POLYPHYLETIC ORIGIN OF ANGIOSPERMS IN THE LIGHT OF XYLOTOMY

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Abstract

The author considers, contrary to Takhtajan's theory of monophyletic origin, that a poly-phyletic origin of the Angiosperms is more probable, and wants to support his opinion by xylotomy of the homoxylous *Drymis*, comparing it with a *Juniperus* and a *Magnolia*. As *Drymis* has only tracheids with simple pits and is without vessels, while in the Magnoliales vessels occur, and as the tracheidic state is more primitive than the vessel-containing one, the homoxylous trees could therefore, not originate from Magnoliales.

It is not only today that the author asserts the polyphyletic origin of Angiosperms, he also did this sixty years ago.

Introduction

According to the system of the prominent Soviet phylogeneticist, TAKHTAJAN, 32 families belong to the order Magnoliales, comprising 165 genera and approxima-tely 700 species. Approximately 45,000 photomicrographs of sections from 16,000 samples of these trees were made by H. GOTTWALD of Hamburg, the Director of the Institute for Wood Research, in order to decide whether the development and relationship of Angiospermae could be ascertained on a xylotomic basis and whether the primitive type is represented by the *Magnoliales* with the other angiosperms — including *Monocotyledons* — descended from the that is to say whether these were the older, i.e. the more primitive ansgiosperms. H. GOTTWALD rendered an account of his work in a particular monograph (Plant. Syst. Evol. Suppl. pp. 111–121, 1977), delivered also at the International Symposium of Botanical Taxonomists. He has sent a reprint of this with a covering letter to the author. In this he writes: "Es geht hierbei um die von TAKHTAJAN wiederholte — aber nicht von den Systematikern geteilte Auffassung — dass alle lebenden höheren Pflanzen von den Magnoliales abzuleiten sind. Nach xylotomischen Merkmalen ist dies nicht vertretbar, da es außerhalb der *Magnoleales* noch primitivere Familien gibt, wie z. B. die *Hetoxica-ceae, Dilleniaceae* u. a., die außerdem ein so differenziertes Strukturbild aufweisen, daß diese *unmöglich* (italics added: P. G.) aus den *Magnoliales* hervorgegangen sein können".

The author already took a completely similar point of view 60 years eralier (1918) and again in his recently (1955, 1964, 1971, 1979) published papers. (Cf. References). When the author received H. Gottwald's reprint, he took out his old sections and now wants to contribute to throwing new light upon this much discussed questions, adducing newer data, and thoughts among them same xylotomical ones. The direct origin of Angiosperms from Gymnosperms is considered as probable by

more than one phylogeneticist, e.g. by the Hungarian Soó, the Viennese EHREN-DORFER, etc. because there are not known any so-called transitional forms, accepted by everybody, between the extant Angiosperms and Gymnosperms. But taking a closer look at the so-called homoxylic trees *(Drymis,* certain xylotomic character-istics of these will appear to be suitable for establishing likely phylogenetic con-nections in our opinion, such a xylotomic relationship is revealed Viennese EHREN-DORFER, etc., because there are not known any so-called transitional forms, accepted by everybody between the extant Angiosperms and Gymnosperms. But taking a closer look at the so-called homoxylic trees *(Drymis, Tetracentron, Trochodendron)* from among the Angiosperms, certain xylotomic characteristics of these will appear to be suitable for establishing likely phylogenetic connections in our opinion, such a xylotomic relationship is revealed for instance by the tropical *Drymis winteri,* on the one hand with the Gymnosperms, more precisely the Conifers and on the other hand with the heteroxylic dicotyledonous *Magnolia acuminata,* and other *Angio-sperms.* In order to be deliberate this question, we considered it desirable to compare with one another the xylotomies of a Conifer *(Juniperus mactropoda),* a homoxylic tree *(Drymis winteri)* and a heteroxylic dicotyledon *(Magnolia acuminata),* reporting on the conclusion drawn from these.

However, in comparing the secondary xylem of homoxylic trees we have to think, in addition to the Conifers, of the Cycadaceae, also from among the Gymnosperms, and the Monocotyledons, more exactly the Arecaceae from the Angiosperms. These trees have, however, a quite different tissue structure. The Cycadaceae have, a very voluminous pith and a mono- or multilayer (monoxylic, polyxylic) xylem and pith ray. The palms, however, have scattered vascular bundles but without definite pith rays. The comparison of them, with homoxylic trees would, therefore, be known in advance to be useless and thus it cannot come into consideration in ascertaining the relationship. This seems, on the other hand, to confirm that among the present-day Angiosperms and the Gymnosperms several maintypes are living, or have lived, which are anatomically quite different and of different origin. They are, therefore, both of polyphyletic descent. The author wants to support the correctness of a comparison like this — separately from the genetic arguments in one (1979) of his latest papers — in the following, with some xylotomic arguments and photographs, on the basis of transverse, tangential and radial sec-tions of trunks.

Plate 1. Photograph 1. Cross-section of *Juniperus macropopoda*, with annual-ring boundary and scanty parenchyma cells; no vessels. (x75).
     Photograph 2. Cross-section of *Drymis winteri*. On the left, there is an aggregate pith ray; no vessels. (x70).
     Photograph 3. Detail of photograph 2. Figures indicate the tracheids, lettersthe pith rays. (x130).
     Photograph 4. Magnolia acuminata. Vessels and clusters of vessel occuring at the bound-aries of annual rings. The ground substance is: xylem-fibres, wood parenchyma and tra-cheids. (x200).
     Photograph 5. Aggregate pith ray of *Alnus glutinosa*, alongside it isolated or grouped vessels. (x150).

Plate 1
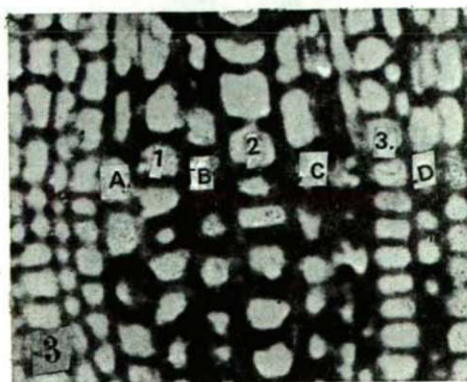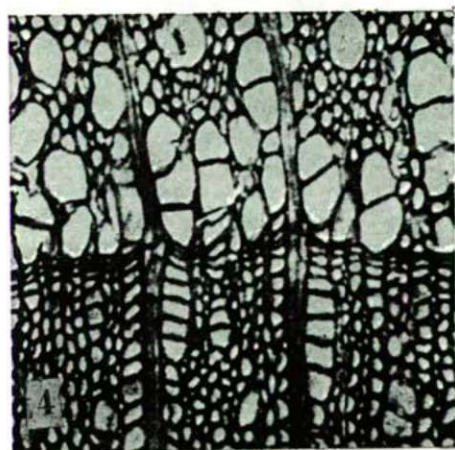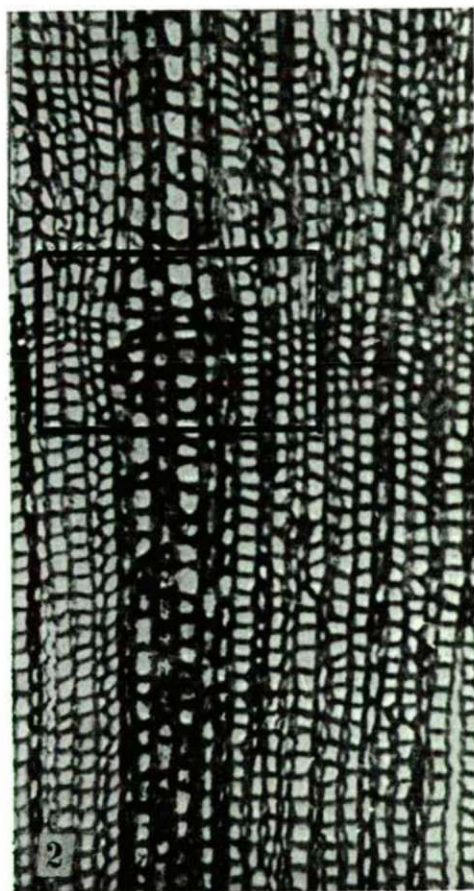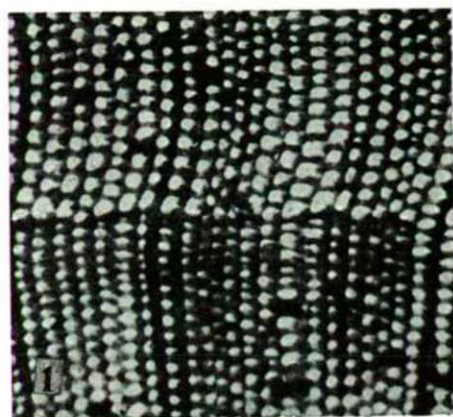
Comparison of transverse sections

Plate 1. Photograph 1 illustrates the structure of a Conifer *(Juniperus macropoda)* in transverse section. In the xylem, there are only tracheids and very scanty wood parenchymas. The tracheids in cross-section are angular or slightly rounded. As to their size, they are entirely homogeneous, there being small differences only at the boundary of annual rings. At the hardly observable annual-ring boundaries, the tracheids slightly flatten out. The pith rays are generally uniseriate. Multiseriate or aggregate pith rays — except in cases of Conifers with intercellular canals containing resin — do not occur in Conifers.

In the middle of the photograph and on the right side, in the "basic substance", 6 to 8 tracheid bundles seem to be separated a little, together with pith rays. Although this separation is not very distinct, yet the cross-sections of the smaller and larger tracheids make us think that this may possibly be the point of origin of aggregate pith rays. Aggregate pith rays first occur in certain types of the dicotyledonous Amentiflorae *(Alnus, Carpinus,* etc.) in which the shorter pith rays of breadth 1–3 are densely arranged, close to one another, and, consequently, there are between them no water conducting (tracheary) elements (Cf. Photograph 5a, x75).

Phot. 2. The structure of *Drymis winteri* in transverse section is generally very similar to that of Coniferae according to the significant observation that the xylem consists here, too, of thick-walled tracheids, rarely of wood fibres, with vessels (and perhaps in this species parenchyma cells, too) completely absent. The broad pith rays consist of short, square pith ray cells. The annual-ring boundary is indicated by slightly flattened tracheid series. On the left of the photograph stretches, a broader so-called aggregate pith ray. These are enclosed by so = called limiting cell series (perhaps primitive transverse tracheids??) which also verifies the heterogeneous structure of the pith ray. The inner pith-ray cells are rather square and much smaller than the tracheid series lying beside them. (Cf. also with Phot. 12) (x70).

Phot. 3 is an detail of phot. 2, in which the pith-ray cells and the tracheid series are seen, at a higher magnification (x130).

Phot. 4. The structure of the heteroxylic *Magnolia acuminata* in transverse section differs fundamentally from the two former tree types in as much as this tree already has vessels and the "basic substance" is filled with tracheids, wood parenchyma, and wood fibres. The vessels, which have large lumina are close to one another in the spring wood and at the boundary of annual rings they form a continuous wood. (tree with porous rings). The vessels in the field of annual rings are solitary or in pairs or groups, sometimes in pore-rays of 6 to 8 members. These three kinds of a new element distinct from former ones seem to make certain the verification of a more recent and higher stage of development (division of labour), i.e. greater perfection (x200).

Plate 2. Photograph 6. Tangential photograph of *Juniperus macropoda.* The pith rays are uniseriate. No vessels. (x150).
Photograph 7. Tangential photograph of *Drymis winteri.* On the right, pith. The pith rays of 1—3 layers. On the left, a broad pith ray. (x100).
Photograph 8. Single pith-ray cells, arranged in the broad pith ray of *Drymis winteri,* in longitudinal rows, in orthostichons and parastychons. These are indicated in the photograph by dotted black lines. (x300).
Photograph 9. Tangential section of *Magnolia acuminata.* In the vessels there is opposed, ladder-like thickening.

Plate 2
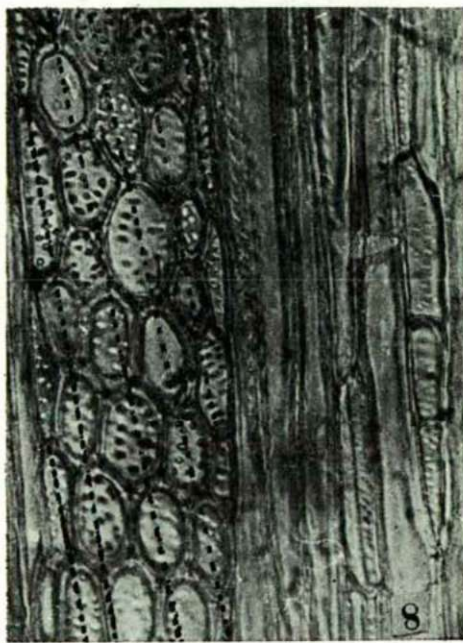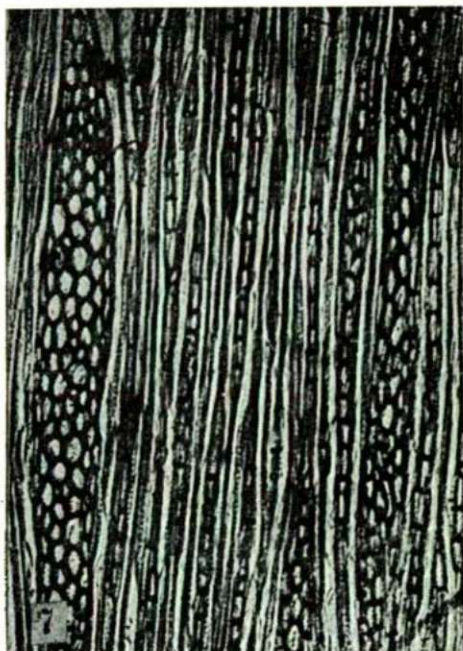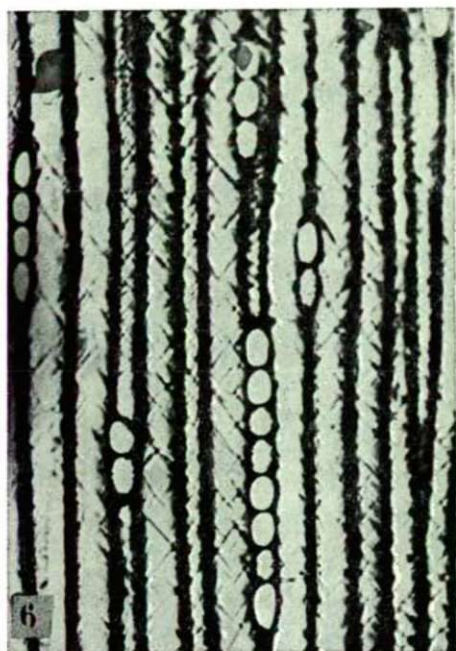
Phot. 5. illustrates the structure of the aggregate pith ray of *Alnus glutinosa*, in transverse section. This belongs to the series of dicotyledonous amentiferous plants (Amentiflorae). The single pith rays draw near to one another in the middle, between the tracheid series, their sum total reminds us of a quite broad pith ray (aggregate ray, gehäufter Markstrahl). This structure is very similar, even in its details, to the aggregate pith ray of *Drymis winteri*. A pith ray, like this, never occurs in the Magnoliae. Accordingly, this characteristic of *Drymis winteri* or *Alnus glutinosa* could not originate from any of the Magnoliales, which do not contain anything like this. This is a quite primitive characteristic, i.e. it is more ancient than the developed vascular state of the Magnoliales. BAILEY and NAST say of this that "in *Tetracentron*, which is placed among the Winteraceae, the primitive nature of the cambium and xylem excludes the possibility that it may once have developed vessels and lost this capacity only later." And elsewhere, they state that "taking into consideration all the evidence obtained from every organ of the plants, there is no convincing argument for deriving *Tetracentron* from Winteraceae, or, the other way round, for referring that these families are phylogenetically in a close relationship. It cannot be supposed, either, that other families, such as in the Ranales, could descend from these vesselless wood substance of Winteraceae with Gymnosperms, then its position should be with the secondary xylem of Pteridospermae and Bennetitales rather than with Coniferae and Cordaitales." As seen later on, we consider as more probable a relationship with the Coniferae and a connection with the dicotyledonous Amentiflorae; all the more so, *as the Drymises have the most primitive carpels among the Dicotyledons.*

It follows from these facts that the homoxylous trees, and thus *Drymis winteri,* are of more primitive origin. In the more advanced Magnoliales, and in several other dicotyledonous families true multiseriate pith rays are frequent and this leads us to conclude from the point of view of food conduction, too, that this is a more recent type of plant organisation. BAILEY's and JEFFREY's opinion was that the homoxyl trees, and thus *Drymis, Tetracentron,* and *Trochodendron* were "degenerate" vesselless trees. Such a degeneration in trees is surly not made by nature. (x150).

Comparison of tangential structures

Phot. 6. As seen in tangential section in *Juniperus macropoda* the pith rays are uniseriate, and 2 to 10 cells tall. Alongside them there are longitudinal tracheids. There can also be observed, exceptionally pith rays two cell layers broad but never any of more cell layers. These can occur only with the origin of aggregate pith rays (Phot. 1). In the wood of *Conifers,* wood parenchyma cells also occur (x150).

Plate 3. Photograph 10. Ray structure of *Juniperus macropoda.* There are in the cross-fields 2 to 4 simple pits; in the tracheids are bordered pits. (x200).
Photograph 11. In the radial walls of *Juniperus macropoda* the bordered pits are arranged in single rows. (x150).
Photograph 12. Simple pits in 1—2 rows. The walls of three tracheids of *Drymis winteri.* (x150).
Photograph 13. Radial structure of the pith of *Drymis winteri.* The parenchyma cells are square-, rectangular or column-shaped, with dense simple pits in their walls. (x200).
Photograph 14. Ray structure of *Magnolia acuminata.* On the left, the vessels has opposed, ladder-like pits with simple apertures. The pith-ray cells are elongated rectangles; in the cross-fields there are several tiny simple pits. (x200).

Plate 3
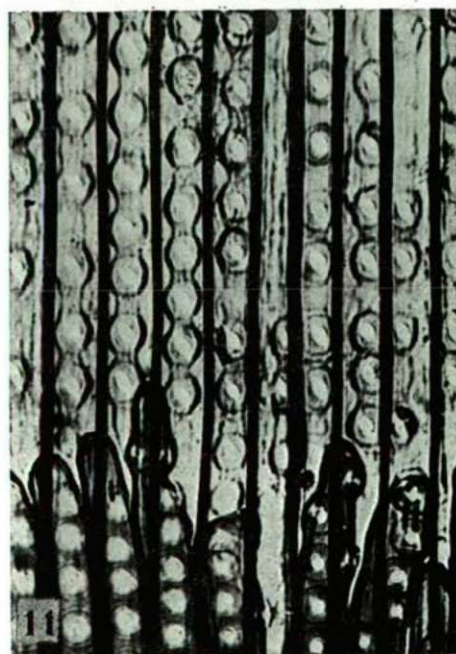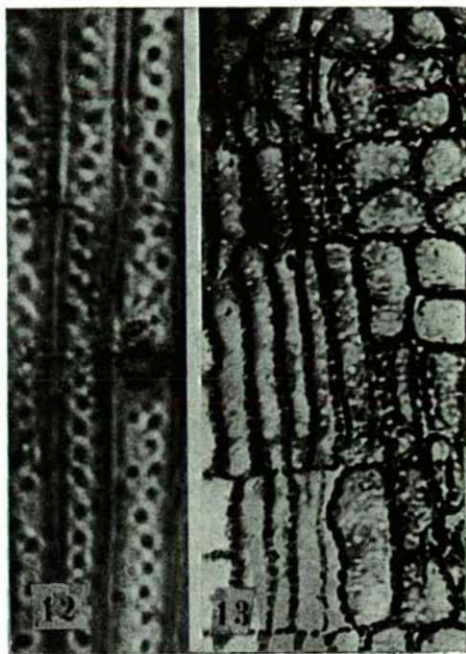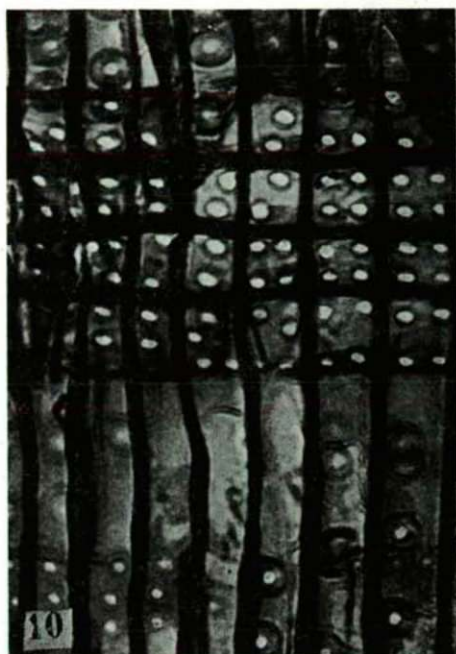
Phot. 7. In the wood of the homoxylic *Drymis winteri*, between the tracheids lie uniseriate pith rays and multiseriate (2–8 cells broad) aggregate and compound pith rays, sometimes 5 mm high. (According to METCALFE it has only "narrow" pith rays). From tangential sections it would be possible to think them uniseriate pith rays because there is no difference between them in transverse section; both of them can be regarded as a perpendicular cell chain. On the left of the photograph the pith rays, of 1 to 3 cell layers, are comparatively dense, 10–12 mm. If they are arranged terminally or round the vessel, then they are really parenchyma cells (x100).

Phot. 8. shows the internal structure of the aggregate pith rays. Observing better, in this pith ray the pith-ray cells and tracheids are aligned in regular longitudinal lines, essentially in single layers. At the endings of the single-cell rows there are corresponding similar, narrower border-cells, while the inner thick-walled pith cells — owing to the twisting of wood — follow one another in somewhat slanting, ortho- and parastichous lines. The inner ones are generally isodiametric; only those at the end of cell-rows seem to be more elongated and flatter, with several simple pits in their wall. This also shows that the aggregate pith rays are in fact composed of cell laminae, which agrees fully with the heterogeneous structure of pith rays (x300).

Phot. 9. shows the structure of *Magnolia accuminata*. The pith rays are 1–2 (−5) cell-layers broad and 10–15 cells high. In the "basic substance" between the vessels (which have wide lumina) xylem fibres, tracheids and parenchyma cells are distributed. The tangential walls of vessels are here and there covered with ladder like thickenings and oppositely arranged pits. (It may be that they got to the tangential side as a result of a cut or twisting (x150).

Comparison of the radial structures

Phot. 10 shows the radial structure of the pith ray and tracheids of *Juniperus macropoda*. In the quadratic cross fields of pith-ray cells there are 2 to 4 simple cupressoid pits. In the radial walls of tracheids, the bordered pits follow one another in one line and are distributed in a scattered manner. The "court" and circular aperture are distinct (x200).

Phot. 11. In the radial wall of the tracheids of *Juniperus macropoda*, the bordered pits are arranged in single rows. An arrangement like this occurs only in homo-xylous trees and conifers (x200).

Phot. 12 is the radial structure of *Drymis winteri*. In the walls of the three longitudinal tracheids large, round, simple pits occur, alternating in single or double lines (Cf. also with photographs 15, 16, 19, (x150).

Phot. 13 is the pith-ray structure of *Drymis winteri*. The pith-ray cells are more or less isodiametric, the bordering cells are somewhat longer, sometimes elongated

Plate 4. Photograph 15. Tracheids by the ray of *Drymis winteri*. The pits are large, located in 1 or 2 rows. (Photograph 19 is the magnifying of phot. 15.)

Photograph 16. In the tracheids, the simple pits are circular, without "court" and torus. (Cf. at the arrow.) (x300).

Photograph 17. Alternate pits, bordered and spiral thickening in the early wood of *Drymis winteri*. (Cf. with the framed square in Phot. 20.) (x150).

Photograph 18. Magnification of the rectangle towards the top of Phot. 17. The edges of the ladder-like thickening are not straight. The apertures came into being by the fusion of the apertures of simple pits. (x300).

Plate 4
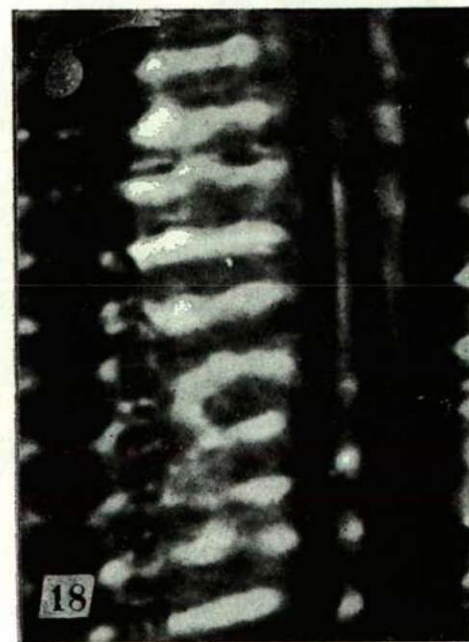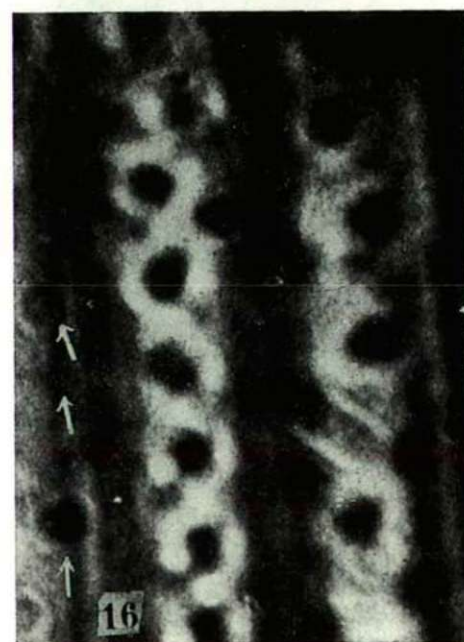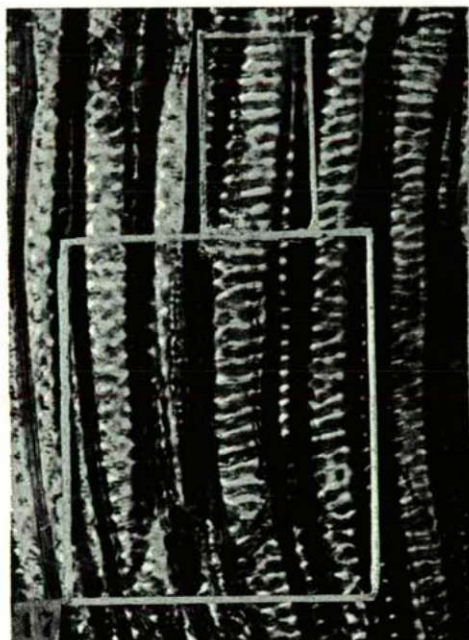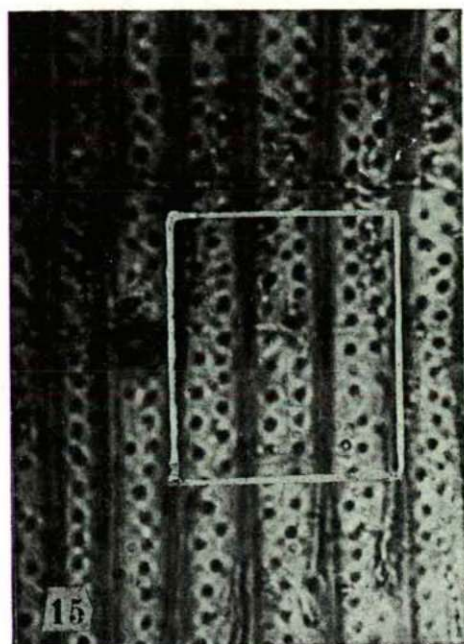
tracheid-like, with single or double- rows of pits in their walls. The simple structure of the pits is similar to that in tracheids (x200).

Phot. 14 is the pith-ray structure of *Magnolia* in radial section. On the right is a simple perforation of a vessel, with long elongated, opposite ladder-like thickenings in its wall. This ladder-like thickening may have come about from the horizontal lengthening of a simple transverse bordered pit. The horizontally lying pith-ray cells — differently from the more primitive *Drymis* — are elongated in the radial direction, with several simple pits in the cross-fields. Between the vessels, which have large cavities, there are longitudinal wood elements (tracheids, xylem fibres and xylem parenchyma cells). This pith-ray structure is somewhat similar to the radial structure of *Drymis winteri*, but there are no vessels in the xylem of *Drymis*. This is a very important difference between the two tree types (x200).

Phot. 15. In the radial walls of the tracheids of *Drymis winteri*, are alternately arranged circular pit apertures in 1–2 rows, which seem to be simple pits, therefore they could even essentially be thick-walled parenchyma cells (they may have formed from such cells). The pits are not quite uniform, and not always regularly circular. They are larger than simple pits or (generally) than the pores of parenchyma cells (Cf. also with photograph 19 (x150).

Phot. 16. The pits are regular or irregular circles. (Cf. at the arrows). Some of them are elliptical. Beside them the marks of "courts" cannot be observed; at most wall thickenings in the longitudinal elements (cf.: right side). In this respect this pittedness is also to be considered as a primitive characteristic. A structure like this has, not been known, up to this point at least not in the tracheids of Conifers. (x300).

Phot. 17. It seems to be another new phenomenon, that in the broader tracheids the alternating pits link up close together, two or three or four at a time. Consequently, the apertures of three or four pits almost meet one another, and in this way ladder-like thickenings come about (x150).

Phot. 18. This ladder-like thickening differs fundamentally from the ladder-like thickening of Magnoliales. While the rangs of the ladder and the apertures in Magnoliales come about from the lengthening of a single bordered pit — i.e. the border of the aperture is a horizontal straight line — in *Drymis winteri* the rungs of the ladders and the apertures come into being from the fusing of several alternating circular pores. Due to this, the two borders of the rungs are not straight lines but irregular ones (x300).

Phot. 19 is a detail of Photograph 15, at higher magnification. We see, in the radial walls of the three longitudinal tracheids, their simple pittedness. In these tracheids, not bordered but simple pits are present, arranged in pairs or alternately. Were they bordered pits, then the apertures and courts (+ −) would be regular circles or apertures of equal size. These apertures, however, are of different size and shape, so this structure points to simple pittedness without any torus. The pittedness of the pith-ray parenchyma is quite similar to that of tracheids, only that there the pits are much larger (Cf. also phot. 21). This is a very primitive peculiarity,

Plate 5. Photograph 19. Magnification of the framed square of Phot. 15. The large pits in the walls of tracheids are generally circular, elongated or angular. Around the apertures there are comparatively wide rings (x350).
Photograph 20. The framed square of phot. 17. Below, at the arrow, the contact two tracheids is to be seen at the upper left white arrow, in the tracheids are 2—3 alternating pits. At the arrow on the right, the apertures of pits are continued in a spiral (x350).

Plate 5
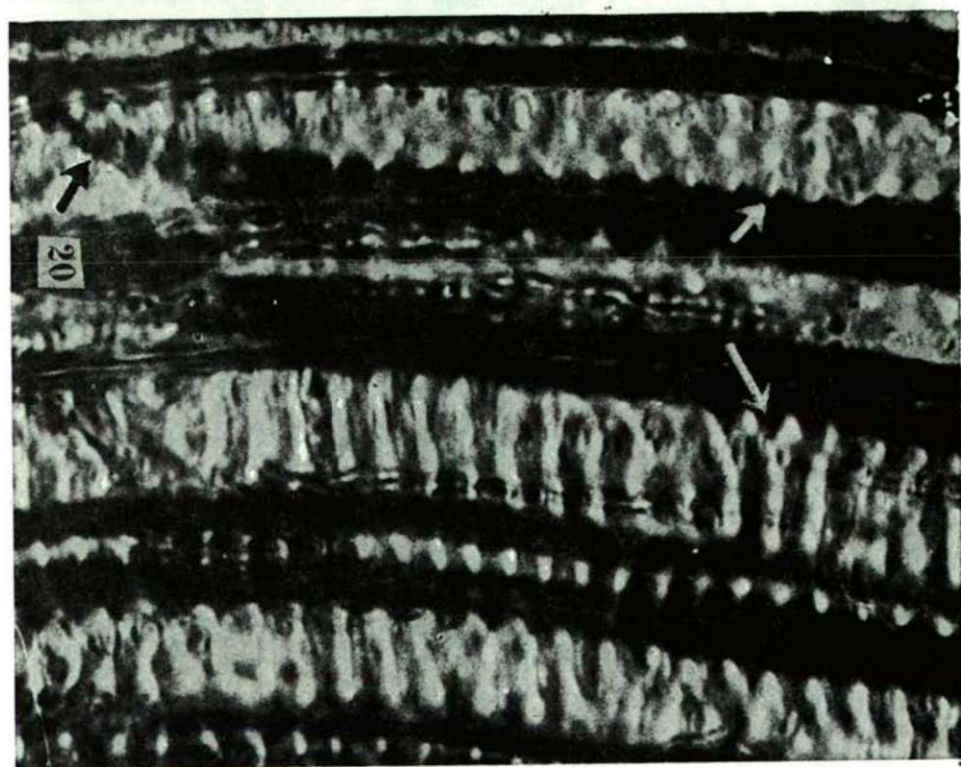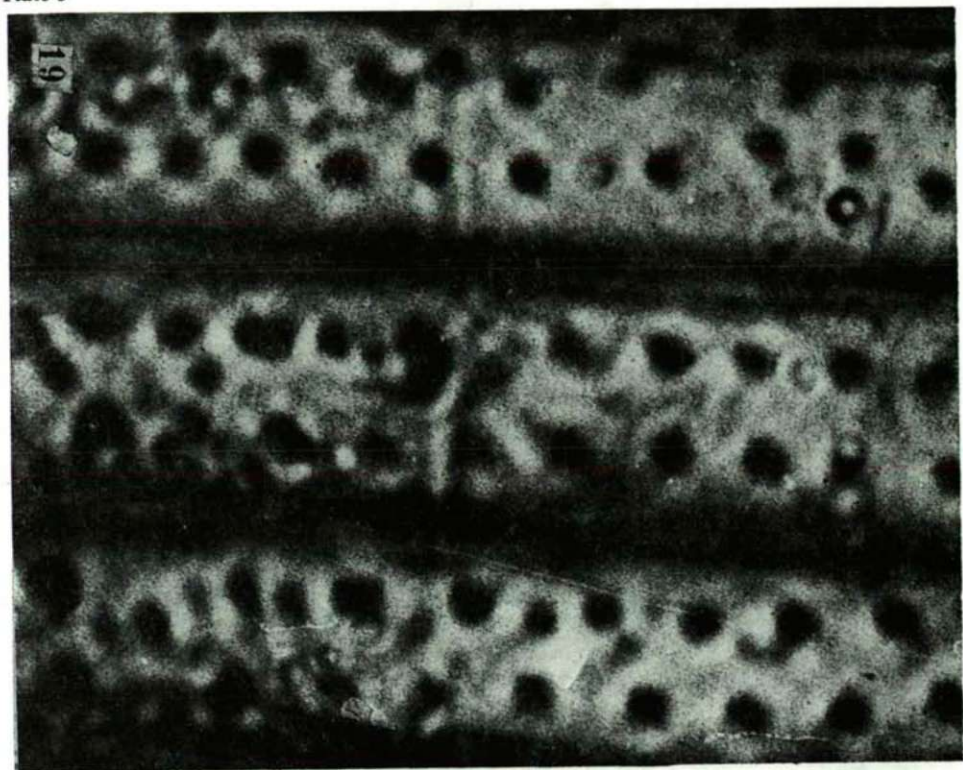
from which it is to be concluded that the tracheids essentially come from the paren-
chyma and that, therefore, their pittedness is similar, as well. In Magnoliales there
is no such primitive feature. Hence homoxylous trees cannot originate from Magno-
liales (x350).

In phot. 20 we can see one of the details of phot. 17, the formation of the ladder-
like and spiral thickenings from the simple, and bordered pits, at a higher magnifica-
tion. Here and there, a border to the pits also appears, and the aperture may even
become rod-like. Pits like this can be observed in the xylem of *Drymis winteri*. At
the black arrow, below, the ends of two tracheids appear. The white arrows show
how the thickening of bordered pits turns into the spiral. This structure occurs
particularly in the tracheids of the season (x350).

Finally, phot. 21 to 24 are presented to confirm that tracheid pitting and pith-
ray structure similar to those in *Drymis winteri*, occur in early dicotyledonous woody
plants as well, and that there is a probable relationship along this line. I have men-
tioned in my book "Occurrence of Tertiary trees in Hungary" that, for instance,
in the tracheids and vessels of *Myristicoxylon hungaricum* GREGUSS and *M. bajnaense*
GREGUSS, the same kinds of simple pits occur as in the living *Drymis* (Phot. 21, 22),
and even the aggregate pith rays show a similar structur (phot. 24). It was possible
to detect similarly large, round pits in another fossil broad-leaved tree, as well,
which could not be determined more exactly (Phot. 2, 3). All this seems to support
the view that it is better to suppose phylogenetic connection with *Drymis* and the
more primitive dicotyledonous deciduous trees than with Bennettites or Pterido-
spermae, as postulated by BAILEY and JAMES (x200).

Summary

Vessels and perhaps parenchyma cells are missing or scanty in *Drymis winteri*
while in Magnolia accuminata, apart from tracheids of her wood elements also
occur: vessels (tracheae), wood parenchyma and wood fibres, these being charac-
teristic of the most highly developed wood structure. Hence, from these considera-
tions, the structure of the wood tissue of the vesselless *Drymis winteri* ist to be con-
sidered as older, i.e. more primitive, than that of Magnoliales. For this reason, the
Drymises could not have descended from Magnoliales.

The phenomenon that in the walls of tracheids instead of the normal bordered
pits, large and simple pits are present, is to be regarded as another primitive feature
and conclusiv proof. But in the walls of the tracheids of *Drymis winteri* the ladder-
like thickening also originates in an essentially different way from those in Mag-
noliae. Another primitive feature in *Drymis* is the occurrence of aggregate pith

Plate 6. Photograph 21. A radial detail of the wood of *Drymis winteri*. In the walls of tracheids,
there are some comparatively large simple pits and also there are several simple pits in the
walls of pith-ray cells (x100).
Photograph 22. In the wall of vessels of *Myristicoxylon hungaricum* large pits, similar
to those in *Drymis*, occur in 1—2 lines (x200).
Photograph 23. In the walls of vessels of an unknown plant fossil from the Oligocene,
large, simple pits are present, similar to those in *Drymis* (x100).
Photograph 24. Aggregate pith rays in *Myristicoxylon hungaricum* (Cf. at the arrows.)
(x200).

Plate 6
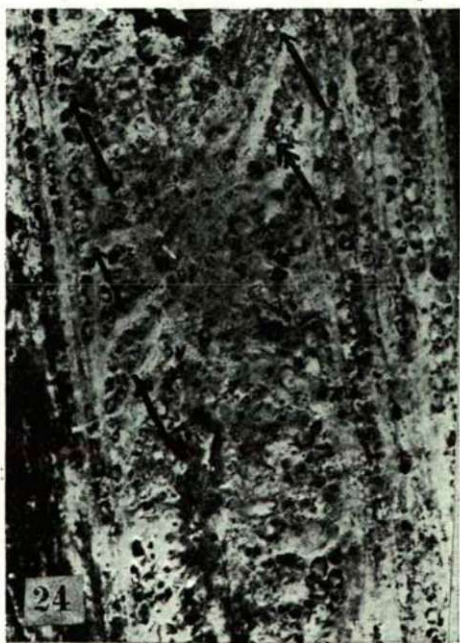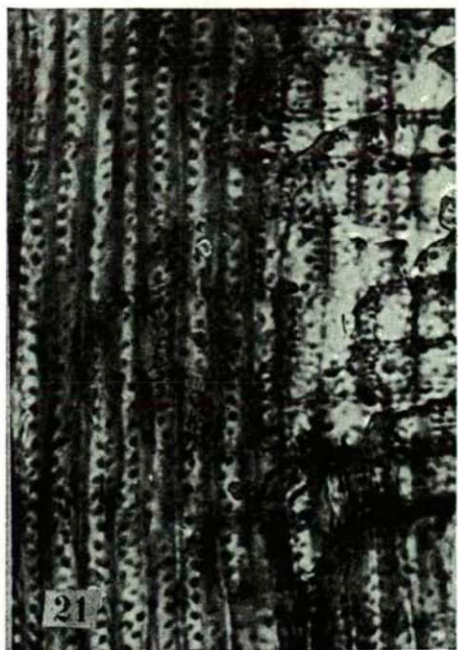
rays. Such rays are absent from Magnoliales. This also supports the view that the origin of homoxylous trees, among of Takhtajan's heteroxylous vascular Magnoliales. Hence *Drymises* could not have originated from Magnoliales. Iincidentally, about 45 species of *Drymises* are known and these occur mainly in the Far East and Australia.

It is also to be considered as primitive, and a conclusive proof, large simple pits are found. In the walls of the tracheids of *Drymis* the ladder-like thickening arises in a way which is essentially different from that in Magnoliales. A further primitive mark in *Drymis winteri* is the occurrence of aggregate pith rays. Rays like these are missing from Magnoliales. It is proved by this, too, that the origin of homoxylous trees, and among them *Drymises,* may have been older than that of Takhtajan's heteroxylous vascular Magnoliales. As already mentioned, "Drymises have, among all the Angiospermae, the most primitive carpel".

Takhtajan derives even the Monocotyledons from Magnoliales, i.e. he consideres the Angiosperms essentially as monophyletic — and this is fundamentally at varience with our polyphyletic conception.

It is a fact that the opposers of polyphyletic origin present some arguments to support their statements. Thus, among others, they mention the double fertilization which takes place in Mono- and Dicotyledons by and large in a similar way. This objection can, however, be easily refuted. Within the Pteridophytes (Lycopsida, Pteropsida, Sphenopsida) zoogamy takes place essentially in a similar way, which seems to verify a monophyletic origin though there are, in many respects, essential differences between them. The structure of the reproductive organs of Lycopodia, horsetails and ferns, archegonia and antheridia, is by and large similar. In the finer, essential details, however, there farreaching differences between them are to be seen. Thus, for example, the absence or presence of the suspensor, or the formation of the bi- or multi-ciliated spermatozoids, etc. Nevertheless, very few botanists may state that these descended from one another, or that Pteridophytes, such as *Calamites, Sigillaria* and *Lepidodendron* that lived side by side in the Devonian and the Carboniferous Period, originated one from the other: the descent of these was also polyphyletic. In this respect, why should the Angiosperms be the exeption?

And if the supposition that Monocotyledons came from the dicotyledonous hermaphroditic Polycarpaceae, or from Magnoliales, is false, then the conclusions drawn from this are also erroneous. Therefore — in our opinion — the opinion cannot be defended that the hermaphroditic flower of Magnoliales is the more primitive flower, the more ancient (originating earlier) hence is also less advanced than the dioecious and monoecious Amentiflorae or the above-discussed *Drymis winteri.* According to such a conception, the flowers of the entomophilous orchids or those of apple-trees would be more imperfect than for instance the flowers of the anemophilous *Typha* or the poplar catkin, or the non-branching palm trunk would be more primitive and imperfect than the branching old oak-tree, or an oak imperfect than, for instance, a *Yucca* leaf or parallel venetaion, or that insect pollination would be less advanced than the pollination by wind, etc. How many contradictions occur, and how much impossibility, if we accept a monophyletic descent of Angiosperms, rather than our polyphyletic conception!

The author has wanted, with this xylotomic paper, to endorse against Takhtajan's conflicting position — H. Gottwald's statements, arived at on the basis of

xylotomy, according to which it is impossible to derive the homoxylous trees of primitive structure, as well as the monocotyledonous trees from Magnoliales. This is supported, apart from morphological, palaeontological and genetic arguments, by xylotomic data.

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