Wulfenia **20** (2013): 43–54

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

Scalariform tracheids in secondary xylem of woody dicotyledons: distribution, function and evolutionary significance

Gorn B. Kedrov †

Summary: The vessel tracheids are inherent in many heteroxylar woody dicotyledons, especially in those having diffuse vessels and tracheidal vessel-to-vessel communications where the tracheids transfer water from one vessel to the next one. The tracheid pitting is identical to that of the vessel segment the tracheid adjoins. Thus, the dicotyledons with scalariform-pitted vessel segments have always scanty to rather numerous scalariform tracheids which always combine with either pitted fiber counterparts or with libriform fibers. The scalariform tracheids are quite effectual water-conducting wood constituents, but they are insufficiently strong to enable the wood to support trunk and crown. Therefore, the scalariform tracheids are invariably vessel ones. Dicotyledonous vessels, fiber tracheids and libriform fibers are additionally confirmed to have evolved from the scalariform tracheids of ancestral dicotyledons. The latter plants must have had wood of only scalariform tracheids. Consequently, those plants must have been manoxylic woody or even herbaceous.

Keywords: dicotyledons, secondary wood, homoxylar plants, heteroxylar plants, scalariform tracheid, wood evolution, growth habit evolution

Scalariform tracheids are rarely revealed in the secondary wood of dicotyledons. Such tracheids are inherent in some homoxylar plants among modern woody dicotyledons. Especially *Trochodendron* and *Tetracentron* have spring wood mostly constituted by distinctively scalariform thin-walled tracheids, whereas only pitted ones are in their summer wood (Fig. 1) (Thompson & Bailey 1916; Bailey & Thompson 1918; etc.). Indistinctive scalariform tracheids are known in *Amborella* (Bailey & Swamy 1948) and *Sarcandra* (Swamy & Bailey 1950). Only few species of *Drymis* (Fig. 2) and *Bubbia* of the family Winteraceae have scalariform tracheids in their spring wood, but their scalariform pitting is hardly discernible. The scalariform tracheids have not been revealed in other members of this family so far (Bailey 1944; Money et al. 1950; Patel 1974; etc.).

Information on the scalariform tracheids in heteroxylar woody dicotyledons is scanty and sometimes controversial. For instance, Jarmolenko (1939) reported these formations in *Liriodendron* and some *Magnolia* species, but this was argued by Yatsenko-Khmelevskiy (1948). The scalariform tracheids seem to have reliably been revealed in secondary wood of Vitaceae members (Record & Hess 1943), *Myrrhidendron donellsmithii* J. M. Coult. & Rose of Umbelliferae (Rodriguez 1957) and *Azorina vidalii* (H. C. Watson) Feer of Campanulaceae (Vasilevskaya & Shulkina 1976). Presence of the scalariform tracheids in woody dicotyledons is considered a keystone of realizing and interpreting wood evolution in these plants.

Most botanists believe now that angiosperm ancestors were homoxylar, i.e. they had vesselless secondary xylem. The early angiosperms are thought to have remained homoxylar for some period of their existence (Yatsenko-Khmelevskiy & Shilkina 1964; Takhtajan 1970; etc.). They then became heteroxylar. Their secondary xylem tracheids differentiated into water-conducting vessel segments and specialized strengthening xylem constituents.

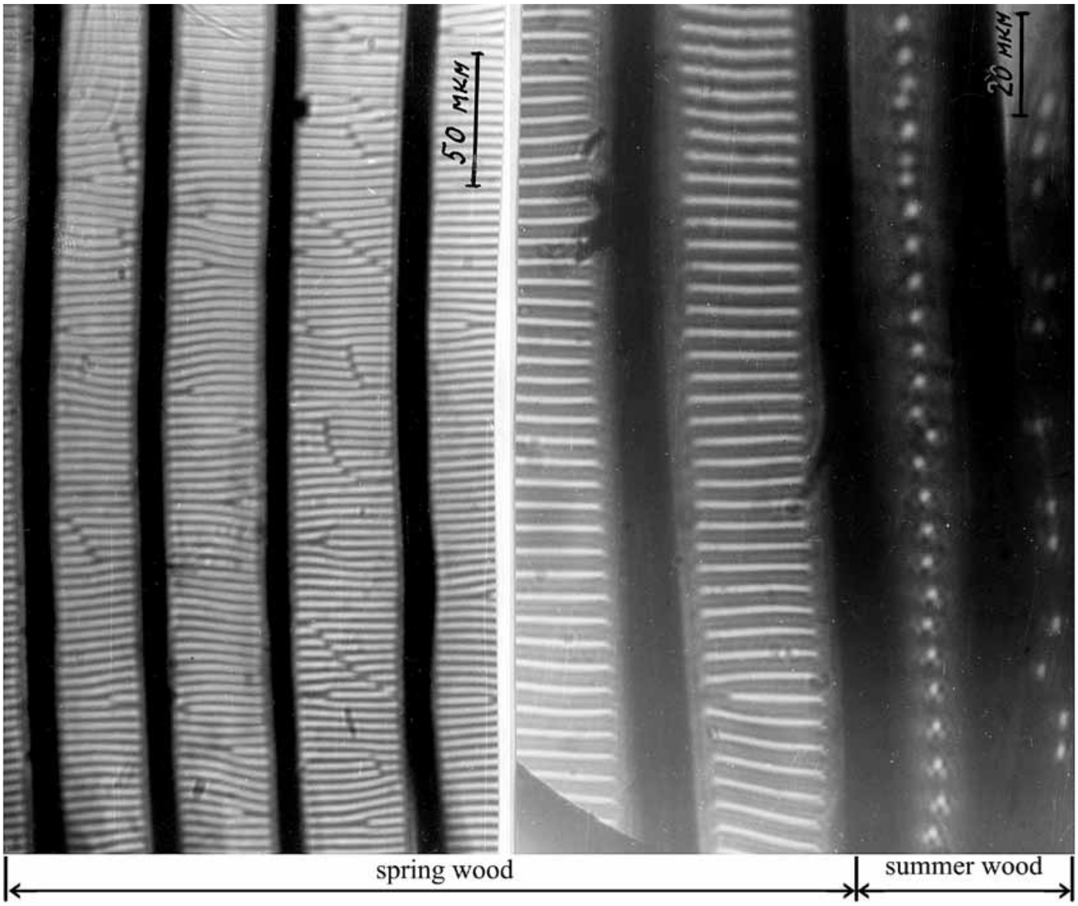

Figure 1. Radial sections of the spring (left) and summer (right) wood of *Tetracentron sinense* Oliv.

The vessel segments in the secondary xylem of woody dicotyledons were shown in the early 20th century to have evolved from the scalariform tracheids similar to those in the spring wood of extant homoxylar angiosperms, specifically to those in the spring wood of *Tetracentron* (Bailey & Tupper 1918; Frost 1930a,b, 1931; Bailey 1944; Yatsenko-Khmelevskiy 1948; etc.). The most primitive vessel segments are usually believed to be more similar to the scalariform tracheids. They have very long oblique perforation plates with numerous (100–150) perforations and bear scalariform pits in their lateral walls. The vessel segments of at least some angiosperms were recently deduced to have derived from the reticulate tracheids or pitted ones, the latter having opposite or alternate pitting (Parameswaran & Liese 1973). However, this theory was concluded to be unsound (Meylan & Butterfield 1975).

The primitive polymerous scalariform perforation plates of ancestral dicotyledonous vessel segments were advancing to oligomerous ones to be changed into simple counterparts. Original scalariform pitting of vessel segment lateral walls evolved to opposite one, the latter being succeeded by the alternate counterparts. A highly advanced vessel segment is a wide cylinder with nearly transversal simple perforation plates each occupied by huge roundish sole perforations.

According to Frost (1930a), the scalariform tracheid to vessel segment evolution would be traceable by co-presence of these tracheids and vessels in wood at least of few extant heteroxylar woody dicotyledons. However, such wood was not known that time. Frost (l.c.) considered

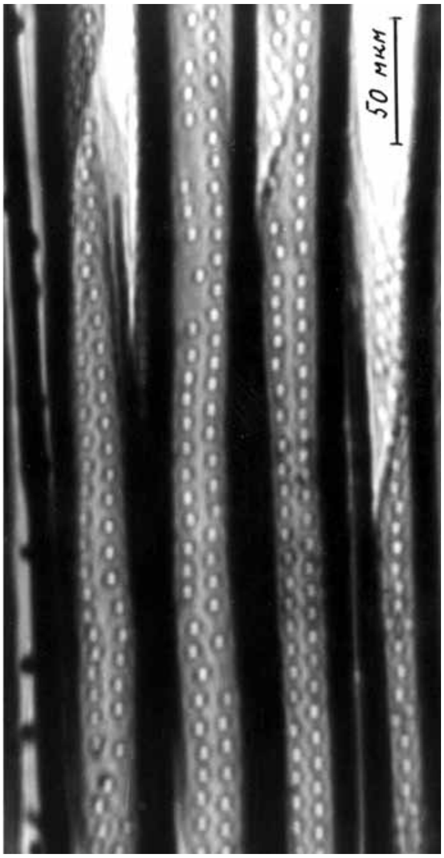

Figure 2. Radial section of the wood of *Drymis winteri* Forst.

such wood a missing link of arguments for the theory that the dicotyledonous vessels had evolved from the scalariform tracheids. To advocate the theory, he assumed that the xylem of extant heteroxylar woody dicotyledons was so highly advanced that it had lost any scalariform tracheid.

The secondary xylem strengthening elements in heteroxylar dicotyledons are fiber tracheids and libriform fibers, the former formations being considered more primitive. The fiber tracheids are bifunctional, as they transfer water and strengthen the wood. Accordingly, they have more or less thickened cell walls and bear clearly visible roundish bordered pits in the walls. Oligomerization of pits, decreasing of pit sizes and bordered pit-to-simple pit transformation are thought to have been specializations of the fiber tracheids. Unifunctional strengthening libriform fibers have resultantly evolved. There are fiber tracheid-to-libriform fiber transitional formations in a set of modern woody dicotyledons.

Yatsenko-Khmelevskiy (1954) hypothesized on the basis of variety of strengthening xylem elements and transitional ones that they all had evolved from the only ancestral strengthening formation. Such an ancestral formation would have been the scalariform tracheid, if only scalariform fiber tracheids and/or transitional scalariform-to-pitted ones had been detected in heteroxylar woody dicotyledons. However, this was not the case at that time. Thereof, Yatsenko-Khmelevskiy (l.c.) concluded that either the scalariform fiber tracheids had not yet been revealed or they had never existed. Because the author clearly inclined to the latter conclusion, he assumed that all scalariform tracheids in ancestral dicotyledons had evolutionary changed into the scalariform-perforated vessel segments in their descendants whereas the pitted tracheids remained. The latter formations were similar to those in summer wood of extant homoxylar woody dicotyledons. Therefore, the pitted tracheids have reasonably given rise to the fiber tracheids of heteroxylar woody dicotyledons.

The question about the structure of initial strengthening xylem elements is part of the major problem of wood composition in homoxylar early angiosperms. Indeed, if the strengthening xylem elements of heteroxylar dicotyledons come from pitted tracheids similar to the ones of summer wood of extant homoxylar dicotyledons and the vessel segments are evolved from the scalariform tracheids, then both pitted and scalariform tracheids must be concluded to have been conterminous constituents of the secondary xylem in the early homoxylar angiosperms. But if the scalariform tracheids have given rise to vessel segments as well as to fiber tracheids, then the homoxylar secondary xylems of ancestral woody angiosperms must have born only scalariform tracheids.

The tracheid structure of initial homoxylar angiosperms can controversially be deduced from that of extant homoxylar woody dicotyledons. The point is that most distinct conterminous scalariform and pitted tracheids are inherent in *Trochodendron* and *Tetracentron*, whereas two-typed tracheids can only arbitrarily be distinguished in more primitive taxa while most homoxylar woody dicotyledons have uniform tracheids in their wood. These uniform tracheids are invariably pitted, though! The typical scalariform tracheids were discovered in secondary xylems of heteroxylar woody dicotyledons after the works of Frost (1930a, b, 1931) and Yatsenko-Khmelevskiy (1954) had been published. Moreover, these tracheids are inherent in rather advanced taxa. Besides, neither exact tracheid localization nor its function have been scrutinized.

Therefore, a wide range of heteroxylar woody dicotyledons, especially the primitive ones, is worth being screened for scalariform tracheids and published data should be checked. Function/s of these tracheids is/are to be further investigated. Such work is of importance for understanding dicotyledonous xylem evolution and also for realizing growth habit/s of the ancestral angiosperms.

Materials and methods

The wood samples of *Magnolia grandiflora* L., *M. hypoleuca* Siebold & Zucc., *M. macrophylla* Michx., *Manglietia* sp., *Talauma sambuensis* Pittier (Magnoliaceae), *Vitis vinifera* L. (Vitaceae), *Clusia minor* L. (Guttiferae) and *Rhizophora mangle* L. (Rhizophoraceae) were taken for the present investigation. The samples are deposited in the wood collection of the Department of Higher Plants, Lomonosov Moscow State University, Moscow. Over 3 mm long wood samples of all species listed but *C. minor* and *R. mangle* were serially transversally sectioned. I failed sectioning wood of these two species, because the former was too brittle and the latter was partly destroyed by some fungus.

The scalariform tracheids were searched for in serial ca. 12 mm^2 large and 15 µm thick sections as follows. A narrow tracheary element situated in between wider vessels or adjoining the wider one laterally was picked up in some middle section of a series. This element was traced through upward and downward the section series. The sectioned element and its surroundings were sketched throughout with drawing device RA-4 to record all structure changes of the wood constituents. If no perforations had been detected on both ends of the picked element, the latter was considered a tracheid.

After the tracheids had been revealed in serial sections, they were tested in macerated wood for their scalariform structure (Fig. 3). Those of *C. minor* and *R. mangle* were directly revealed and tested in macerated wood. The wood samples were boiled in strong nitric acid to be macerated. Unstained tracheids were photographed under transmissive λ_{343} light with luminescent microscope ML-2 equipped with camera MFN-1.

Results

The scalariform tracheids were revealed in all sectioned wood samples but that of *Manglietia* sp. They were not detected in macerated wood of *Manglietia* sp. and *Talauma sambuensis*. All

Figure 3. Scalariform tracheid of macerated wood of *Magnolia grandiflora* L.

tracheids revealed were of vascular type. They were observed in spring wood as well as in summer wood.

The scalariform tracheids were always associated with the vessels. They were in between the latter formations and contacted them mostly by tangential walls (Fig. 4). These tracheids did not constitute longitudinal files separated from the vessels. The tracheids were as long as their associated vessel segments (Fig. 5).

Vitis vinifera had long wide vessels and also narrow ones consisting of 2 to 3 vessel segments. Such narrow vessels hardly exceeded 1 mm in length.

Discussion

Function and importance of the vascular tracheids

According to the wood advancement code (Yatsenko-Khmelevskiy 1948, 1954), deviating lines of strengthening xylem element evolution resulted in vascular tracheids in heteroxylar dicotyledons. Such tracheids repeatedly evolved in variously advanced wood. This conclusion obviously need be corrected.

There are vessels that are nearly always considered the principal water-conducting constituents of the dicotyledonous heteroxylar wood. If the vascular tracheids are present, they are thought to participate accessorily in water-conducting. Consequently, they are believed to be wood

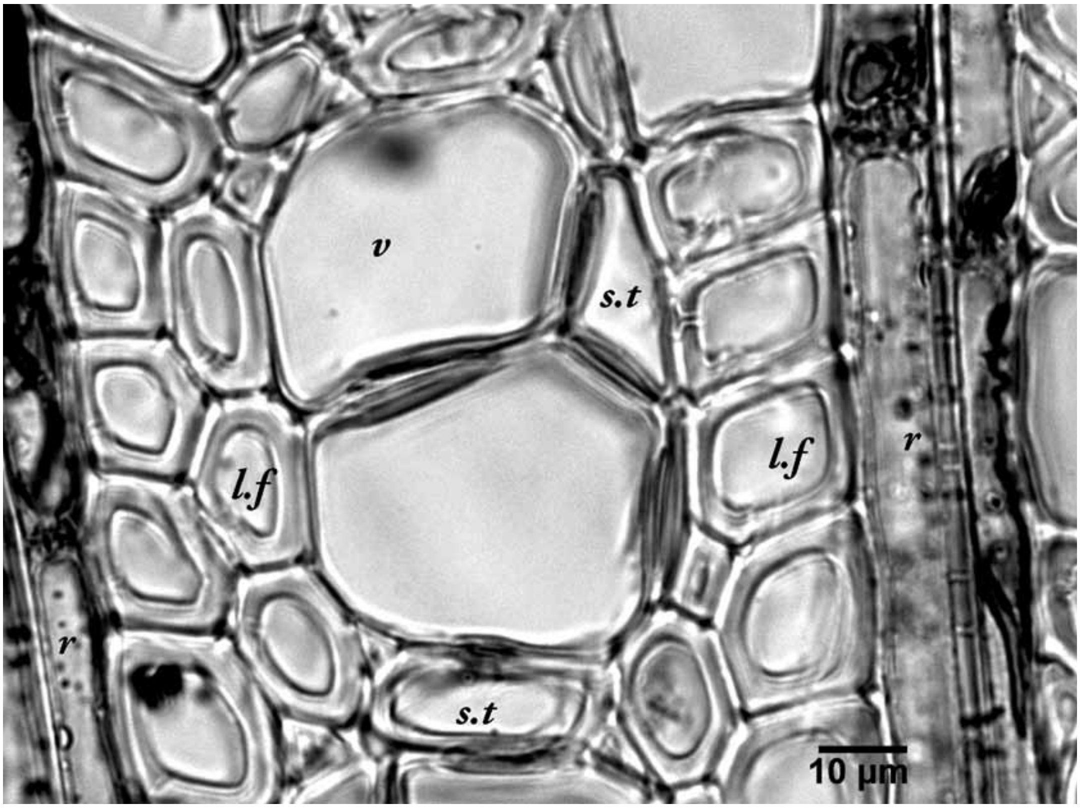

Figure 4. Cross-sectioned secondary wood of *Magnolia grandiflora* L. *l.f* – libriform fiber; *r* – ray; *s.t* – scalariform tracheid; *v* – vessel.

constituents of minor importance. This notion seems relevant if only the vessels and vascular tracheids are separately concerned with. Indeed, the vessels are mostly much wider and longer pipes than the tracheids. Thereof, they transfer water much more efficiently. However, when the vessels and vascular tracheids are jointly analysed as constituents of integral water-conducting system, the vascular tracheids prove to be as important for water transport as the vessels in many heteroxylar plants.

The vessel is well known to consist of a set of segments intercommunicated by perforation plates. The vessels vary from 1 mm (*Vitis vinifera*, present data) to 15 m long to even longer (Greenidge 1952; etc.), but there is no vessel that extends through the whole water transfer

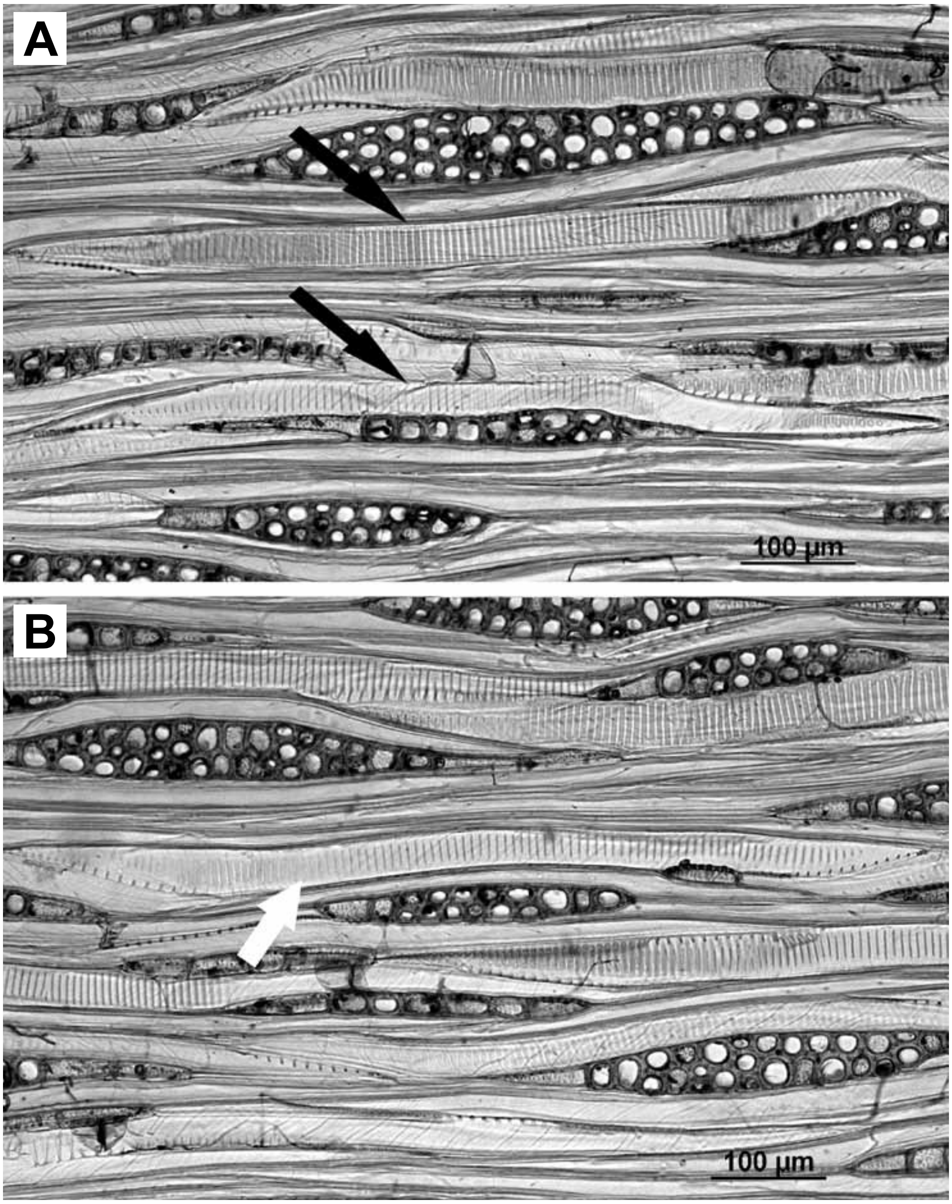

Figure 5. Tangentially sectioned secondary wood of *Magnolia grandiflora* L. A – scalariform tracheids (black arrows); B – scalariform vessel segment (white arrow).

system. Every vessel bears terminal segments on both ends that have only vesselward perforation plates, whereas all other segment walls are imperforate and bear bordered pits. Thus, the whole vessel is a terminally closed pipe similar in this respect to the shortest tracheids. Then, vessel-to-vessel communications are of importance for conducting water through the xylem. Like tracheids, they intercommunicate by the bordered pits in their contiguous walls. Non-storied tracheids are typical of all homoxylar woods. Thereof, the tracheids are interlocked for rather long parts of their lengths to result in a fairly large intercommunication area (Kedrov 1984).

Serial transversal sections of wood show that the vessels are similarly interlocked (Kedrov 1965; Zimmermann 1978; etc.). However, vessel-to-vessel communications are quite different in various plants. Three communication modes, viz. (i) tracheidal, (ii) direct and (iii) combined (= tracheidal + direct), have been recognized elsewhere (Kedrov 1968). If tracheidal-communicated, the vessels are completely separated throughout by the vascular or by the fiber tracheids. Such vessels are seen solitary and dispersed in the bulk of tracheids in wood transversal sections. Tracheids contact vessels and each other by their pitted walls maintaining vessel-to-vessel communications in such wood. There are no tracheids at all in wood that has direct vessel-to-vessel communications. The vessels inevitably contact each other laterally for more or less their lengths there. Then, solitary as well as grouped vessels are visible in wood transversal sections in this case. Contiguous vessel walls bear numerous bordered pits (these walls and vessels are sometimes termed 'contacts' and 'contacting vessels', respectively), and these pits directly maintain vessel intercommunications. Just like the tracheids, the contacting vessels intercommunicate by bordered pits. There are many other plants having combined vessel-to-vessel communications whose vessels communicate through 'contacts' and adjoining tracheids. The tracheids variously participate in vessel communications in different species.

The tracheids are thus sine qua non constituents of wood with solitary vessels. They should not be considered accessory to the vessels, unimportant conducting elements of wood. The tracheids of wood with combined vessel-to-vessel communications should not be considered unimportant either, if the contacts are small and scanty. If the wood has only advanced direct vessel intercommunications, its tracheids (if present) are worth being considered insignificant conducting elements. Accordingly, vascular tracheids are rather widespread in heteroxylar dicotyledons. These tracheids are clustered with the vessels to constitute various masses (radial files, oblique tangential bands etc. as seen in wood transversal sections). The vascular tracheids constitute 1- to 2-layered sheaths round solitary vessels in some heteroxylar species. It is important to take into account that the vascular tracheids strikingly differ from fiber counterparts and libriform fibers in their pitting, but they are quite similar in this trait to vessel segments of the same species (Yatsenko-Khmelevskiy 1954).

Ancestral dicotyledonous tracheids

Solitary vessels should be considered primitive according to the wood advancement code (Yatsenko-Khmelevskiy 1948, 1954). They were evolutionary succeeded by the grouped vessels in most dicotyledons. Therefore, the vessels initially did not contact each other. They unavoidably communicated through intermediate tracheids. Then, the vascular tracheids are irrelevantly thought to be results of deviating evolutionary lines of wood axial element progress that repeatedly arose in differently advanced wood. On the contrary, such tracheids must have been immanent elements of ancestral unspecialized wood. If so, which tracheids initially maintained vessel-to-vessel communications in ancestral heteroxylar angiosperms?

Accepting Yatsenko-Khmelevskiy's theory, all ancestral vascular tracheids should be considered to have changed into the vessel segments and only pitted tracheids should be thought to have remained in heteroxylar wood. Thereof, only the pitted tracheids must be considered to have connected solitary vessels in ancestral heteroxylar angiosperms. Because of the tracheid pitting and its vessel counterpart are the same, the ancestral vessel segments should be thought to have born roundish pits. However, certainly ancestral scalariform vessel perforation plates are relevantly interpreted to have derived from the scalariform tracheid pits. Thereof, the tracheids of ancestral heteroxylar dicotyledons would have born scalariform pits in their end parts and roundish ones in their middle parts (Fig. 6). The former pits would have given rise to the scalariform perforation plates of vessel segments, whereas the latter ones would have remained in lateral walls of pitted vessels of primitive heteroxylar wood.

However, the above-outlined tracheids have never been observed in vascular plants. Besides, very many heteroxylar dicotyledons have scalariform vessel-to-vessel pitting of their directly connecting vessels (Metcalfe & Chalk 1950). This pitting is reasonably believed to have come directly from the scalariform pitting of their initial tracheids (Frost 1931; Yatsenko-Khmelevskiy 1954). Thus, the vessel segment generating tracheids as well as vessel connecting ones must have been scalariform throughout in the ancestral heteroxylar dicotyledons. However, this conclusion is not apodictic. The point is that scalariform vessel-to-vessel pitting could arise only after solitary vessels had been succeeded by grouped ones. Initial solitary vessels certainly had no vessel-to-vessel pitting at all. Those of extant plants have no scalariform pits, because they are intercommunicated through vascular and fiber tracheids with exclusively roundish pits in their walls. Quite similar pits are accordingly born by the vessel segments, though their perforation plates are mostly scalariform. Even if a few vessels of these plants occasionally contact each other directly, they develop roundish vessel-to-vessel pitting, if any.

To solve the apparent contradiction, the dicotyledonous vessels should be assumed to have been surrounded by the scalariform tracheids when they arised. Contrarily to Yatsenko-Khmelevskiy's (1954) theory, not all but some scalariform tracheids should be considered to have changed into vessel segments. These tracheids are connected with solitary vessels and interconnected to maintain vessel-to-vessel communications in the primitive heteroxylar wood. The scalariform pitting is highly efficient in conducting water, because the pits are rather large and densely located in the walls and therefore they have a large area to be penetrated by the water-current. In other words, the scalariform tracheids are advanced water-conducting formations. That is why they had been performing the water-conducting function till the grouped vessels succeeded the solitary counterparts. Thereafter, the direct vessel-to-vessel communications arose and the tracheids lost their importance as water-conducting formations. The scalariform pitting has correspondingly remained only in contiguous vessel-to-vessel walls of the vessel segments. When discharged from water-conductance, the tracheids evolved as follows. They got shorter and changed their scalariform pitting first to opposite, then to alternate pitting and transformed into strengthening fiber tracheids.

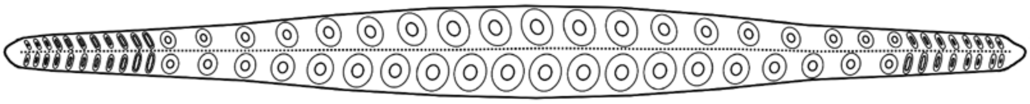

Figure 6. Imaginary combined scalariform/pitted tracheid.

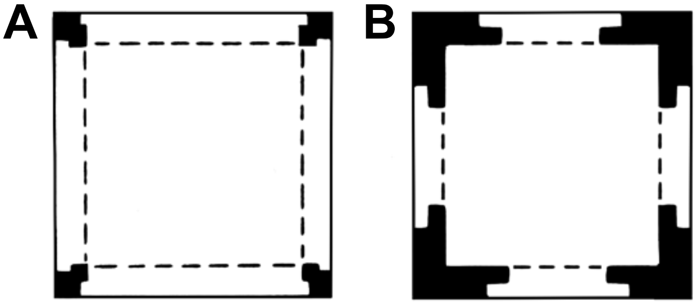

Figure 7. Specific areas of cross-sectioned tracheid walls. A – scalariform; B – pitted.

The contradiction solution just outlined is seemingly confirmed by the presence of scalariform tracheids in modern heteroxylar dicotyledons. These tracheids still maintain communications between the vessels, though they are of less importance now, because the water is mostly transferred directly through vessel-to-vessel pitting. Thus, these tracheids are worth being considered as the missing link Frost (1930a) wrote about.

Thus, at least some pitted fiber tracheids are likely to have evolved from the scalariform counterparts that surrounded solitary vessels in ancestral dicotyledons. The scalariform tracheids occupy the spring wood and pitted ones occupy the summer wood in extant homoxylar dicotyledons which have distinctly dimorphic tracheids. Thereof, one could assume that the dicotyledonous vessels have come from the scalariform tracheids of the spring wood of homoxylar ancestors whereas the pitted fiber tracheids have partly originated directly from the pitted tracheids of their summer wood. However, investigated woods including the primitive ones of members of the family Magnoliaceae do show that the vessels and associated residual scalariform tracheids are in spring and in summer wood. Therefore, the ancestral heteroxylar dicotyledons are likely to have had no pitted tracheids but scalariform ones throughout the growth rings. In other words, ancestral homoxylar dicotyledons are reasonably thought to have had uniform scalariform tracheids. Dimorphic tracheids in heteroxylar dicotyledons seem to have evolved after the originating of their vessels. Consequently, all pitted tracheids of extant heteroxylar dicotyledons are relevantly concluded to have come from initial scalariform counterparts.

Strength property of the scalariform tracheids

The scalariform tracheids are unable to make wood strong. The wood strengthening elements are known to withstand to longitudinal tensions and compressions. Their strength is directly determined by the specific transversal area of longitudinally continuously thickened parts of element walls.

Figure 7A shows that scalariform-pitted cell walls can resist to longitudinal stresses only by their tiny edge parts (black). The other parts are unable to resist such stresses, because they are interrupted by transversally long scalariform bordered pits. Like those in the metaxylems of many ferns and in secondary xylems of some cycads, the dicotyledonous scalariform tracheids bearing pits in all their walls (Fig. 3) are hardly stronger than their protoxylem spiral counterparts which are rather tensile than longitudinally stress resistant.

The middle S_2 layer is a principal part of the cell wall of strengthening wood elements. Its parallel cellulose fibrils are longitudinal to mostly somewhat oblique to constitute large-pitched spirals

(Frey-Wissling 1968, 1976). The cellulose fibril orientation is reflected by those of elliptic to slitting inner orifices of the pits. The strengthening element walls are thus reinforced due to orientation of their cellulose fibrils which are usually nearly parallel to stress vectors in the walls. Continuous spiral structure of the cellulose fibrils is impossible in the scalariform tracheid walls, even though they would bear distant pits (Fig. 8).

Figure 8 A shows a part of a fiber tracheid wall with typical round pits. This wall is quite similar with its imaginary scalariform counterpart (Figs 7, 8 B) in width and thickness, as well as in bordered pit numbers, total pit membrane areas and total pit orifice areas. The two walls only differ in pit shapes. These walls must be equally water-permeable, but the pitted ones resist stresses as a whole (Figs 7 B, 8 A). Besides, the large-pitched spirals of the cellulose fibrils are feasible in pitted tracheid walls but impossible in scalariform tracheid ones. Therefore, the round-pitted wall is much stronger against longitudinal stresses than the scalariform-pitted one, the latter resisting stresses only by its small edge parts.

The drawn comparison shows that evolutionary scalariform-to-round pitting transformation was of great importance. It has resulted in such high amelioration of wood element strength that any extant woody angiosperm is unlikely to have retained scalariform strengthening constituents in its wood.

Thereupon, the scalariform tracheids would irrelevantly be interpreted as strengthening wood elements. They should be classified as vascular tracheids. Like the vessels, the scalariform tracheids mostly transfer water trough the wood. After this conclusion, *Trochodendron* was erroneously reported to have no vascular tracheids at all (Sokolov 1949) and the short pitted tracheids were irrelevantly thought to be the only vascular tracheids in *Tetracentron* (Metcalfe & Chalk 1950). Every scalariform tracheid in *Trochodendron* and *Tetracentron* and any other plant should be considered with confidence to be vascular irrespectively of whether it is in the metaxylem or in the secondary xylem.

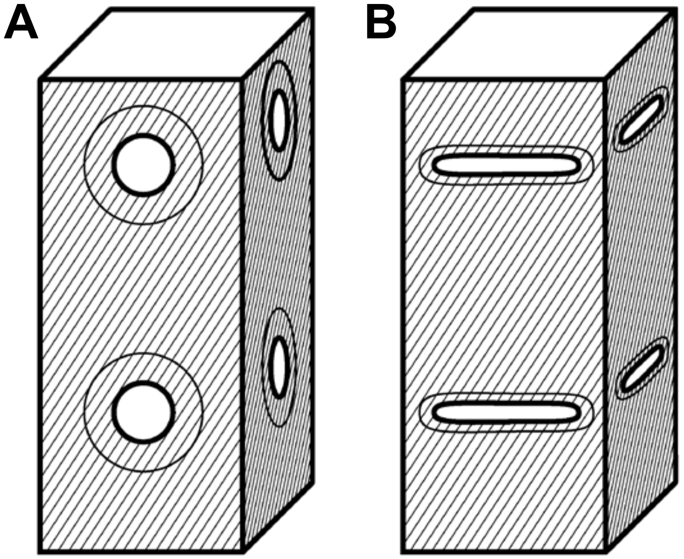

Figure 8. Spiral cellulose fibrils in the tracheid walls. A – mostly continuous in pitted tracheid; B – mostly discontinuous in scalariform tracheid.

Original growth habit of angiosperms as evidenced by specific functioning of the scalariform tracheids

Available facts prove that dicotyledonous fiber tracheids and vessel segments must have come from scalariform tracheids. Consequently, the ancestral angiosperm wood must have had only scalariform ones. Thereof, those plants were not woody, i.e. pycnoxylic in the strict sense of the term. The secondary wood takes the most specific volume of the pycnoxylic stem and it is the only strengthening tissue there. Therefore, it always has variously advanced strengthening elements (fiber tracheids, libriform fibers) that constitute the bulk of the wood. The scalariform tracheids were shown above to be unclassifiable as strengthening wood elements. There are no pycnoxylic homoxylar plants which would have exclusively scalariform tracheids in their wood.

The ancestral angiosperms could have been manoxylic plants whose primary wood or primary plus pure secondary wood took insignificant specific volumes of their stems. Such wood were secondary or insignificant strengthening constituents of the stems. Peripheral extraxylar stem tissues mostly strengthen the manoxylic stem. In this context, it is worth to be noted that all plants with wood having only scalariform tracheids are exclusively manoxylic (e.g. lepidodendrons, some cycads). Otherwise, the ancestral angiosperms could have been rather small herbs and the strengthening of their stems must not yet have been urgent at all.

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Address of the corresponding author:

Univ.-Prof. Dr Alexander C. Timonin
Lomonosov Moscow State University
Faculty of Biology
Department of Higher Plants
Vorobyevy Gory 1(12)
119992 Moscow
Russia
E-mail: timonin58@mail.ru

Zeitschrift/Journal: Wulfenia

Jahr/Year: 2013

Band/Volume: 20

Autor(en)/Author(s): Kedrov Gorn B.

Artikel/Article: Scalariform tracheids in secondary xylem of woody dicotyledons: distribution, function and evolutionary significance. 43-54