Wood-remains from the Lower Pleistocene of Tegelen (The Netherlands)

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Burgh, J. van der. Wood-remains from the Lower Pleistocene of Tegelen (The Netherlands). Scripta Geol., 25: 1 - 35, 2 tables, 6 pls., Leiden, November 1974.

Wood-remains of the Lower Pleistocene type locality of the Tiglian have been described and identified. The resulting flora is compared with Recent European forest-vegetations and a strong affinity with flood plain forests has been established.

Also a comparison with flood plain forest vegetations of North America, East Asia and the Pontic area is made. The Tegelen wood-flora can at best be compared with the floras found in N. E. Asia and in the Pontic area. The climatic implications of this comparison and of the floristic composition of the Tegelen wood-flora are discussed.

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Introduction

GENERAL SCOPE

Plant macrofossils, especially fruits and seed-remains have been known from the Lower Pleistocene type locality of the Tiglian at Tegelen (Province of Limburg, The Netherlands) for a long time. The study of these remains, together with the palynological investigation by Zagwijn (1963), has provided considerable insight in the composition of the Tiglian flora.

On the other hand the locally abundant wood-remains from Tegelen have been neglected. Since the study of wood-remains could well provide additional botanical information, collections were made by Mr A. Voorrips and the author (ca 100 specimens) and Dr W. H. Zagwijn, Rijks Geologische Dienst, Haarlem (ca 30 specimens) from the clay-pit Russel Tiglia Egypte.

The wood-remains originate from a sand-filled channel. Although definitely representing allochthonous elements, the wood does not show any marks diagnostic for long-distance transport. Consequently it is assumed that the wood-remains reflect part of a vegetation situated in the direct vicinity of the channel. The objective of the present study is to provide information about 1) the qualitative composition of the vegetation, and 2) the possible environmental and climatological conditions.

ACKNOWLEDGEMENTS

The author is indebted to Dr W. H. Zagwijn for his help and useful comments, to Prof. Dr F. P. Jonker for the helpful discussions, and to the staff of the Laboratory of Palaeobotany and Palynology and of the Division of Systematic Wood Anatomy of the Institute for Systematic Botany, for their assistance. Special gratitude goes to Miss Dr A. M. W. Mennega for making available slides and samples of the wood-collection of the Division of Systematic Wood Anatomy, as well as literature concerning the anatomy of Recent wood.

The author is grateful to the Rijks Geologische Dienst (the Geological Survey of the Netherlands) at Haarlem for putting Dr Zagwijn's material at his disposal.

The help of Messrs H. A. Elsendoorn and T. Schipper in preparing and mounting the photographs has greatly improved this publication.

METHODS

Part of the samples was stored in water. Dried samples were boiled before slides were made. The sections were prepared with a razor blade and mounted with glycerin jelly. Some of them have been bleached with NaOCl and stained with methylgreen.

The samples have been stored in the fossil-wood collection of the Laboratory of Palaeobotany and Palynology, Utrecht, under the numbers mentioned below in the descriptions.

Descriptions

CONIFEROSPERMAE
PINALES
PINACEAE

Pinus cembra L.
Pl. 1, figs. 1 - 3

Description — The growth rings are rather narrow, 9 - 40 tracheids wide.

The tracheids are angular in cross section.

Measures of tracheids in µm	radial	tangential	wall thickness
early wood	50	43	4 - 5
late wood	7	32	8

One vertical row of bordered pits with a diameter of 18 - 19 µm was found in the radial walls of the tracheids; numerous small bordered pits with a diameter of 7 - 9 µm occur in the tangential walls of the late wood. Parenchyma has not been observed.

Uniseriate rays are up to 15 cells high and show ray-tracheids, or not. Multiseriate rays, up to 3 cells wide and up to 25 cells high, have a resin duct and 20 - 22 µm high ray-parenchyma cells. The 2 - 3 µm thick horizontal and tangential walls are lignified and pitted. The crossfields generally have a single fenestriform pit with a maximum diameter of 25 µm. One or two tracheids above each other are present at the margin of the ray; the walls are nearly smooth or have a very weak dentition (Hudson gradation 1 - 2); the bordered pits have a diameter of 10 µm.

The vertical and horizontal resin ducts have both thick- and thin-walled epithelium and surrounding parenchyma. The diameter of the vertical ducts is 50 - 80 µm; of the horizontal ducts 20 - 40 µm.

Identification — According to the identification key of *Pinus* wood published by van der Burgh (1973), the wood under consideration can be classified within the Section *Strobus*.

In Europe the Recent species of this section are *P. cembra* and *P. peuce*. Our wood resembles *P. cembra* in every respect and is therefore described under this name. The walls of the ray-tracheids in the wood of *P. peuce* show a more developed dentition. Outside Europe there occur two other Recent species showing an amount of dentition in the ray-tracheids similar to that in *P. cembra*, viz. *P. koraiensis* and *P. albicaulis*. However, in these species the crossfield pits are different: wider in *P. koraiensis* and smaller with a narrow aperture and wide borders in *P. albicaulis*. *P. pumila*, which is often described as a variety of *P. cembra*, has lower rays.

Samples — no 1431, 1483, 1494.

Young wood of *Pinus cembra*

One of the samples investigated (no 1483) represents the wood of a rather young branch. It differs from the above description in the following respects: (1) in cross section the tracheids are rounded, the lumina are narrower; (2) the rays are lower (uniseriates up to 8 cells, multiseriates up to 17 cells high); (3) the

crossfield pits are fenestriform, but frequently one can observe two pits above each other in a crossfield; (4) the horizontal resin ducts have a diameter of 30 µm, the vertical ducts a diameter of 50 µm; (5) ray tracheids are almost completely lacking.

The occurrence of more than one fenestriform pit in a crossfield, as well as the absence of ray tracheids, is typical for young wood of the Section *Strobus*. The above described wood may therefore be compared with young wood of *P. cembra* and also with that of *P. pumila* described and illustrated by Greguss (in Greguss & Vanhoorne, 1961, Plate III-1). The wood illustrated shows low rays, a single fenestriform pit in a crossfield and the presence of ray tracheids. Therefore one may conclude that Greguss' sample represents rather young wood, though older than our sample 1483.

Pinus cf. *tabulaeformis* Carrière
Plate 1, figs. 4 - 5.

Description — The growth rings are 5 - 6 mm wide, the transition from early wood to late wood is gradual.

The tracheids are rounded to angular in cross section.

Measures of tracheids in µm	radial	tangential	wall thickness
early wood	45	30	6
late wood	10	25	8

Bordered pits with a diameter of 18 - 20 µm occur in a vertical row in the radial walls of the tracheids; they were not observed in the tangential walls. Parenchyma has not been observed.

Uniseriate rays, up to 23 cells high, show tracheids, or not. Multiseriate rays are up to 3 cells wide and up to 28 cells high, with a resin duct. Ray-parenchyma cells, up to 22 µm high, show very thin unpitted horizontal and tangential walls; in most parts of the sections they are, however, degraded. The crossfields have one or two fenestriform pits with a diameter of 25 µm. Ray-tracheids occur along the margins of the rays, sometimes also between the ray-parenchyma; up to four ray-tracheids are found on top of each other; the walls are provided with slender teeth (Hudson graduation 7); the bordered pits have a diameter of 10 - 12 µm.

The vertical and horizontal resin ducts have thin-walled epithelium and surrounding parenchyma.

Identification — Our sample shows all the characteristics of the wood of *Pinus*, Section *Pinus*. In particular it resembles the wood *P. tabulaeformis*. However, in *P. tabulaeformis* there is a stronger dentition in the ray tracheids, according to Hudson (1960) with a gradation 10, according to material from the Utrecht wood collection with a gradation 8 - 9. Therefore our wood is not considered to be identical with that of *P. tabulaeformis*, but certainly there is a very close relation. Identical wood has been described by Greguss as *Pinus (tabulaeformis* v. *funebris)* (in Greguss & Vanhoorne, 1961).

Sample — no 1429.

Other comparable material — According to the measurements by Zagwijn (1963)

most of the pollen grains of *Pinus* found in the channel sediment could well be referred to the species *P. peuce* and *P. sylvestris*. This assumption was not confirmed by our wood analysis.

Picea abies (L.) Karsten
Plate 1, figs. 9 - 11.

Description — The transition from early wood to late wood is gradual in the growth rings.

The tracheids are rounded in cross section, no spiral thickenings were observed.

Measures of tracheids in µm	radial	tangential	wall thickness
early wood	30	25	3
late wood	5	10	10

A single vertical row of bordered pits with a diameter of 15 µm was found in the radial walls of the tracheids. Parenchyma has not been observed.

Uniseriate rays, up to 19 cells high, show ray-tracheids, or not. Multiseriate rays, up to 4 cells wide and 28 cells high, have a resin duct. The ray-parenchyma cells are about 13 µm high and have pitted walls, up to 6 µm thick. The crossfields have one to four piceoide pits with a diameter of 6 µm. Tracheids occur along the margins of the rays, one to three on top of each other; the bordered pits have a diameter of 5 - 6 µm.

The vertical and horizontal resin ducts have both thick- and thin-walled epithelium and thick-walled parenchyma. The lumina have a diameter of 7 - 8 µm. The diameter of vertical ducts is 50 - 80 µm, that of horizontal ones 20 - 45 µm.

Identification — This species closely resembles *P.* cf. *omorika,* described hereafter, and therefore the identifications will be discussed together.

Samples — no 1406, 1412, 1425, 1433, 1462, 1490, 1500, 1501, 1517, 1518.

Picea cf. *omorika* (Paue) Purk.
Plate 1, figs. 6 - 8.

Description — This wood shows some minor, but constant, differences with the above described type of wood; (1) in the radial walls of the tracheids one or two rows of bordered pits can be observed, sometimes there is a single tracheid with spiral thickenings in the walls, (2) the walls of the ray parenchyma cells are up to 8 µm thick and the crossfield pits show a diameter of 6 - 7 µm, (3) the diameter of the vertical resin ducts is up to 90 µm. In all other characters there is a complete conformity with the above described species.

Identification — These wood types can be compared with the woods of the genera *Larix* and *Picea*. According to Greguss (1967, 1972), virtually all tangential walls of the ray tracheids are very oblique or even partly horizontal in *Larix,* and less so in wood of *Picea*. However, according to our own investigations of the wood structure of the latter genus, this feature can be commonly observed

in *Picea*. Therefore it cannot be used for separating the two genera.

If we compare the Recent European species of *Larix* and *Picea*, it appears that *Larix decidua* is characterised by much narrower lumina in the surrounding parenchyma of the horizontal resin ducts than *Picea abies* and *P. omorika* as well as the above described wood types. The second type described shows the most thick-walled surrounding parenchyma and is therefore comparable to *Picea omorika*. The lumina of the ray parenchyma cells, however, are slightly narrower. The first type is exactly comparable with the wood of *P. abies* and has therefore been described under this name.

Samples — no 1436, 1447, 1482, 1525.

Other comparable material — Zagwijn (1963) recorded pollen of *Picea* in rather big quantities, which he considered to represent a few different species. This is confirmed by the presence of at least two different types of *Picea* wood. From the channel, from which the present material originates, also cones of this genus *(Picea florschützii)* have been described (van der Hammen, 1951).

Abies alba Miller
Plate 2, figs. 1 - 3.

Description — The growth rings are 10 - 20 tracheids wide, the transition from early wood to late wood is abrupt.

The tracheids are rounded to angular in cross section.

Measures of tracheids in µm	radial	tangential	wall thickness
early wood	45	25	2 - 3
late wood	10	22	4 - 5

One, sometimes two, vertical rows of rather densely spaced bordered pits occur in the radial walls of the tracheids; they are round to elliptical and have a diameter of 16 - 18 µm; crassulae are sometimes present. In the tangential walls of the tracheids many small bordered pits occur with a diameter of 6 - 8 µm. Sparse parenchyma occurs at the margins of a growth ring; the walls are pitted.

All rays are uniseriate, up to 21 cells high. The shape of the marginal cells is somewhat irregular; the cells are 16 - 18 µm high; the horizontal and tangential walls have many small pits. In the crossfields there are one or two piceoide pits with a diameter of 6 - 7 µm. The thickness of the horizontal walls is 5 - 6 µm, of the tangential walls 7 - 8 µm.

Resin ducts were not observed.

Identification — According to the pitting of the walls of the ray cells, this wood can be recognised as derived from a member of the Pinaceae. It must be compared with the wood of the genera *Abies, Cedrus, Pseudolarix, Tsuga,* and *Keteleeria*. Contrary of the wood of *Cedrus* and *Tsuga,* our wood does not show ray tracheids. *Keteleeria* and *Pseudolarix* are characterised by the presence of much more parenchyma with thin horizontal walls, in *Abies* the bordered pits in the radial walls of the tracheids are usually situated in a single vertical row; in the widest tracheids one may however observe double pits. In all other respects the above described wood can be compared with the wood of *Abies alba* and therefore our sample is included in this species.

Sample — no 1458.

Other comparable material — According to Zagwijn (1963) *Abies* pollen is relatively rare at Tegelen. There is a continuous low percentage in all spectra representing the first climatic optimum (Tc 3), the second climatic optimum, during which the present material was deposited, is characterised by spectra in which *Abies* pollen occurs only sporadically. The discovery of cone remains of *Abies* cannot be expected, only separated scales perhaps, but they have not been found so far.

CUPRESSALES
CUPRESSACEAE

Chamaecyparis cf. *thyoides* Britton, Stern & Poggenberg
Plate 6, figs. 1 - 3.

Description — The growth rings are narrow, 0.5 - 1 mm wide, early wood and late wood are difficult to distinguish. The margin of a growth ring is indicated by one or two rows of radially contracted elements.

The tracheids are rounded in cross section.

Measures of tracheids in µm	radial	tangential	wall thickness
early wood	25 - 30	14 - 17	3 - 5
late wood	3 - 6	14 - 17	3 - 5

One vertical row of bordered pits occurs in the tracheids with a diameter of 12 - 15 µm. Bordered pits are sparsely distributed in the tangential walls, their diameter is 5 - 7 µm. Parenchyma is sparse, the crosswalls are up to 7 µm thick and pitted.

The rays are uniseriate, up to 10 cells high. The cells are up to 15 µm high, the horizontal walls are up to 5 µm thick and pitted; the tangential walls are 2 µm thick and smooth, sometimes with faint knots, indentures are present. The crossfields have two to four taxodioide or simple pits, mostly two above each other, 5 - 7 µm in diameter.

Identification — This material corresponds exactly with the Belgian wood described as *Chamaecyparis (thyoides* Britton, Stern & Poggenb.?) by Greguss (in Greguss & Vanhoorne, 1961). According to Greguss the presence of taxodioide pits is characteristic of, among other species, *Chamaecyparis thyoides.* The slides of the Utrecht collection of this species show the presence of pits with horizontal apertures in the early wood. However, the long axis of the pit does not coincide with that of the aperture; in fact one can observe an obtuse angle (U 7412, U 7346). Moreover, the combination of taxodioide pits with some simple pits can also be found in the genus *Thuja* (e.g. *T. occidentalis,* U 10317). The latter wood shows some more parenchyma. Although there are some important differences if compared with *Chamaecyparis thyoides* and our material, the samples show a rather strong resemblance with *C. thyoides.* Therefore they have been identified as *Chamaecyparis* cf. *thyoides* Britt, Stern & Pogg.

Samples — no 1430, 1454.

Other comparable material — Pollen of the Cupressacceae are regular constituents of the spectra by Zagwijn (1963), especially from his zones Tc 3 and

Tc 4. The pollen could not be identified on a generic level. Also in the channel sediments Cupressaceae pollen has been found; it occurs, however, in lower percentages. Macrofossil records of the family are unknown from these deposits.

ANGIOSPERMAE
RANUNCULALES
MAGNOLIACEAE

Magnolia sp.
Plate 2, figs. 4 - 6.

Description — The growth rings are narrow, 1 - 1.5 mm wide, they can be distinguished by the wide vessels in the early wood and the terminal parenchyma band along the margin.

The vessels have a diameter of 70 - 90 μm in the early wood, but are narrower in the late wood; they occur single or in radial multiples of maximum three vessels. The perforations are simple or scalariform with up to 15 bars. The pits to the rays are coarse and have a diameter of 6 - 8 μm. The intervascular pits as well as the pits to parenchyma are scalariform; the circular bordered pits to the fibers have a diameter of 7 - 9 μm. Thylloses are sometimes present. The walls have spiral thickenings.

The fibers have bordered pits in the walls with a diameter of 7 - 9 μm. The material is too degraded to measure the wall thickness. Both paratracheal and apotracheal-diffuse parenchyma was found, and also a terminal band. The small pits occur in groups together.

The rays are homogeneous or weakly heterogeneous, one to three, mostly two, cells wide, and up to 60 cells high (1.2 mm). The cell-walls are lignified and up to 4 μm thick. Pits lay in lines along the corners of the lumina.

Identification — The combination of the presence of (1) both simple and scalariform perforations, (2) spiral thickenings in the vessel walls, (3) typical scalariform as well as irregular coarse pits, and (4) the characteristic shape of the rays is known from the wood of the genus *Magnolia*. On a specific level, however, our material does not completely correspond with the wood of any of the species described; therefore it is identified as *Magnolia* sp.

Samples — no 1477, 1486, 1493, 1598.

Other comparable material — Zagwijn (1963) recorded a rather large number of seeds from the channel sediments, which he ascribed to *Magnolia kobus* DC (according to Kirchheimer, 1957, the name should be *Magnolia ultima).*

URTICALES
ULMACEAE

Ulmus sp.
Plate 2, figs. 7 - 9.

Description — The growth rings are ca 1 mm wide, definitely ring-porous.

The vessels are arranged in irregular bands or groups, their diameter is in

the early wood 100 - 180 µm, in the late wood 20 - 40 µm. The perforations are simple. In the walls of the narrow vessels 1 µm wide spiral thickenings occur. The pits to the rays are circular or irregular, their diameter is 3 - 5 µm. The pits to parenchyma are elliptical and have a diameter of 5 - 6 µm. Intervascular pitting is by bordered pits, either circular with a diameter of 7 - 8 µm, or elliptical with a horizontal slitlike aperture with a length of 2 - 4 µm.

The fibers have small pits in the walls. The walls are 3 µm thick in early wood and 5 µm in late wood. The parenchyma is paratracheal vasicentric.

The rays are homogeneous, 1 to 5 cells wide and up to 60 cells high (0.7 mm). The cells are 10 - 12 µm high and have 1.5 - 2 µm thick walls.

Identification — The characteristic arrangement of the vessels, combined with the spirals in the narrow vessels of the late wood, and the simple perforations point to the Ulmaceae. In this family, *Ulmus* is characterised by homogeneous rays. Because of the uniformity of the wood-anatomical characters of the various species of *Ulmus,* it is impossible to point out a single species to which the above described wood may be referred. Therefore it is identified as *Ulmus* sp.

Samples — no 1449, 1591, 1603.

Celtis sp.
Plate 2, figs. 10 - 12.

Description — The growth rings are narrow, only 0.25 - 0.75 mm wide; there is an abrupt transition from early wood to late wood.

The arrangement of the vessels is often obscure due to the narrow growth layers. The vessels are up to 170 µm wide in the early wood and 20 - 30 µm in the late wood. In the walls of the narrow vessels of the late wood 1 µm wide spiral thickenings occur. The perforations are simple. Circular bordered pits with a diameter of 7 µm occur between the vessels. The pits to the rays are 3 - 4 µm in diameter; the pitting to the parenchyma is by horizontally widened pits with a diameter of 3 - 8 µm.

The fibers have small bordered pits with a diameter of 1 µm in the walls which are 5 µm thick. Some paratracheal parenchyma is present.

The heterogeneous rays have one to three marginal rows of upright cells and sheath cells; they are 1 to 10 cells wide and up to 70 cells high (1 mm). The cells in the middle of the rays are 14 - 15 µm, and the sheath cells up to 25 µm high. The walls are 1.5 - 2 µm thick. The cells in the uniseriate rays are rather wide, up to 20 µm, in the multiseriate rays they are narrower, up to 12 µm.

Identification — This wood shows a striking resemblance with the above described *Ulmus* sp. The only difference is formed by the structure of the rays. In this respect it can be compared with the wood of the genera *Celtis* and *Zelkova,* the latter genus, however, does not show an abrupt transition between early wood and late wood. Since our wood can be referred to no species of *Celtis* in particular with certainty, it is identified as *Celtis* sp.

Samples — no 1418, 1426, 1443, 1595, 1597.

Other comparable material — Zagwijn (1963) mentioned a slight increase of *Ulmus* pollen in his zone Tc 5, to which the present material belongs. Seeds of *Ulmus* have not been found in the channel filling. According to Zagwijn this may be the result of corrosion.

Neither pollengrains, nor seeds of *Celtis* have been reported.

GERANIALES
TILIACEAE

Tilia sp.
Plate 3, figs. 1 - 3.

Description — Growth rings were not observed due to the flattening of the wood.

The vessels are single or occur in irregular groups and have a diameter of 50 - 60 μm. The perforations are simple. The walls have 2 μm wide spiral thickenings. The intervascular pits are pentagonal or hexagonal in shape and have a diameter of 7 - 8 μm. The pits to rays and parenchyma are circular and 2 - 3 μm in diameter. The bordered pits to the fibers have a diameter of 4 - 6 μm.

The fiber walls are thin without spirals. The bordered pits in the walls have a diameter of 4 - 6 μm. Paratracheal parenchyma is represented by some isolated fibers along the vessels. Also some apotracheal parenchyma is present.

The rays are nearly or entirely homogeneous; at the margins of the heterogeneous rays there is usually one row of quadratical or upright cells. The rays are one to three cells wide and up to 1 mm high. The cell walls are 2 - 3 μm thick, the procumbent cells 12 - 13 μm high.

Identification — The spiral thickenings in the vessel walls, the shape of the pits and the homogeneous rays are typical for the genus *Tilia*. Between the species of the genus no choice can be made, not only because of the bad preservation of the fossil material, but also because of the uniform wood-structure within the genus. The wood is therefore identified as *Tilia* sp.

Sample — no 1416.

Other comparable material — Though *Tilia* pollen has regularly been recorded in the sediments, no seeds were observed (Zagwijn, 1963). For this reason it was supposed that *Tilia* together with *Quercus, Carya,* and *Corylus* did not grow in the direct environment of the channel, but occurred on somewhat higher ground. The discovery of wood, however, makes it probable that the absence of seeds of *Tilia* and *Carya* must be ascribed to different causes.

RUTALES
RUTACEAE

Phellodendron sp.
Plate 3, figs. 4 - 7.

Description — The growth rings are rather narrow, 0.5 - 1 mm wide; the transition from early wood to late wood is gradual.

The vessels are exclusively solitary and have in the early wood a diameter of 150 - 250 µm, in the late wood of 50 µm. In the walls spiral thickenings occur; the perforations are simple. The pits to rays and parenchyma are circular and have a diameter of 3 - 5 µm; the apertures to the vessels are fused to grooves. Intervascular pitting occurs in the tips of the vessel members by circular bordered pits with a diameter of 8 µm. Due to fossilisation the grooves formed by the apertures have become deepened and widened, which makes the pitting seemingly scalariform.

The fiber walls are 5 µm thick, the lumina 10 - 18 µm wide. Only paratracheal vasicentric parenchyma is present as a uniseriate often interrupted layer around the vessels.

Uniseriate rays are composed of only upright cells; multiseriate rays have a central part of procumbent cells with on both sides tips of upright cells, up to 60 cells high (0.7 mm) and 2 - 5 cells wide. The cells are 8 - 12 µm high and have 3 - 4 µm thick pitted walls.

Identification — This wood resembles that of *Phellodendron*. The vessel pits and the diameter of the vessels are comparable to those of *P. amurense, P. sachalinense,* and *P. japonicum*. *P. amurense* and *P. sachalinense,* however, can be distinguished by the presence of tangential bands of parenchyma and narrow vessels, the vessels in the early wood often occurring in radial pairs. The rays are homogeneous with only procumbent cells or weakly heterogeneous ones. *P. japonicum* has stronger heterogeneous rays than *P. sachalinense* and *P. amurense,* but they are considerably less heterogeneous than those of the above described wood. Radial vessel pairs are also present in the early wood of *P. japonicum,* but the bands of parenchyma and narrow vessels in the late wood are lacking.

Another genus of the Rutaceae characterised by wood with spiral thickenings, which has been quoted in the literature concerning Tertiary and Early Pleistocene plants in Europe, is *Ptelea*. In *P. trifoliata* the vessels occur in irregular groups together with much parenchyma; rather many radial rows of two or three vessels are present.

In view of the above-mentioned resemblance with wood of the Recent species of *Phellodendron,* our wood is identified as *Phellodendron* sp.

Sample — no 1413.

Other comparable material — Zagwijn (1963) recorded pollen and seeds of *Phellodendron* from the sandy channel deposit.

SAPINDALES
ACERACEAE

Acer campestre L.
Plate 3, figs. 8 - 11.

Description — The growth rings are narrow, 0.25 - 0.75 mm wide; late wood has distinctly less pores than early wood.

The vessels occur solitary, or in radial rows of maximal three vessels; in cross section there are 120 - 140 vessels per mm^2. The intervascular pits are

alternating and have a diameter of 6 - 7 μm. Pits to parenchyma and rays are circular and have a diameter of 5 - 7 μm. Spiral thickenings are often present, perforations are simple.

The fibers have a diameter of 10 - 15 μm and 4 - 5 μm thick walls. The bordered pits in the walls have a diameter of 4 - 5 μm. Parenchyma is scanty, vasicentric, and paratracheal diffuse.

Wide rays are homogeneous, 1 - 10 cells wide, 6 - 100 cells high. The cell walls are 3 - 4 μm thick and pitted. The cells are 75 - 100 μm long and 10 μm high. Narrow rays are sometimes weakly heterogeneous because of the shorter and higher border cells: 12 - 14 μm high, 35 - 50 μm long.

Identification — The rather large pits between rays and vessels, the long ray cells, and the spirals are characteristics of the genus *Acer*. Within this genus a comparison was made with the wood of the following species: *A. barbatum, A. campestre, A. ginnala, A. macrophyllum, A. monspessulanum, A. negundo, A. nigrum, A. palmatum, A. plantanoides, A. pseudoplatanus, A. rubrum, A. saccharinum* and *A. saccharum*. Only *A. campestre* shows the same number of vessels per mm² in cross section. Moreover, the size and shape of vessels and rays are identical. Therefore our wood has been identified as *A. campestre* L.

Samples — no 1423, 1440, 1441, 1466, 1472, 1502, 1596, 1602.

Other comparable material — Zagwijn (1963) mentioned some pollen grains of *Acer* in the sandy channel sediment. Fruits of quite a number of species of this genus, e.g. *A. campestre,* are met with in the same locality.

RHAMNALES
VITACEAE

Vitis sylvestris Gmelin
Plate 3, figs. 12, 13.

Description — The growth rings are ca 1 mm wide; in the wide early wood one or two vessels, in the late wood radial multiples of narrow vessels occur.

In the early wood the vessels are 130 - 150 μm wide, in the late wood 10 - 20 μm. The broad early wood vessels are mostly solitary; the late wood vessels occur in radially stretched groups or rows. The perforations are simple. Intervascular pitting by up to 100 μm wide scalariform pits; the apertures are narrow (1.5 - 2 μm) and long (up to 90 μm). Pits to parenchyma are up to 20 μm wide and have up to 3 μm wide apertures. Pits to rays are circular with a diameter of 3 - 4 μm and are arranged in horizontal lines.

The fibers are septate. The walls have small bordered pits with a diameter of 2 - 3 μm. Paratracheal vasicentric parenchyma occurs as a uniseriate layer around the vessels.

The rays are 10 - 14 cells wide, up to 6 mm high, some narrower homogeneous and/or weakly heterogeneous rays are present; the latter have a single row of quadratic cells along the margin.

Identification — This wood resembles that of *Vitis vinifera* in every respect. It is, however, here included in the direct ancestor of the cultivated grape, viz. *Vitis sylvestris*.

Sample — no 1420.

Other comparable material — Zagwijn (1963) mentioned a great amount of seeds of *Vitis* cf. *sylvestris* from the channel sediment. He also observed some pollen grains of *Vitis*, as well as some tendrils.

APIALES
CORNACEAE

Cornus mas L.
Plate 4, figs. 1 - 3.

Description — The growth rings are narrow, 0.1 - 0.6 mm wide, the margins are only visible by the radially shortened elements.

The vessels have a uniform diameter (30 - 60 μm) all over the growth ring; they are solitary, they have an angular cross section shape and thin walls (2 μm). The perforations are scalariform with up to 25 bars. Pits to parenchyma and rays are circular or scalariform; their horizontal diameter is 4 - 10 μm. Pitting to fibers is by circular bordered pits with a diameter of 8 - 9 μm. Intervascular pits are scalariform and restricted to the tips of the vessel members.

The fibers have 4 - 5 μm thick walls with many 7 - 8 μm wide circular pits, scanty paratracheal and apotracheal diffuse parenchyma is present.

The rays are two to four, mostly three, cells wide and up to 30 cells high. Uniseriate rays are composed of upright cells. Multiseriate rays are heterogeneous, composed of procumbent and upright cells; the procumbent cells are 18 - 20 μm high and have 3 - 5 μm thick, pitted walls; the pits are circular with a diameter of 1 μm. Sheath cells are sometimes present.

Identification — The narrow solitary vessels, scalariform perforations, fibers with bordered pits, and heterogeneous rays are indicative for *Cornus*. Of the two Recent West-European species of this genus, *C. sanguinea* has rather low ray cells (10 - 14 μm). The height of the ray cells in *C. mas* (15 - 18 μm) closely resembles that in our wood. In all other respects the anatomy is identical and therefore our wood has been identified as *C. mas*.

Samples — no 1437, 1470.

Other comparable material — Zagwijn (1963) observed three fruits of this species in the sandy deposits from which our wood has been collected. Pollen has not been recorded.

ROSALES
ROSACEAE

Sorbus aucuparia L.
Plate 4, figs. 4 - 7.

Description — The growth rings are rather wide (1.5 mm) and have some rows of flattened elements at the margins.

The vessels are solitary; in the early wood they are somewhat more crowded than in the late wood. All have more or less the same diameter; 60 µm in radial, 40 µm in tangential direction. They are rounded to angular in cross section; in the crowded areas the vessels are at different places in contact with each other. The walls are 3 - 4 µm thick, with simple perforations. Spiral thickenings have often been observed, sometimes branched, usually nearly horizontal. Pits to parenchyma and rays are circular, 3 µm in diameter. Pitting to fibers by circular bordered pits with a diameter of 5 - 6 µm.

The fibers have bordered pits in the walls, 5 - 6 µm in diameter; no spiral thickenings were observed. Some scanty paratracheal vasicentric and apotracheal diffuse parenchyma is present.

The rays are homogeneous, uni- or bi-seriate, up to 25 cells high. The cell walls are 5 - 6 µm thick, pitted.

Identification — This wood is almost identical with that of *Sorbus aucuparia;* therefore our wood has been ascribed to that species.

Samples — no 1432, 1434, 1446.

Crataegus sp.
Plate 4, figs. 8 - 10.

Description — Growth rings are difficult to observe, at the margin a narrow layer of radially shortened elements occurs.

The vessels are solitary, with a uniform diameter all over the growth ring, they measure 40 µm in radial and 24 µm in tangential direction and are angular in cross section. The walls are 3 - 3.5 µm thick, spirals are present, perforations simple, and the average length of vessel members is 184 µm. The pits to rays and parenchyma are circular or horizontally elliptical with a diameter of 3 - 4 µm; pitting to fibers is by circular bordered pits with a diameter of 6 µm.

The fiber walls are 5 µm thick and have bordered pits with a diameter of 6 µm. The diameter of a lumen is 8 µm. Paratracheal vasicentric and apotracheal diffuse parenchyma is present.

The rays are homogeneous or weakly heterogeneous with only one row of upright cells; 1 - 3 (4) cells wide and 2 - 24 cells high. The walls are up to 3 µm thick, pitted.

Identification — Among the wood samples of Recent European trees and shrubs showing the combination of uniform narrow vessels and simple perforations, only that of *Crataegus* resembles the wood described above in all respects. Within the genus it is impossible to identify the species on the basis of wood anatomy, therefore our wood is described as *Crataegus* sp.

Samples — no 1428, 1459.

Prunus sp.
Plate 4, figs. 11 - 13.

Description — The margins of the growth rings are marked by a few rows of 0.2 - 1 mm wide radially flattened elements.

The vessels are mostly solitary and have a diameter of 40 - 60 μm; oblique spiral thickenings occur in the walls. The perforations are simple. Pits to parenchyma and rays alternate and are circular with a diameter of 3 - 4 μm. Pitting to fibers is by circular bordered pits, 4 - 5 μm in diameter. Intervascular pits alternate and have a diameter of 5 - 7 μm.

The fiber walls have elliptical bordered pits with a shortest axis of 2 μm and a longest one of 4 μm. The walls are 3.5 μm thick. Both paratracheal vasicentric and apotracheal diffuse parenchyma is scarcely present.

Two to nine cells wide heterogeneous multiseriate rays with sheath cells have at the margins up to five rows of upright cells and they are up to 60 (120) cells high. Uniseriate rays composed of upright cells are 4 to 12 cells high. The cell walls are 3 - 6 μm thick, pitted.

Identification — This wood closely resembles the wood of some species of *Prunus*. It differs from the wood of the genus *Acer* by the oblique widely spaced spiral thickenings, the smaller pits between vessel and ray, and the heterogeneous rays. Within the genus *Prunus* there is some resemblance with the wood of *P. mahaleb* and *P. spinosa* from Europe and *P. maximowiczii* from eastern Asia. These three species show rather wide rays in their wood *(P. maximowiczii* and *P. spinosa* up to six cells, *P. mahaleb* up to eight cells wide). Therefore *P. maximowiczii* and *P. spinosa* differ from the above described wood by the narrower rays. Moreover, in *P. maximowiczii* there are radial multiples of three or four vessels, whereas *P. mahaleb* has much more weakly heterogeneous rays. Consequently there is no species, to which the fossil wood can be ascribed with sufficient centainty, and therefore it has been identified as *Prunus* sp.

Samples — no 1410, 1411, 1444, 1460, 1465, 1471, 1503.

Other comparable material — Zagwijn (1963) recorded pollen from *Sorbus* and *Prunus* from the clay deposits at Tegelen but not from the source-sediment of our fossil wood. Among the fruits and seeds, *Crataegus* and *Prunus* could be identified. Macrofossils of *Sorbus* are still unknown.

PAPILIONACEAE

cf. *Cytisus* sp.
Plate 5, figs. 1 - 3.

Description — Growth rings were not observed in our small single specimen.

Vessels are arranged in groups, connected by tangential parenchyma bands. The diameter of the wider vessels is up to 60 μm, that of the narrow vessels up to

20 µm; the walls show spiral thickenings. Pits to parenchyma and rays are elliptical, up to 6 µm wide; sometimes they are scalariform, up to 15 µm wide. Intervascular pits have a diameter of 6 - 7 µm, the apertures are fused to superficial grooves. The perforations are simple.

No normal fibers are present; parenchymatical substitute fibers with narrow lumina and storied structure occur instead. In addition to the above mentioned parenchymatical fibers, paratracheal parenchyma is present in irregular tangential bands, also with storied structure.

The rays are 1 - 12 cells wide, homogeneous, up to 2 mm (180 cells) high.

Identification — The structure of the pits, the presence of substitute fibers, and the spiral thickenings in the narrow vessels are indicating for wood of the Papilionaceae. Within this family there is some resemblance with the wood of *Cytisus*. However, this wood always shows some fibers. Because of the absence of fibers it is impossible to identify the fossil wood with certainty on a generic level. Therefore it has been described as cf. *Cytisus*.

Sample — no 1475.

Other comparable material — Pollengrains and seeds of the Papilionaceae have not been recorded from the deposits in the vicinity of Tegelen.

OLEALES
OLEACEAE

Fraxinus excelsior L.
Plate 5, figs. 4 - 6.

Description — Growth rings are clearly visible, the wood is definitely ringporous.

The diameter of the vessels in the early wood is 200 - 250 µm, in the late wood 30 - 50 µm. The walls are 7.5 µm thick, the vessel members are short (250 µm), the perforations are simple. The intervascular pits are circular or horizontally elliptical, alternating, and have a diameter of 6.5 µm. Pits to rays are circular with a diameter of 3.2 µm.

The fibers in the early wood have lumina of 12.5 µm diameter. The walls of the fibers are 3 - 4 µm thick and have bordered pits with a diameter of 2 µm. Paratracheal vasicentric parenchyma occurs as a one or two cells wide layer around the vessels; especially in the early wood they are often fused to irregular tangential bands.

The rays are one to three, generally two, cells wide and 1 - 15 cells high, weakly heterogeneous. Their walls are 5 µm thick, pitted. Along the margins there is a single row of square cells.

Identification — This wood is identical with that of *Fraxinus excelsior*. The other European species of *Fraxinus, F. ornus,* is less definitely ring-porous and has rays up to 30 cells high. According to Jane (1970) the other non-European species of the genus, with the exception of *F. nigra,* are difficult to separate from *F. excelsior* on wood-anatomical characters. Therefore our wood could also be compared with these species. However, for reasons of probability it has been included in *F. excelsior* rather than any American or Asiatic species.

Samples — no 1405, 1407, 1408, 1409, 1415, 1417, 1421, 1435, 1438, 1439, 1442, 1445, 1448, 1450, 1451, 1453, 1456, 1457, 1463, 1468, 1478, 1479, 1485, 1487, 1488, 1491, 1519, 1520, 1522, 1527, 1529, 1531, 1532, 1533, 1592, 1599, 1601.

Other comparable material — The pollen grains of *Fraxinus* are quite common in the Tegelen deposits (Zagwijn, 1963). Fruits of this genus have not been recorded; their absence is considered to be the result of rapid desintegration.

SALICALES
SALICACEAE

Populus nigra L.
Plate 5, figs. 7 - 9.

Description — The growth rings are narrow, 1.5 - 2 mm wide.

The vessels occur solitary and in radial multiples of mostly three, maximum four. The diameter of solitary vessels is 80 - 90 µm. The perforations are simple. Intervascular pits are circular with a diameter of 8 - 10 µm, their aperture is horizontally elliptical. Pits to parenchyma were not observed; pits to rays are coarse, irregular, and have a diameter of 7.5 - 10 µm.

The fibers are thin-walled, no pits were observed. Very scanty vasicentric parenchyma is present.

The rays are uniseriate, homogeneous, up to 20 cells high. The height of the cells is 15 - 18 µm. Horizontal walls are 3 - 4 µm thick and pitted. Pits to fibers are simple, small (0.8 - 1 µm). Pits to vessels occur only in the marginal rows, sometimes, however, over the entire height of the rays.

Identification — Because of its simple vessel-perforation, coarse vessel-ray pits, and uniseriate homogeneous rays, this wood has been included in the genus *Populus*. Within the genus it has been compared with the wood of *P. alba, P. tremula,* and *P. nigra*. The wood of *P. alba* differs by its lower ray cells (12 - 15 µm), higher rays (up to 34 cells), smaller intervascular pits (7 - 8 µm) with slit-like apertures, stronger irregularly formed coarse vessel-ray pits with a diameter of 7 - 11 µm, and its radial rows of up to six vessels.

Also, the wood of *P. tremula* has rather strongly irregular pits with a range in diameter of 6 - 11 µm, as well as radial rows of up to six vessels. In addition, it shows rather abundant solitary vessels. The rays can well be compared with those of our wood. This also applies to the height of the ray cells but the horizontal walls are thicker (up to 5 µm).

The wood of *P. nigra* has radial rows of 3 - 4 (5) vessels. The coarse pits between vessels and rays (diameter 7.5 - 9 (10) µm) are irregular, though not as strongly as in *P. alba* and *P. tremula*. It shows circular intervascular pits with elliptical apertures and a diameter of 8 - 10 µm. It resembles in every respect our fossil wood, and the latter has therefore been included in *P. nigra*.

Samples — no 1419, 1452.

Other comparable material — Zagwijn (1963) recorded pollen of *Populus* from the clay deposits at Tegelen, but not from the source-sediment of our fossil wood. In his list of seeds and fruits the genus is not mentioned.

JUGLANDALES
JUGLANDACEAE

Carya sp.
Plate 6, figs. 4 - 6.

Description — Growth rings were not observed.

The vessels occur solitary or in short radial rows. The wall thickness is variable in the preparations. According to the size of the intervascular pits the original thickness of a double wall must have been 20 - 25 μm. The perforations are simple. Intervascular pitting is by sexangular bordered pits; pits to rays and parenchyma are sometimes very irregular and coarse having a diameter of 8 - 10 μm.

The fibers have thick-walled circular bordered pits with a diameter of 3 - 4 μm. Paratracheal vasicentric parenchyma and also apotracheal uniseriate tangential bands are present.

The rays are one to three, generally two, cells wide, homogeneous or weakly heterogeneous with up to three rows of square cells at the margins. The height of the procumbent cells is 20 μm, the wall thickness 3 μm.

Identification — The almost homogeneous rays, reticulate parenchyma, and the shape of vessels and pits are known from the wood of certain genera of the Juglandaceae. According to Müller-Stoll and Mädel (1960) the presence of very thick intervascular walls is a characteristic of the genus *Carya*. Any identification beyond the rank of the genus is impossible because of the similarity in wood structure of the different species of *Carya*.

Samples — no 1526, 1600.

Pterocarya sp.
Plate 6, figs. 7 - 9.

Description — The growth rings are narrow, about 1 mm wide, bordered by a terminal uniseriate parenchyma-band.

The vessels occur solitary or in short radial rows of up to three vessels. In the early wood they have a diameter of 90 - 150 μm, which in the late wood gradually decreases to 40 μm. The perforations are simple. The walls are thin, a double wall measuring only 5 - 6 μm. Pits to rays and parenchyma are coarse and circular to elliptical with a diameter of 6 - 9 μm. The alternating intervascular pits are flattened to sexangular and have a diameter of 10 μm.

The fibers are rather thin-walled (up to 6 μm) and have circular bordered pits with a diameter of 3 - 4 μm. Paratracheal vasicentric parenchyma occurs as a uniseriate band around the vessels; apotracheal parenchyma is reticulate; uniseriate and uniseriate-terminal bands occur.

The rays are one to three, mostly two, cells wide, up to 22 cells high and

weakly heterogeneous with a single row of square cells along the margins.

Identification — Also this type of wood is known from the Juglandaceae. According to Müller-Stoll and Mädel (1960) the presence of thin walls, vessels, and fibers is a characteristic of *Pterocarya* as well as some species of *Juglans (J. cinerea, J. sieboldiana, J. mandschurica, J. stenocarpa).* If compared with our wood and *Pterocarya, J. cinerea* has vessels with a smaller diameter. Moreover, the latter species can be distinguished by the more pronounced horizontally elliptical shape of the coarse pits between vessels and rays or parenchyma. This also applies to the Asiatic species of *Juglans.* The resemblance with the wood of *Pterocarya fraxinifolia* is striking. The other species of the genus could, however, not be examined. Therefore our material has been identified as *Pterocarya* sp.

Samples — no 1404, 1414, 1424, 1455, 1461, 1464, 1467, 1469, 1473, 1474, 1476, 1480, 1481, 1484, 1489, 1492, 1495, 1496, 1497, 1498, 1499, 1521, 1523, 1524, 1528, 1530, 1593, 1594.

Other comparable material — Zagwijn (1963) mentioned pollen both of *Carya* and *Pterocarya* from Tegelen. Although pollen of *Carya* has been found only in small amounts, it is regularly present. The pollen of *Pterocarya,* which is far more abundant, can be divided in two types. The first type, found in the clays below the channel from which our material has been collected, is considered to be identical with pollen of *Pterocarya fraxinifolia.* The other type, which is present in the channel deposits, has not been included in a Recent species. A large amount of seeds of *Pterocarya* has been collected, referred to the fossil species *P. limburgensis,* which is, as was pointed out by Kirchheimer (1957), different from *P. fraxinifolia.* Fruits of the genus *Carya* are unknown from the deposits of Tegelen.

Discussion

COMPARISON WITH RECENT EUROPEAN FOREST VEGETATIONS

The general qualitative and quantitative composition of our wood flora (Table 1) indicates that the source vegetation has been a deciduous forest with some coniferous elements.

With regard to the vegetation-type there seems to be a fair degree of similarity with the flood-plain forests of western Europe (Oberdorfer, 1953; Doing, 1962). The following of our angiosperm taxa are known to be more or less regular components of the latter vegetation type: *Tilia, Cornus mas, Vitis sylvestris, Ulmus* sp., *Populus nigra, Crataegus* sp., *Prunus* sp., *Acer campestre,* and *Fraxinus excelsior.* In our material these taxa represent 49.9% of the samples.

A striking difference, however, is the total absence of conifers from European flood plain forests (17,7% of our samples). At present *Picea omorika* is restricted to a small area in the Balkan peninsula; no stringent conclusions with regard to the fossil vegetation type can be drawn from the environment of this species. *Picea abies* can be observed in the lower plains of northern Europe.

However, more to the south the species is restricted to mountain ranges and does not occur in conjunction with the above-mentioned angiosperm flora. The occurence of *Abies alba* is exclusively limited to these mountain ranges. *Pinus cembra* is a montane-sub-alpine species.

Another difference is the absence of a number of our taxa in the flood plain forest. Most of these taxa are not indicative for specific vegetation types, with the exception of *Pterocarya* and *Celtis*. The latter genera (25.4% of our samples) are important constituents of the humid forests of the Pontic area.

Because of the dominance in our material of the genera *Pterocarya, Fraxinus, Acer,* and *Prunus* as well as the presence of *Vitis,* the fossil vegetation must have been a humid one having very strong affinities to the Recent flood plain forests. The problem of the occurrence of coniferous elements in such a vegetation will be discussed below.

COMPARISON WITH FLORAS OUTSIDE EUROPE

North America — A comparison between the composition of the European and

Table 1. Comparison between the fossil wood-flora of Tegelen and related taxa in some Recent floras.

	European flood-plain forest	Manchurian deciduous forest	Hokkaido deciduous forest	mixed mesophytic forest of eastern Asia	eastern North American flood-plain-forest and upland forest	Pontic forest	number of samples	percentage of samples
Pinus spp.	—	+	+	—	+	—	4	3.1
Picea spp.	—	—	—	+	+	+	15	11.5
Abies alba	—	—	—	+	+	+	1	0.8
Chamaecyparis cf. *thyoides*	—	—	—	—	—	—	2	1.5
Magnolia sp.	—	+	+	+	+	—	4	3.1
Ulmus sp.	+	+	+	+	+	+	3	2.3
Celtis sp.	—	+	+	—	—	+	5	3.8
Tilia sp.	+	+	+	+	+	+	1	0.8
Phellodendron sp.	—	—	+	+	+	—	1	0.8
Acer campestre	+	+	+	+	+	+	8	6.2
Vitis sylvestris	+	+	+	+	+	+	1	0.8
Cornus mas	+	+	+	—	+	+	2	1.5
Crataegus sp.	+	—	+	+	+	+	2	1.5
Sorbus aucuparia	—	—	+	+	+	+	3	2.3
Prunus sp.	+	+	+	+	+	+	7	5.5
cf. *Cytisus* sp.	—	—	—	—	—	—	1	0.8
Fraxinus excelsior	+	+	+	+	+	+	37	28.3
Populus nigra	+	+	+	—	—	—	2	1.5
Carya sp.	—	+	+	—	—	—	2	1.5
Pterocarya sp.	—	—	+	+	—	+	28	21.6
Indet.	—	—	—	—	—	—	1	0.8
Percentage of taxa	45	60	80	75	75	70		
Percentage of samples	48	60	85	89	70	88		

the North American flood plain forests clearly shows the higher degree of species diversity in America, as well as the abundance of vines. Here the following of our genera occur: *Tilia, Cornus, Vitis, Carya, Ulmus, Celtis, Populus, Prunus, Acer* and *Fraxinus*. In the surrounding upland forests one can observe *Tilia, Cornus, Carya, Magnolia, Prunus, Acer* and *Fraxinus* (Knapp, 1965, Küchler, 1964; Braun, 1950). Together these genera represent 60% of our flora (also 60% of our samples; see Table 1).

Eastern Asia — According to Wang (1961) and Hara (1959) one may observe in the mixed mesophytic forest of eastern Asia *Tilia, Cornus, Carya, Magnolia, Phellodendron, Vitis, Pterocarya, Ulmus, Celtis, Populus, Crataegus, Sorbus, Prunus, Acer* and *Fraxinus*, with eventually some *Pinus*. Other conifers are not to be found. Together these genera represent 80% of our flora (85% of our samples). According to Hara (1959) the following woody plants may be observed in S. W. Hokkaido: *Tilia, Magnolia, Phellodendron, Vitis, Ulmus, Populus, Sorbus, Prunus, Acer,* and *Fraxinus*. At some places there is an admixture with montane coniferous-forest elements, e.g. *Abies* and *Picea*. Similar forests occur on the northern part of Honshu; here also *Pterocarya* and *Crataegus* can be found. This extremely rich flora contains 75% of our genera (89% of our samples).

Another rich flora has been described by Wang (1961) from N. Manchuria. He mentions *Tilia, Cornus, Magnolia, Phellodendron, Vitis, Ulmus, Populus, Crataegus, Sorbus, Prunus, Acer, Fraxinus, Pinus tabulaeformis* and *P. koraiensis*. Especially the latter species is a common element. It is a near relative of *P. cembra* and is very tolerant with regard to a wide range of climatic conditions. The adjoining montane forests contain, among other taxa, *Picea, Abies, Pinus koraiensis* together with an admixture of *Acer, Prunus, Sorbus, Phellodendron, Tilia, Fraxinus,* and *Vitis*. The forests of this region contain 75% of our genera (70% of our samples; see Table 1).

Pontic region — Another occurrence of a comparable flora is found in the Pontic region. Here we find in the low elevations (0 - 500 m) restricted occurrences of forests. These forests include *Tilia, Cornus, Vitis, Pterocarya, Ulmus, Celtis, Populus, Crataegus, Sorbus, Prunus, Acer, Fraxinus, Picea,* and *Abies*. *Pterocarya* occurs especially along brooks and streams in elevations lower than 360 m, and together with *Celtis* and *Alnus* in and along marshes in the plain. *Picea* and *Abies* on the contrary are to be observed only in the higher parts (Radde, 1899; Rikli, 1945). According to Rikli the enormous precipitation enables the montane and plain elements to form a mixed vegetation. The Pontic forests contain 70% of our genera (88% of our samples; see Table 1).

CLIMATE

The best vegetations for comparison with our flora are to be found in the Pontic region and in N. E. Asia (N. E. Manchuria and Hokkaido). By using the climatic data from these areas, we can now try to reconstruct the Tiglian climate at the time of the deposition of the channel sediments (Table 2).

The climatic data and the occurrence of *Picea, Pinus,* and *Abies* in our material point to a situation with a rather indistinct zonation from which a high amount of precipitation may be concluded. Whereas both *Celtis* and *Pterocarya* are present in our material but unknown from N. E. Manchuria and Hokkaido,

the palaeoclimate must have been less severe than the Recent climate in these regions. This is in agreement with the present day distribution of the other identified species. The reconstruction of some climatic conditions is as follows: mean annual temperature: ca 10°C, mean temperature warmest month: ca 20°C, mean temperature coldest month: 4 - 6°C, amount of precipitation: more than 1200 mm. These conditions corresponds with a rather soft and moist climate.

Table 2. Climatic data concerning regions with floras comparable to the Tiglian forest.

Region	mean annual temperature	mean temperature warmest month	mean temperature coldest month	amount of precipitation
NE Manchuria	2 - 4°C	22°C	—18 - —20°C	500 - 700 mm
Hokkaido	6 - 10°C	21 - 23°C	—2 - —5°C	< 1500 mm
Pontic region	14 - 15°C	23 - 26°C	4.5 - 6°C	1200 - 2600 mm
Tegelen during the Tiglian second climatic optimum	± 10°C	± 20°C	4 - 6°C	> 1200 mm

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Manuscript received 28 May 1974.

Plate 1

Pinus cembra

1. Cross section, 40 x.
2. Radial section, crossfield, 400 x.
3. Tangential section, 100 x.

Pinus cf. *tabulaeformis*

4. Cross section, 100 x.
5. Radial section, ray-tracheids, dentition, 400 x.

Picea cf. *omorika*

6. Cross section, 100 x.
7. Radial section, 400 x.
8. Tangential section, ray with resin duct, 400 x.

Picea abies

9. Cross section, 100 x.
10. Radial section, 400 x.
11. Tangential section, 100 x.

PLATE 1

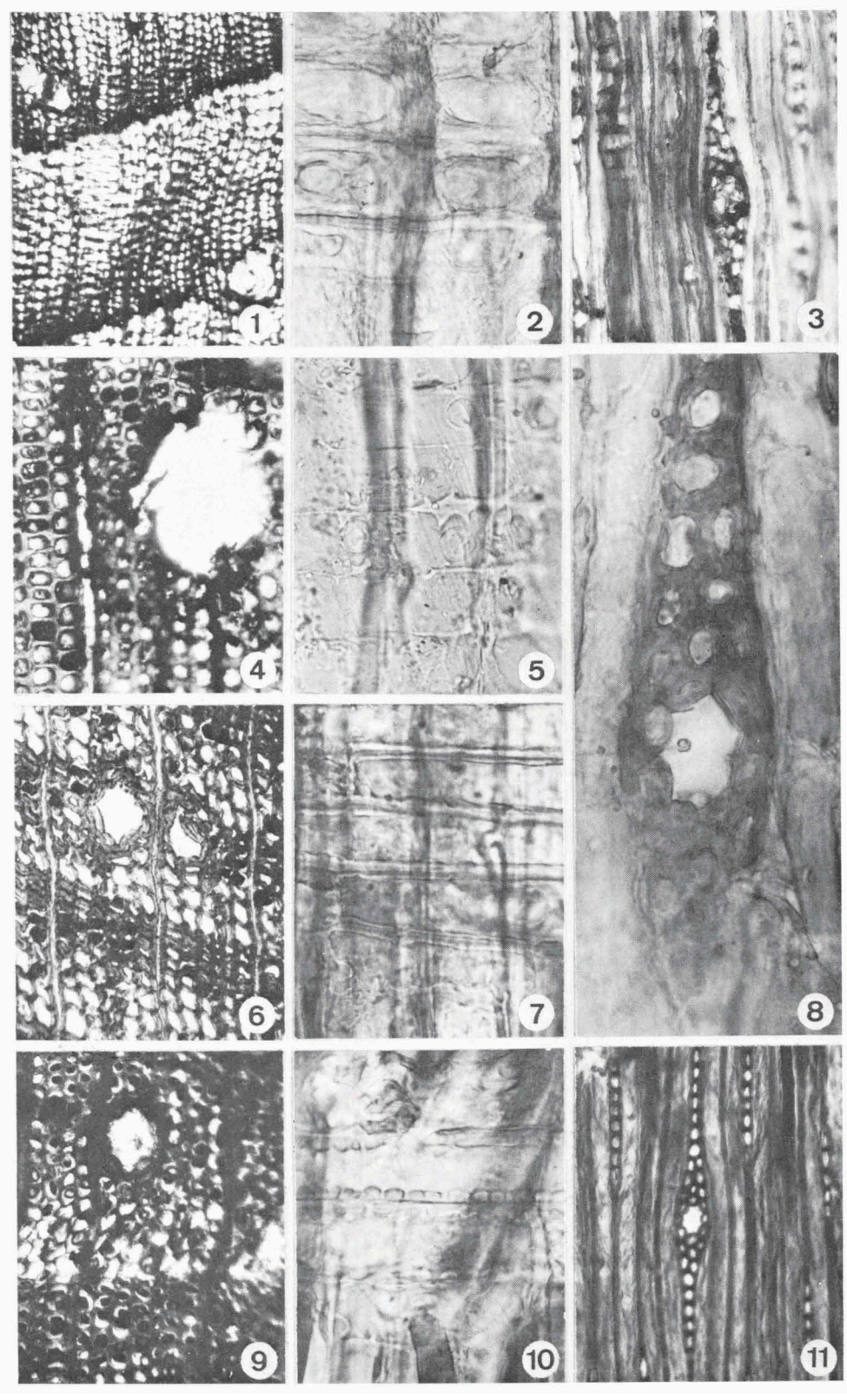

Plate 2

Abies alba

1. Cross section, 40 x.
2. Radial section, 400 x.
3. Tangential section, 100 x.

Magnolia sp.

4. Radial section, wood-parenchyma with pits, 700 x.
5. Radial section, vessel-ray pits, 700 x.
6. Tangential section, ray, 400 x.

Ulmus sp.

7. Cross section, 100 x.
8. Tangential section, narrow vessels with spirals, 600 x.
9. Tangential section, 100 x.

Celtis sp.

10. Cross section, 100 x.
11. Radial section, early wood vessel with spirals, 400 x.
12. Tangential section, 100 x.

PLATE 2

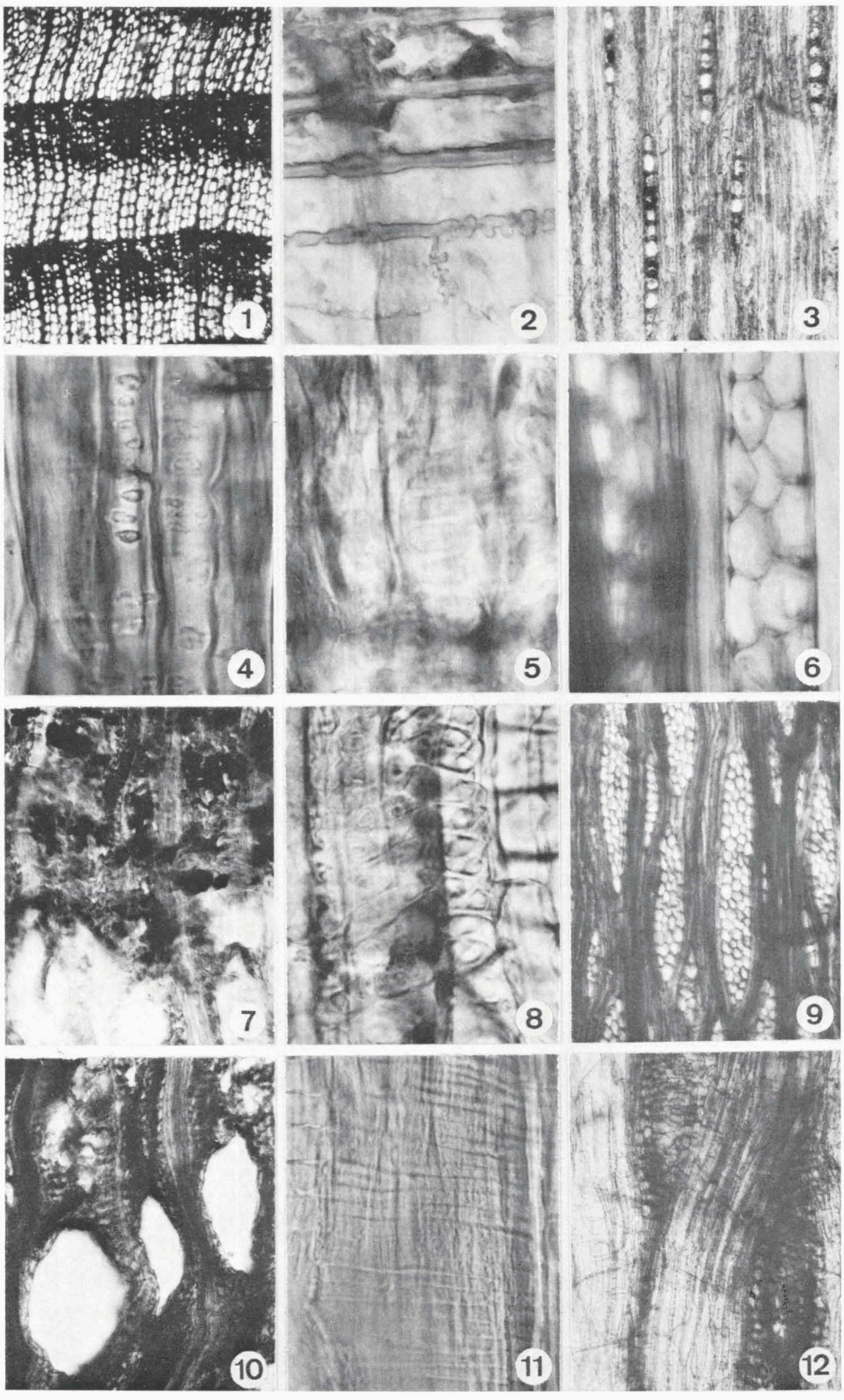

Plate 3

Tilia sp.

1. Radial section, pits in vessel walls, 400 x.
2. Radial section, spirals in vessel wall, 1000 x.
3. Tangential section, 100 x.

Phellodendron sp.

4. Cross section, 100 x.
5. Radial section, spirals in vessel wall, 600 x.
6. Radial section, pits in vessel wall, 700 x.
7. Tangential section, 100 x.

Acer campestre

8. Cross section, 40 x.
9. Radial section, pits in vessel wall, 400 x.
10. Tangential section, 100 x.
11. Radial section, spirals, 400 x.

Vitis sylvestris

12. Cross section, vessels, 100 x.
13. Tangential section, vessel and ray, 100 x.

PLATE 3

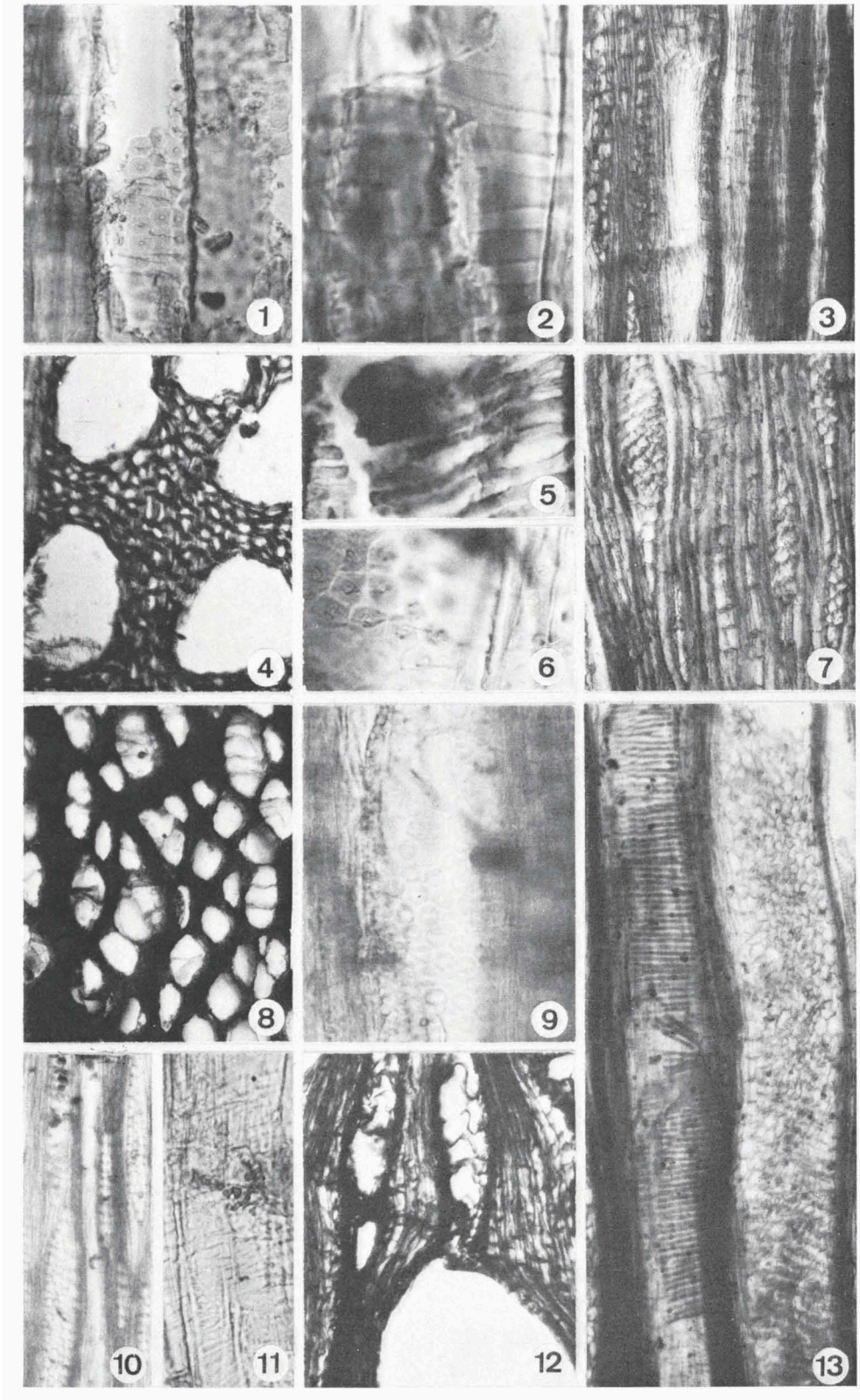

Plate 4

Cornus mas

1. Cross section, 100 x.
2. Radial section, part of a scalariform perforation, 400 x.
3. Tangential section, 100 x.

Sorbus aucuparia

4. Cross section, 40 x.
5. Radial section, pits, 400 x.
6. Radial section, pits, 400 x.
7. Tangential section, 100 x.

Crataegus sp.

8. Cross section, 100 x.
9. Radial section, pits, 600 x.
10. Tangential section, 40 x.

Prunus sp.

11. Cross section, 100 x.
12. Radial section, pits and spirals in vessel wall, 700 x.
13. Tangential section, 100 x.

PLATE 4

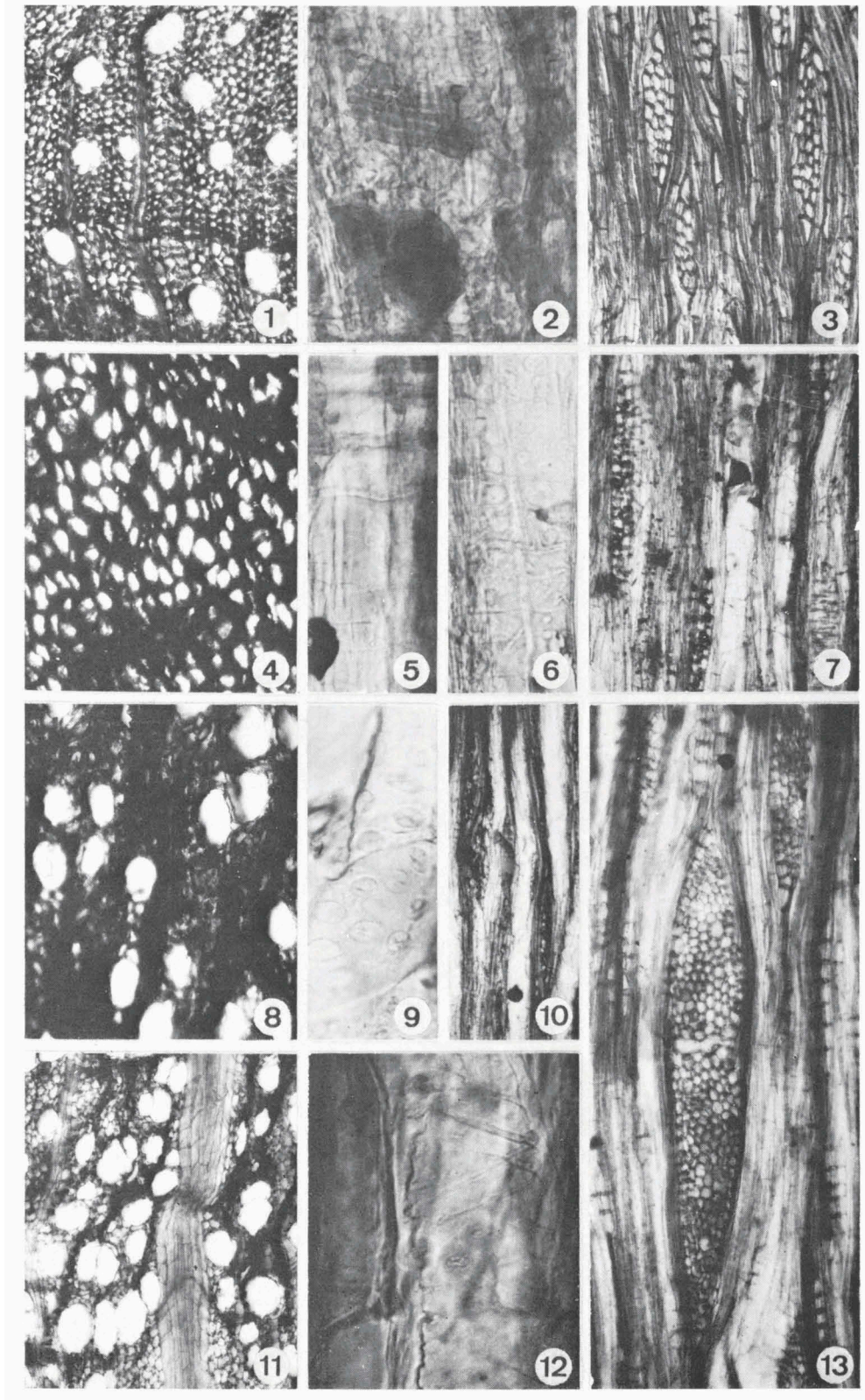

Plate 5

cf. *Cytisus* sp.

1. Cross section, 40 x.
2. Radial section, vessel with pits, 400 x.
3. Tangential section, 40 x.

Fraxinus excelsior

4. Cross section, 40 x.
5. Radial section, pits in vessel wall, 400 x.
6. Tangential section, 40 x.

Populus nigra

7. Cross section, 100 x.
8. Tangential section, 100 x.
9. Radial section, vessel-ray pits, 600 x.

PLATE 5

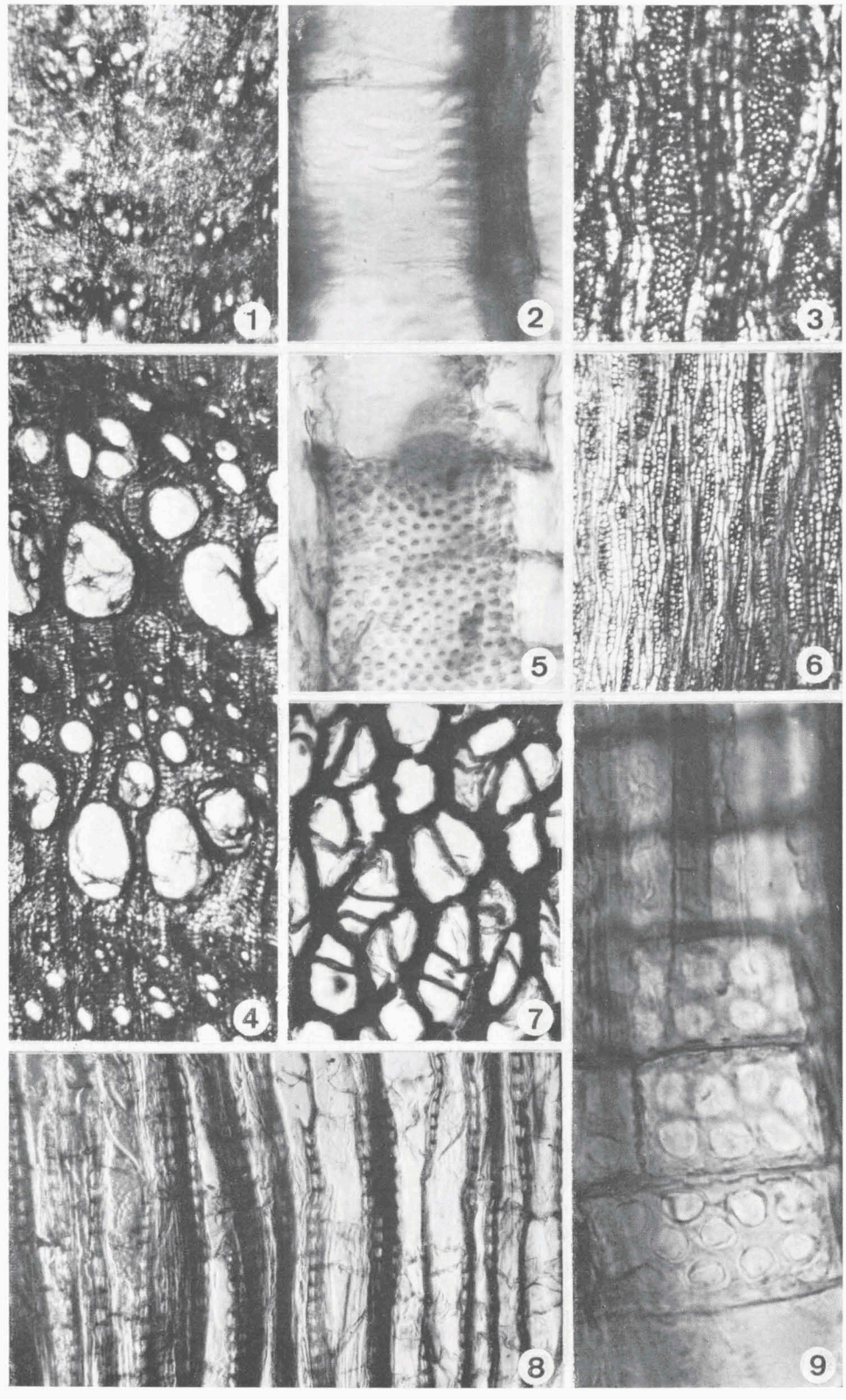

Plate 6

Chamaecyparis cf. *thyoides*

1. Cross section, 40 x.
2. Radial section, crossfields, 400 x.
3. Tangential section, 100 x.

Carya sp.

4. Radial section, 400 x.
5. Tangential section, 100 x.
6. Tangential section, 100 x.

Pterocarya sp.

7. Cross section, 100 x.
8. Radial section, pits in vessel wall, 400 x.
9. Tangential section, 40 x.

PLATE 6