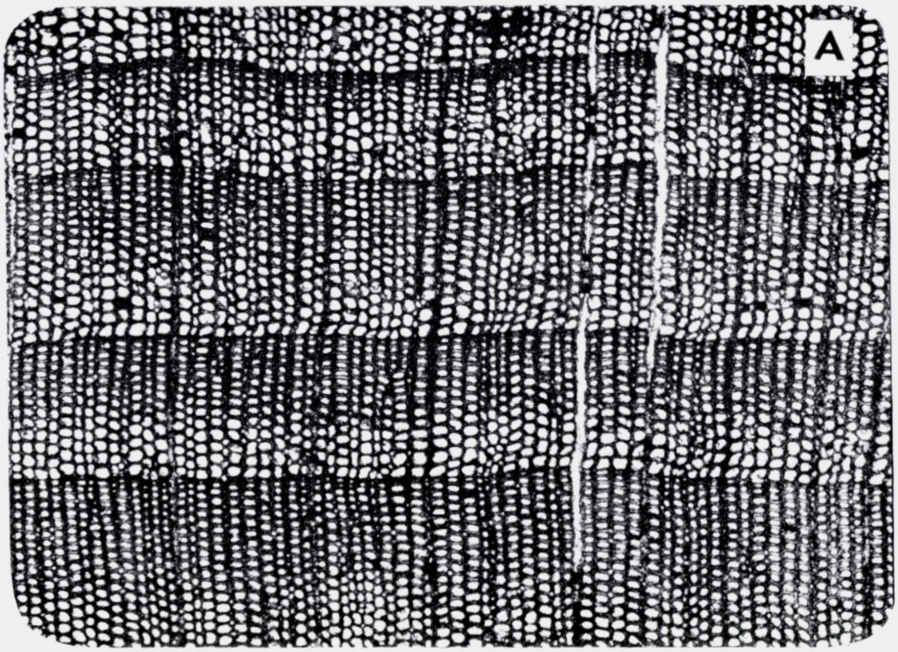
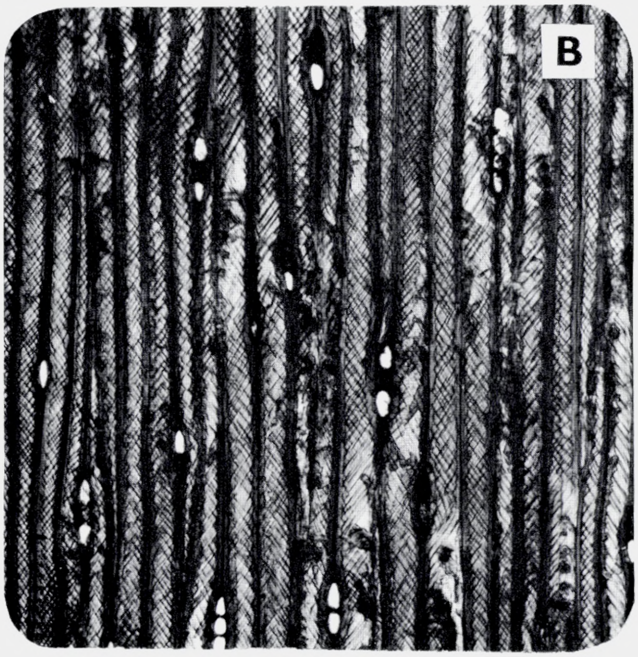


PLATE XXVII

Cupressinoxylon thujoides n.sp. A, transverse section. B, tangential and C, radial section. (A ×60, B and C ×175). Troldhede State Quarry.


A

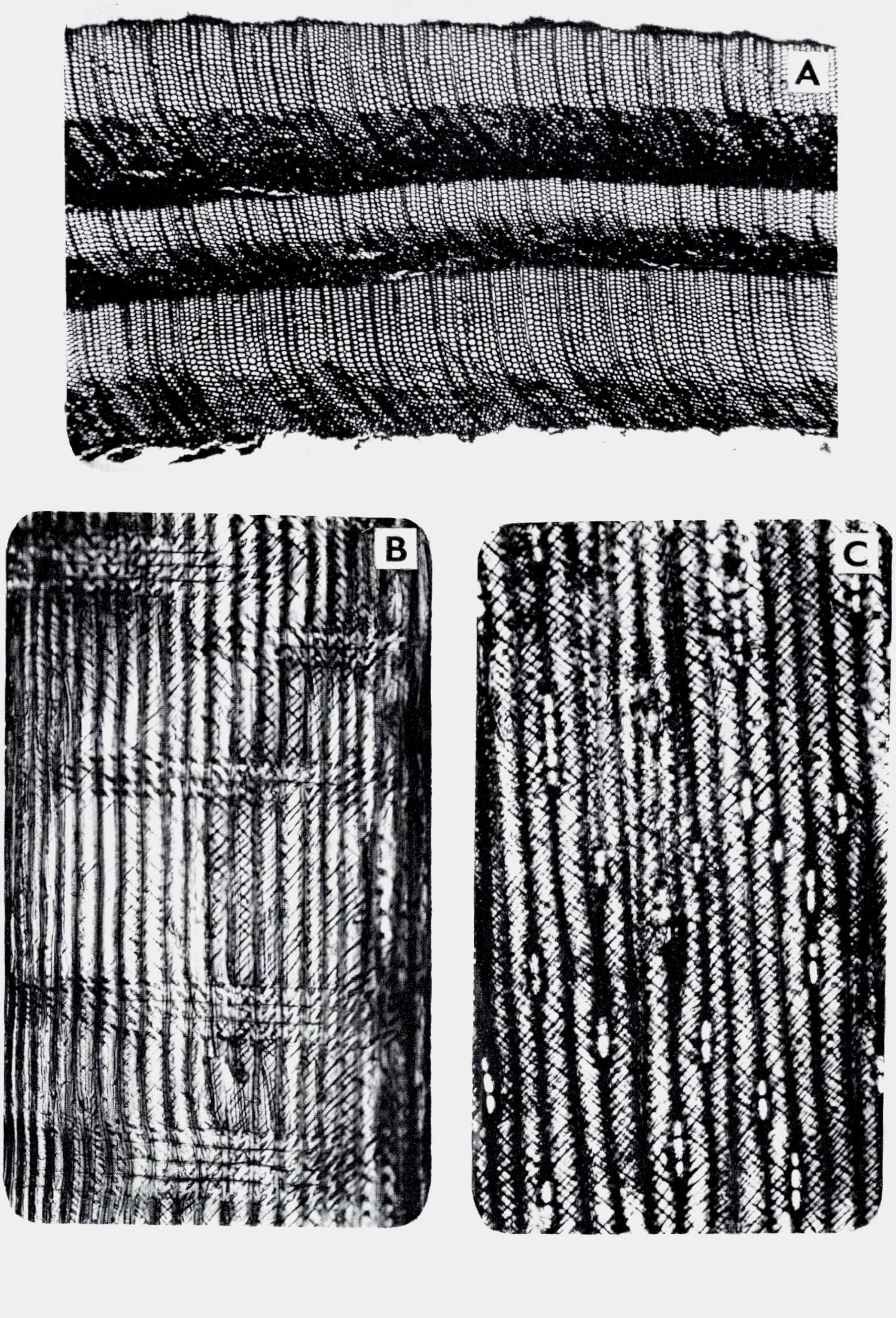

B


C

Plate XXVIII

Cupressinoxylon biotoides nov. comb. (*Biota orientalis* (L.) St. Endlicher var. *miocenica* R. Prill). A, transverse section, the growth rings of the early wood has partly collapsed. B, radial and C, tangential sections. The regular spiral structure of the innermust thickening layer of the tracheidal wall is standing in high relief caused by the solution of the terminal lamella. (A ×60. B and C ×175). Lystrupsminde.

Pl. XXVIII



Det Kongelige Danske Videnskabernes Selskab

Biologiske Skrifter

Biol. Skr. Dan. Vid. Selsk.

Bind **11** (kr. 162.–)

		kr. ø.
1.	Foged, Niels: Diatoms from Afghanistan. 1959	30.–
2.	Einarson, Lárus, and Telford, Ira R.: Effect of Vitamin-E Deficiency on the Central Nervous System in Various Laboratory Animals. 1960	38.–
3.	Larsen, Kai: Cytological and Experimental Studies on the Flowering Plants of the Canary Islands. 1960	24.–
4.	Böcher, Tyge W.: Experimental and Cytological Studies on Plant Species. V. The *Campanula rotundifolia* Complex. 1960	33.–
5.	Böcher, Tyge W., and Lewis, Martin C.: Experimental and Cytological Studies on Plant Species. VII. *Geranium sanguineum*. 1962	14.–
6.	Böcher, Tyge W.: Experimental and Cytological Studies on Plant Species. VIII. Racial Differentiation in Amphi-Atlantic *Viscaria alpina*. 1963	23.–

Bind **12** (kr. 173.–)

1.	Rasmussen, H. Wienberg: A Monograph on the Cretaceous Crinoidea. 1961	173.–

Bind **13** (kr. 155.–)

1.	Hammer, Marie: Investigations on the Oribatid Fauna of the Andes Mountains. II. Peru. 1961	42.–
2.	Hammer, Marie: Investigations on the Oribatid Fauna of the Andes Mountains. III. Chile. 1962	30.–
3.	Hammer, Marie: Investigations on the Oribatid Fauna of the Andes Mountains. IV. Patagonia. 1962	13.–
4.	Køie, M., and Rechinger, K. H.: Symbolae Afghanicae. Enumeration and Descriptions of the Plants Collected by L. Edelberg and M. Køie on "The 3rd Danish Expedition to Central Asia" and by G. Kerstan, W. Koelz, H. F. Neubauer, O. H. Volk, and others in Afghanistan. – Vol. V. 1963	70.–

Bind **14** (kr. 190.–)

1.	Salomonsen, Finn: Some Remarkable New Birds from Dyaul Island, Bismarck Archipelago, with Zoogeographical Notes. (Noona Dan Papers No. 9). 1964	20.–
2.	Nygaard, Gunnar: Hydrographic Studies, especially on the Carbon Dioxide System, in Grane Langsø. 1965	40.–
3.	Wingstrand, Karl Georg, and Munk, Ole: The Pecten Oculi of the Pigeon with Particular Regard to its Function. 1965	25.–
4.	Køie, M., and Rechinger, K. H.: Symbolae Afghanicae. Enumeration and Descriptions of the Plants Collected by L. Edelberg and M. Køie on "The 3rd Danish Expedition to Central Asia" and by G, Kerstan, W. Koelz, H. F. Neubauer, O. H. Volk and others in Afghanistan. – Vol. VI. 1965	25.–
5.	Bendix-Almgreen, Svend Erik: New Investigations on *Helicoprion* from the Phosphoria Formation of South-East Idaho, U.S.A. 1966	30.–

	kr. ø.
6. Mathiesen, Fr. J.: Palaeobotanical Investigations into some Cormophytic Macrofossils from the Neogene Tertiary Lignites of Central Jutland. Part I: Introduction and *Pteridophytes*. 1965	15.–
7. Böcher, Tyge W.: Experimental and Cytological Studies on Plant Species. IX. Some Arctic and Montane Crucifers. 1966	35.–

Bind **15** (kr. 133.–)

1. Foged, Niels: Freshwater Diatoms from Ghana. 1966	50.–
2. Hammer, Marie: Investigations on the Oribatid Fauna of New Zealand. Part I. 1966.	45.–
3. Nørvang, Aksel: *Textilina* nov. gen., *Textularia* Defrance and *Spiroplectammina* Cushman (*Foraminifera*). 1966	8.–
4. Hammer, Marie: Investigations on the Oribatid Fauna of New Zealand. Part II. 1967.	30.–

Bind **16**

(*uafsluttet/in preparation*)

1. Perch-Nielsen, Katharina: Der Feinbau und die Klassifikation der Coccolithen aus dem Maastrichtien von Dänemark. 1968	60.–
2. Hammer, Marie: Investigations on the Oribatid Fauna of New Zealand, with a Comparison between the Oribatid Fauna of New Zealand and that of the Andes Mountains, South America. Part III. 1968	50.–
3. Böcher, Tyge W., and Lyshede, Ole B.: Anatomical Studies in Xerophytic Apophyllous Plants. I. *Monttea aphylla, Bulnesia retama* and *Bredemeyera colletioides*. 1968	30.–
4. Christensen, Tyge: Vaucheria Collections from Vaucher's Region. 1969	18.–
5. Jespersen, Åse: On the Male Urogenital Organs of *Neoceratodus forsteri*. 1969	12.–

Bind **17**

(*uafsluttet/in preparation*)

1. Degerbøl, Magnus, and Fredskild, Bent: The Urus (*Bos primigenius* Bojanus) and Neolithic Domesticated Cattle (*Bos taurus domesticus* Linné) in Denmark. With a Revision of *Bos*-Remains from the Kitchen Middens. Zoological and Palynological Investigations. 1970	160.–
2. Hansen, Hans Jørgen: Electron-Microscopical Studies on the Ultrastructures of some Perforate Calcitic Radiate and Granulate Foraminifera. 1970	32.–
3. Mathiesen, Fr. J.: Palaeobotanical Investigations into some Cormophytic Macrofossils from the Neogene Tertiary Lignites of Central Jutland. Part II: *Gymnosperms*. 1970	55.–

Printed in Denmark
Bianco Lunos Bogtrykkeri A/S