

I. NOMENCLATURE OF AXIAL XYLARY ELEMENTS: A
MORPHOLOGICAL AND PHYSIOLOGICAL APPROACH

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SUMMARY

The views of BAILEY & TUPPER (1918) of main lines of specialization of tracheary elements and fibres are based on the supposed intermediate forms between tracheary elements and other fibres such as libriform fibres. This work has been confirmed by many other publications since, but the way of classifying of particularly nonperforate fibrous elements in the secondary xylem has remained a point of controversy. The perceptions of BAILEY & TUPPER (1918) and also more recently VAN DER SCHOOT & VAN BEL (1989) are derived from macerated xylem. However, this method is not suited to judge the position and mutual relations of individual elements. After scrutiny of two special cases of dispute, *Alnus viridis* (Chaix) DC. and *Solanum lycopersicum* L., the question of the intermediate forms, basis of the general view of xylem evolution, is posed again. Physiological phenomena as the way of differentiation of xylary elements by the cambium and other morphological characteristics and manifestations of the non-perforate fibrous elements in the xylem are considered. This time the mutual relation between tracheary elements and libriform fibres is investigated carefully with the help of sections and accurate microscopic observations. As result an alternative for the "diagrammatic illustration of average size and structure of tracheary elements in the mature wood of Coniferae and various groups of Dicotyledoneae" as published by BAILEY & TUPPER (1918, Fig. 6) is presented. The axial xylary elements are herein classified in a different way, viz. two main groups: a complex of tracheary elements with bordered pits and a complex of parenchymatous and sclerenchymatous fibres with simple and funnel pits.

1. INTRODUCTION

BAILEY & TUPPER(1918) based their view of the main lines of specialization of tracheary elements and fibres only on measurements of length of vessel members and all fibrous elements in slides of macerated xylem of 154 gymnosperm and 279 angiosperm wood species. They distinguished only two types of axial elements in the secondary xylem: vessel-segments and "other tracheary cells", under which both septate and nonseptate libriform fibres, fibre-tracheids and tracheids. All these fibres "grade into one another and appear to

be interchangeable in many plants". The authors concluded from their measurements that as vessel-segments become shorter in more specialized wood species the borders of the pits in the "other tracheary cells" become smaller and smaller and finally have entirely disappeared from fibres of wood species with shortest vessel-segments. Both vessel-segments as well as fibres have become shorter. With increasing specialization, certain tracheary cells became highly specialized and served principally as conductors of liquids, whereas others gradually ceased to serve in that capacity and became modified as mechanical or skeletal elements. Thus BAILEY & TUPPER (1918) departed from the idea that in both gymnosperm and angiosperm woods only long tracheids were the precursors of all axial elements in the secondary xylem. TIPPO(1938) concluded that correlated with the decrease in length of fibrous tracheary elements together with vessel evolution, the fibrous tracheary elements became increasingly specialized. That is, bordered pits became smaller and smaller, until ultimately a libriform fibre with simple pits was produced. In addition BAAS (1986), CARLQUIST (1986a,b, 1988), VAN DER SCHOOT & VAN BEL (1989) considered the fibrous elements in the secondary xylem as a tracheid-fibre continuum from fibres with pure bordered pits like those in the vessel walls until fibres with simple pits. BAAS (1986) recommended radially split surfaces of common wall parts of fibres and rays to judge the nature of these pits. Moreover BAAS (1986) found bordered pits in bundle sheath fibres of monocotyledons and in phloem fibres, and CARLQUIST (1988) in living parenchymatous ray cells. Bordered pits developed along a very precise evolution line during circa 100 million years from changes in the configuration of wall strengthening structures in the primitive conductive elements in the xylem of fossil plants and are originally a type of bordered pit fields (HENES, 1959; EDWARDS, 1992), and not homologous to simple pits. The existing ideas about the relation between and nomenclature of xylem elements are based on the so-called tracheid-fibre continuum of intermediate forms between bordered pits and simple pits. Whether these transitional forms really exist in such a great number in "transitional" tissue is tested. Accurate microscopic observations of the different way in which the several kinds of pits can present themselves in microscopic images of sections only indicate the existence of bordered pits, and several forms of simple pits.

2. MATERIALS AND METHODS

Observations on *Alnus viridis* (Chaix) DC. and *Vitis vinifera* L. wood were made on slides obtained through courtesy of Dr R.W. den Outer, Dept of Plant Cytology and Morphology, Wageningen Agricultural University. Plant material of *Solanum lycopersicum* L. cv. Moneymaker was grown in the greenhouse. In hand-made transverse, radial and tangential sections of fresh material from a piece of the stem of a 1 m high plant at a distance of 10-20 cm above the cotyledons, the elements of the secondary xylem were studied. Slides with sections of seedlings and tubers of older plants of *Raphanus sativus* L. cv. Saxa Nova were the same as used in MAGENDANS (1991). Slides of *Fraxinus excelsior* L. were prepared from branches in a stage of late rest and in which cambial activity was induced by applying auxin in lanolin paste on the cut surface under the bud. Sections of about 12 μm were made with a microtome. Slides of *Malus sylvestris* Miller and *Fagus sylvatica* L. were prepared from sections made by hand of young branches with much cambial activity. All observations were made with a Wild microscope using oil immersion and 1,500 x magnifying optics. Camera lucida drawings have been made by means of a Wild drawing tube.

3. OBSERVATIONS

3.1. The case of *Alnus viridis* (Chaix) DC.

Dr R.W. den Outer recommended this tree with a type of wood considered by wood anatomists as problematical to judge the character of the fibrous imperforate elements in the ground tissue. The fibres of this tissue would show intermediates between tracheids and libriform fibres: fibre-tracheids (*sensu* CARLQUIST, 1986a). In Figs 1-8 the different types of pits in the wood of *Alnus viridis* are shown. In Fig.1 a real bordered pit-pair is shown between two tracheary elements, characterized by a regular lenticular pit cavity, and a calyciform (=funnel-shaped, BAAS, 1986) pit between a libriform fibre (*sensu* CARLQUIST, 1986a) and a parenchyma cell. The bordered pit-pair is well co-ordinated, i.e. the pits form each other's mirror image or each complementary half forms congruence-co-ordination (HENES, 1959). The funnel-shaped pit, funnel pit in short, is not a congruent pit-pair but is complemented by an indistinct simple pit in a parenchyma cell. In Fig. 2 parts of two tracheary

elements are shown with many bordered pits and in Fig. 3 parts of libriform fibres are shown without pits in this part of the drawing illustrating the rather scarce occurrence of pits in libriform fibres. In Fig. 4A a funnel pit-pair is shown in the radial walls of two adjacent libriform fibres and in Fig. 4B the transverse sections at three different levels through a pit-pair with the same shape is shown. This pit-pair consists of two not really complementary halves that are partly blind. The pit cavity is not a distinct lenticular space, but is actually composed of two half slit-formed spaces that show strongly variable positions to the complementary half. The two slit-formed spaces will partly form a very narrow and hardly visible widening near the pit membrane (Fig.4A, w; B, s). In fact in the funnel pit a true pit cavity, as in the bordered pit-pair, does not exist at all. The funnel pits are distinctly smaller than the bordered pits in the wood of *Alnus viridis*. In Fig. 5 other images are shown of pits in radial walls of libriform fibres. Figs 5A,B are more or less interpretable yet, but Figs 5C,D are more difficult to understand. However it should be clear that these images do not represent well co-ordinated bordered pit-pairs with a definite lenticular pit cavity, but smaller funnel pits depicted in some oblique way. In Fig. 6 transverse sections of funnel pits are shown and one longitudinal section (H). Specially in Figs 6 B-F the funnel pits are shown being crooked: the complementary halves are by no means mirror images as in bordered pit-pairs. No definite lenticular pit cavities are present. We can only find two complementary pit canals not identical in shape. Fig. 6H shows a longitudinal section of this type of funnel pit in which the pit cavity appears totally absent, as happens in transverse sections of bordered pits. In Fig. 6A the funnel pit is partly blind and in Fig. 6G a definite pit cavity is also lacking.

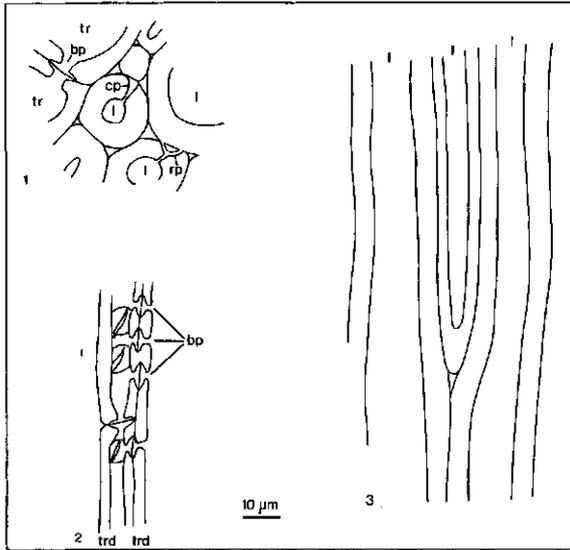
Summarizing it may be said that the libriform fibres of *Alnus viridis* showed simple pits and funnel pits with many irregular shapes and varying sizes. Unlike the bordered pit, the funnel pit showed a large variety of forms in the same wood. In more detail the following types of pits may be found. Simple pits occurred, some of which are ramiform with a branched canal (Fig. 1, rp) and some may be blind, without complementary structure. Most pits have cross, slit-formed canals (Figs 4, 5) and the canals widen in a regular way, i.e. without a distinct limit as a boundary between canal and widening pit cavity, in the direction of the pit membrane (funnel pits). No definite lenticular pit cavity exists, but because of the widenings of the pit canals a four lobed space comes into being corre-

sponding with the directions of the pit canals. In different optical sections the two complementary halves of the funnel pit shifted in relation to each other, making both complementary halves partly blind. All types of pits were smaller, relatively scarce and irregularly spread on the walls of the fibres in contrast with the numerous, larger and distinctly bordered pits of the tracheary elements in the usual regular hexagonal configuration (HENES, 1959).

Intermediate forms between the tracheary elements (Figs 1, tr; 2) and the libriform fibres (Figs 1, l; 3) seem to occur, but are rare. At the very most an isolated transitional element could be found between a tracheary element and a libriform fibre. The characteristics of this transitional form may be summarized as follows. The thickness of the wall of this element is intermediate; these elements are rare and only in the adjacent wall parts of such a fibre and a tracheary element, i.e. at the interface between libriform tissue and the tracheary tissue or elements, transitional types of pits seem to occur. In these adjacent wall parts the number of pits is smaller and the pits are smaller than in other walls of the tracheary element. The pits in these wall parts are scattered or occasional and did not occur in a definite (hexagonal) configuration. These pits (Fig. 7) seem to show characteristics of both, funnel pits and bordered pits. There seems to be a round border (b) but the diameter is much smaller than in the bordered pits of the other walls of the tracheary element. This observation (Fig. 7) was an exception, the other pits in this wall part showed variable shapes in contrast with the normal bordered pits in the other walls of the tracheary element which were almost uniform. In such an, only occasionally present, 'transitional' element, in fact a libriform fibre, funnel pits did occur of which the number may be greater than in other fibres, also in the tangential walls.

Funnel pits do not show a real and sufficiently extensive series of transitional forms to the bordered pits. So-called intermediate forms (Fig. 7) are only occasionally present and these forms belong to the category of funnel pits or are structurally combinations (Fig. 8). The form and size of pits is influenced by the neighbouring element, but does not change the real nature of the pits.

Finally Fig. 8 shows the type of pits between tracheary elements and libriform fibres. This type must be called half-bordered pit-pair and is structurally a combination of a bordered pit and a funnel pit. Only in face view the error can be made to call this type a bordered pit-pair and the fibre element an intermediate form between libriform fibre and tracheary element.



Figs 1-3; Details of secondary xylem of *Alnus viridis*. 1, Transection, two tracheary elements (tr) with real bordered pit-pair (bp) in common wall; libriform fibres (l) with funnel pit (fp) with a rather constantly dilating canal, and ramiform pit (rp); 2, Radial section, vasicentric tracheids (trd) with many closely packed, real bordered pit-pairs (bp); 3, Radial section, libriform fibres (l) without visible pits in large wall parts.

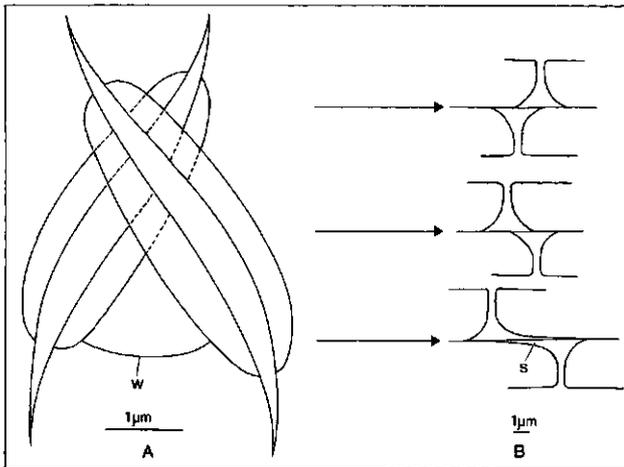


Fig. 4; Secondary xylem of *Alnus viridis*. A, details of radial surface view of funnel pit-pair in libriform fibre ; B, transsections of this type of pit (smaller) at three levels. A regular lenticular pit cavity consisting of two identical complementary halves does not exist. The slit-formed spaces show strongly variable positions to the complementary half. Measurement of this type of pit-pair only allowed for one complementary half.

s, narrow and hardly visible widening near the pit membrane; w, limit of space s.

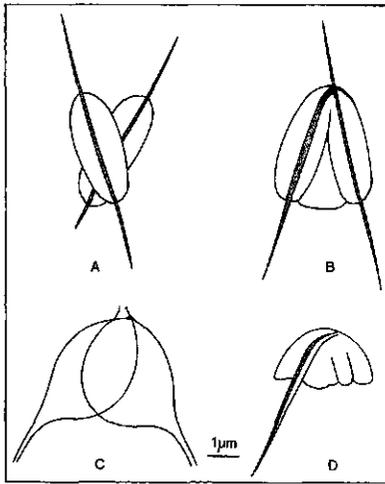


Fig. 5; Secondary xylem of *Alnus viridis*. Details of radial surface views of funnel pit-pairs in libriform fibres; A, B, these images resemble more or less Fig. 4; C, D, funnel pit-pairs depicted in an oblique way.

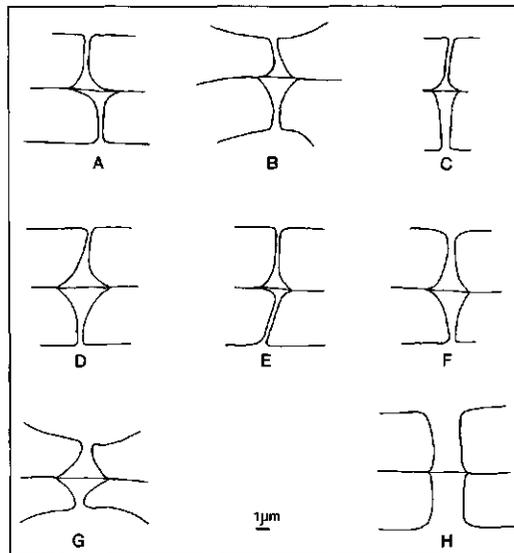


Fig. 6; Secondary xylem of *Alnus viridis*. A-G, transverse sections of funnel pit-pairs in libriform fibres; A, section probably below the centre, cp. Fig. 4; B, in the centre this pit-pair does not show uniformity, but a small degree of "blindness"; C-F, funnel pit-pairs are always more or less crooked: the complementary halves are not mirror images; G, pit canals evenly dilating as two dissimilar calyces upside down to each other ('calyciform' pit) and no distinctly limited pit cavity is present; H, longitudinal section, no pit cavity visible.

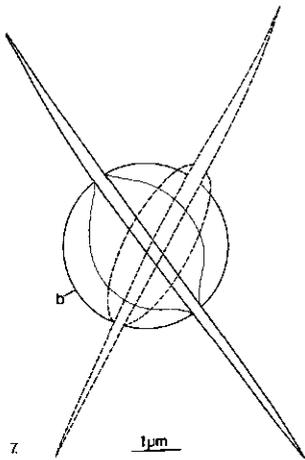


Fig. 7; Secondary xylem of *Alnus viridis*. Radial surface view of pit in common wall of tracheary element and a 'transitional element', in fact a libriform fibre, see text. This very uncommon pit-pair seems to show approximately congruence-co-ordination and a round border. The 'border' is much too small and the position in relation to the other pit-pairs in this wall is too much isolated however, as to call it a real bordered pit-pair in a tracheary element of this xylem. b, 'border'.

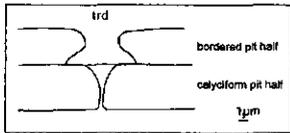
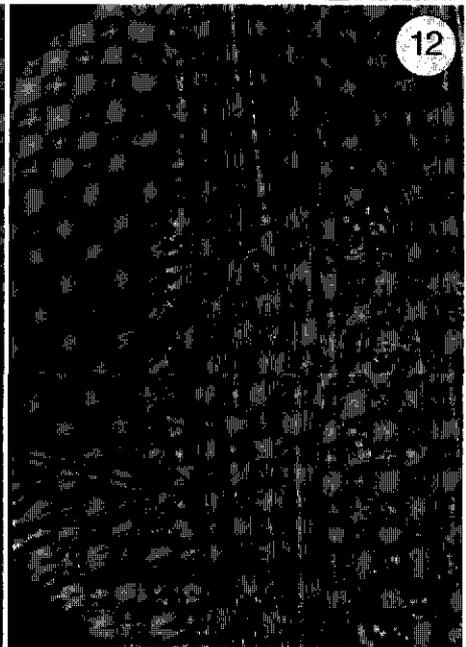
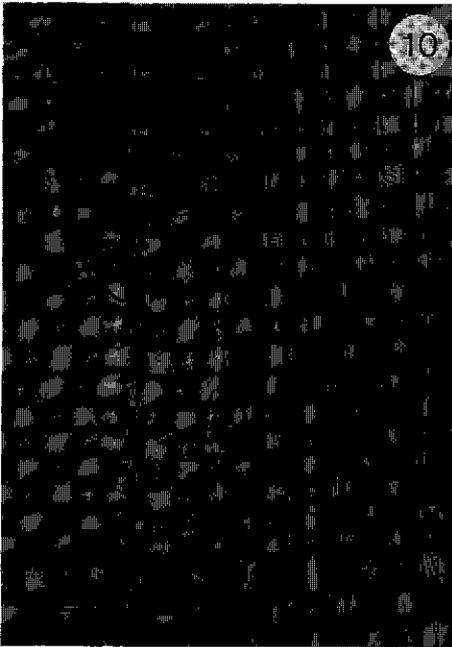
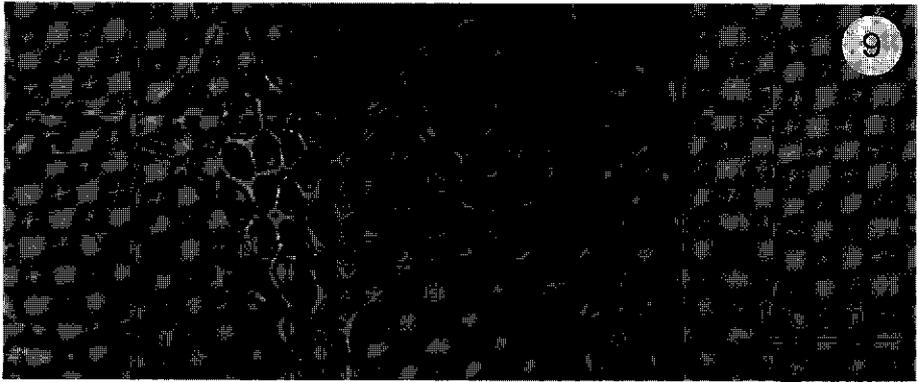


Fig. 8; Secondary xylem of *Alnus viridis*. Transsection of pit-pair in common wall of tracheid (trd) and a so called 'transitional form' between tracheid and libriform fibre, in fact a libriform fibre (l), see text. Half-bordered and half-funnel pit-pair. Also a greater number of this type of pit-pairs in this wall does not convert the fibre into an evolutionary 'intermediate form'.

3.2. The case of *Solanum lycopersicum* L. cv. Moneymaker.

VAN DER SCHOOT & VAN BEL (1989) tried to give a detailed description of the xylem elements in the internodes of a 1 m high plant at a distance of 10-20 cm above the cotyledons. The results of this investigation were exclusively obtained by maceration of the secondary xylem. This method does not allow a proper study of the relative positions of the individual elements in the xylem, nor can it reveal the exact shape of the pit-pairs. In my investigation of the secondary xylem, tracheary elements, which are probably all vessels, libriform fibres (*sensu* CARLQUIST, 1986a), axial parenchyma and ray parenchyma were found (Figs 9-12). The transverse section (Fig. 9) shows a fraction of one of those large parts of the secondary xylem situated between the primary xylem and primary phloem of one of the three large vascular bundles. These areas are characterized by the presence of many tracheary elements, all of them with perforations: vessels (v). Libriform fibres (l) and paratracheal xylem parenchyma (pp) are also present in this section. In radial sections (Figs 10, 11) the vessels (v) are shown with definite bordered pits (bp) in a not strict hexagonal configuration (HENES, 1959) (hc). The



perforations (p) are not visible in every section. The small vessels are adjacent to the libriform fibres (l) which possess funnel pits (fp) or pits with slit-formed canals (sp). In tangential section (Fig. 12) vessels (v) with definite bordered pits (bp) and perforations (p) are easily recognizable. The small vessel to the right borders upon libriform fibres (l) with few funnel pits (fp). The ray parenchyma cells (rp) are living and contain starch. Figure 13 shows the cambial zone of an active growing plant from the greenhouse. The tracheary complexes, left and right of the multiseriate ray (mr), differentiate much earlier than the libriform ground tissue and consist only of large vessels with small vessels around them and sometimes a single paratracheal parenchyma cell. In Fig.14 the tracheary complex in the cambial zone is connected by way of small vessels (1-6) with an older tracheary complex; the differentiation of libriform fibres (l) lags behind.

Transitional forms between vessel members and libriform fibres do occur but seem to be very rare. These transitional forms were only found adjacent to a small tracheary element, as in the wood of *Alnus viridis*. The transitional form is a libriform fibre which shows less and partly smaller bordered pit like structures in the collective wall part with the vessel. Such structures are more scattered, while in the other walls of this libriform fibre mostly simple pits with slitlike pit canals occurred. When mostly smaller bordered pit like structures occurred in the collective wall between a vessel and a fibre, the other walls of the fibre showed simple pits with slit-like canals. The "bordered" structures in the collective wall are often blind, i.e. the complementary half is lacking in the fibre wall. To put it briefly: the pits between a tracheary element and a libriform fibre do not fit properly as in vessels and libriform fibres mutually. A fact that is not to be expected in case of evolutionary transitional forms.

Figs 9-12; Light micrographs of sections from basal internodes of *Solanum lycopersicum*. 9, Transverse section showing vessels (v), libriform fibres (l) and paratracheal xylem parenchyma (pp). Simple pit-pairs (sp), funnel pit-pairs (small, fp) and half-bordered pit-pairs (hbp) are visible; 10, Radial section showing large and small vessels (v) with bordered pit-pairs (bp) and perforations (p), as well as libriform fibres (l) with funnel pit-pairs (fp) and simple pit-pairs with slit-formed canals (sp); 11, Radial section showing vessels (v) with bordered pits in a not strict hexagonal configuration (alternate pitting; hc), libriform fibres (l) with funnel pit-pairs (fp) and simple pits with slit-formed canals (sp), and paratracheal xylem parenchyma (pp) with simple pits; 12, Tangential section showing large and very small vessels (v) with bordered pits and perforations (p), libriform fibres (l) with rather few funnel pits, and ray parenchyma cells (r). Scale bar 100 μm .

4. OBSERVATIONS AND PHYSIOLOGICAL AND MORPHOLOGICAL INTERPRETATIONS

Two main categories of axial xylary elements: tracheary, and parenchymatous or fibrous.

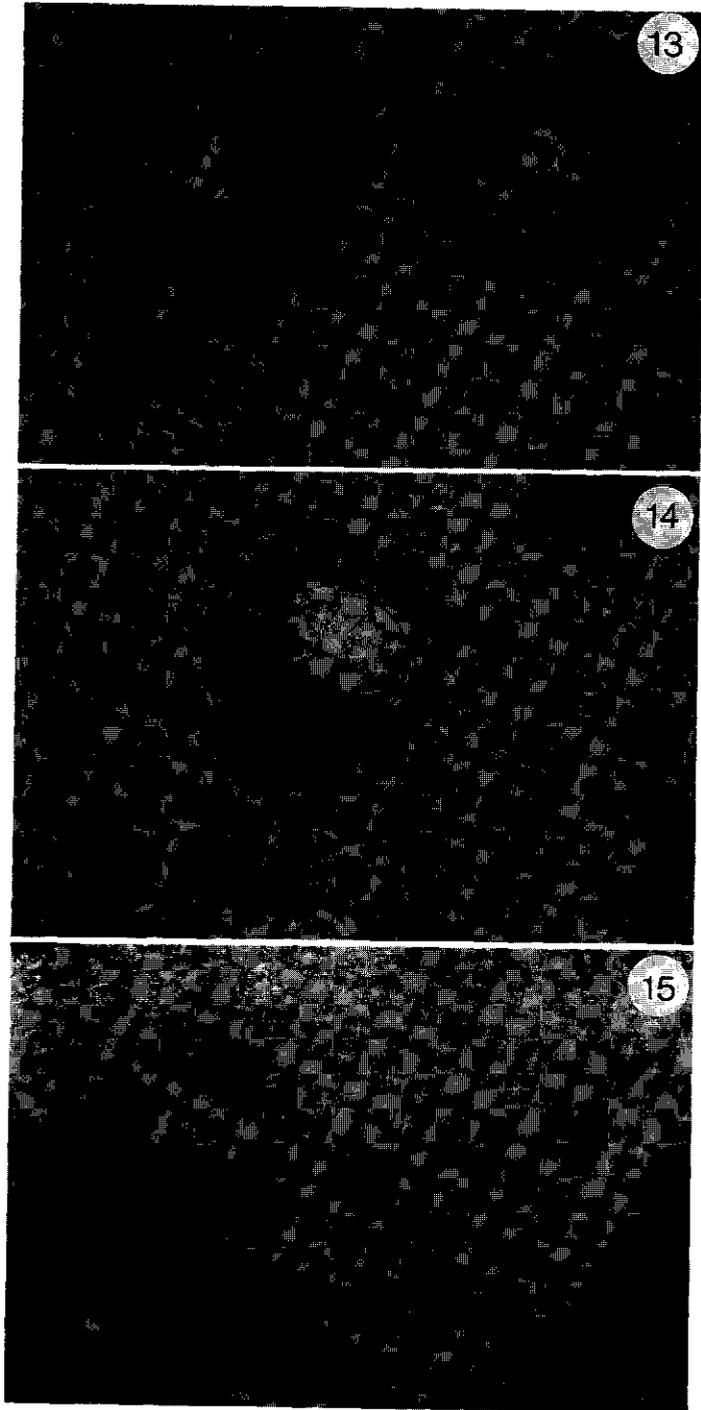
4.1. Physiological indications.

The differentiation into the tracheary elements is 'stable'. An attained state of this type of differentiation continues to exist also after removal of the modifying factors (MOHR & SCHOPFER, 1993). Some young fusiform xylary initials dilate, the walls stretch and thicken and attract the transpiration transport in the cambial zone as indicated by the colouring with eosin (Fig. 15) (MAGENDANS, 1991). This transpiration stream will also contain apoplastic stimuli (MADORE & WEBB, 1981), probably active as modifying factors. These factors will only be operative a short time: differentiation into a tracheary element leads to its death in the cambial zone already and with that to a strong enhancement of the apoplastic transport capacity of the tracheary element.

The differentiation into the other axial xylary elements, parenchyma and libriform, is reversible and not stable ("modulation type" of differentiation); at least there exist many indications for this type of differentiation as being not stable. The modifying factors must be operative during a longer period (MOHR & SCHOPFER,

Figs 13, 14. Light micrographs of transverse sections from basal internodes of *Solanum lycopersicum*. 13, Two aggregates of tracheary elements left and right of a multiseriate ray (mr), differentiated much earlier than the libriform ground tissue (l), composed mainly of large vessels (v) with smaller vessels around them. Only few paratracheal parenchyma cells (pp) are present. The walls of the tracheary elements do always look darker than the brightening walls of the libriform fibres because of the very many large bordered pits (cp. Fig. 11, hc) in the tracheary elements and the relatively few small pits in the libriform tissue: a change in refraction of light occurs. c, cambial initials. 14, As 13, The early differentiated aggregate of tracheary elements with one large vessel (v) is connected via a row of six small vessels (1-6), with many bordered pits, to an older tracheary complex; the differentiation of libriform (l) lags behind. c, cambial initials. Scale bar 100 μm .

Fig. 15. Light micrograph of transverse section of tuber of *Raphanus sativus*. The route of the transpiration stream in the cambial zone becomes visible after 1 hr absorption of an eosin solution by the taproot. The vessel primordia (vp) show thicker, dark-coloured walls although the protoplast is still present. c, cambial initials; n, nucleus. Scale bar 100 μm .



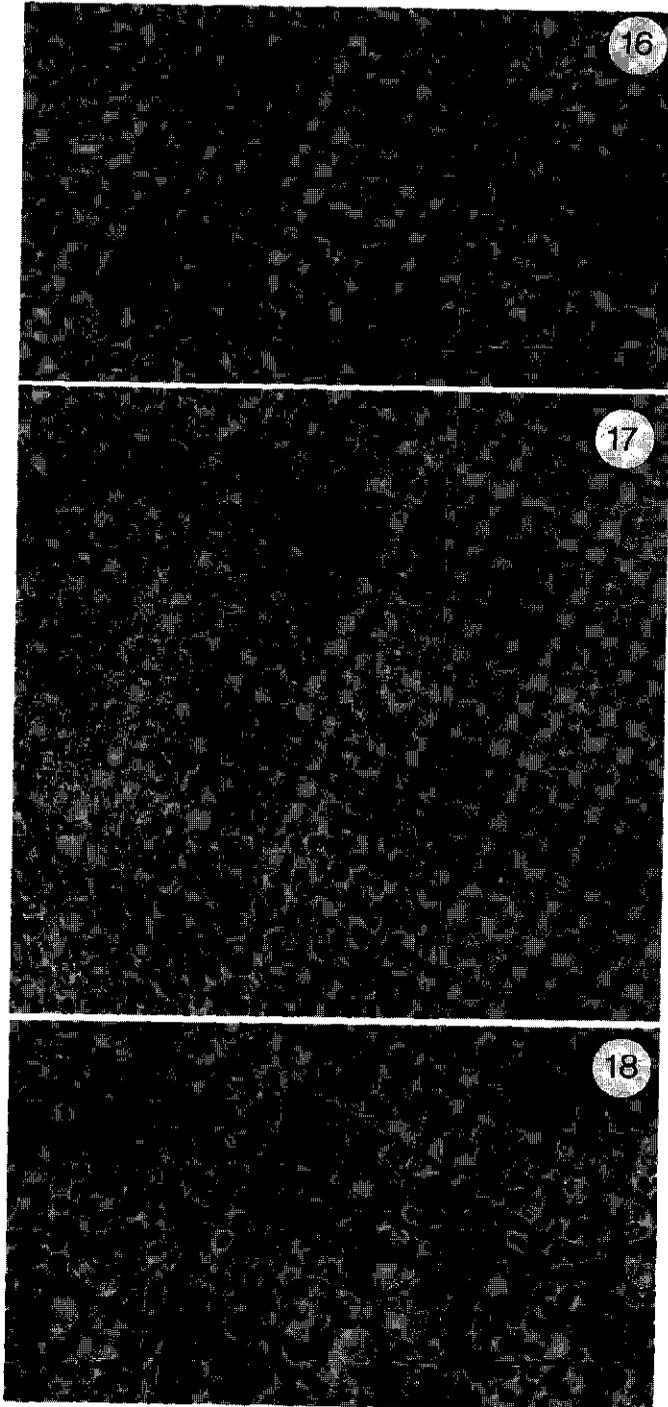
1993) before a state of unstable differentiation is reached. The xylary axial parenchyma remains alive; at least much longer than the other axial elements and so do the real fibres. These elements keep the capacity to dedifferentiate and redifferentiate a longer time, for example in regeneration as in graftings. But also in normal development many indications are found for looking upon these differentiations into parenchyma and fibres as being different from differentiation into tracheary elements. The first approximately four cell layers of the secondary xylem of a small tuber of *Raphanus sativus* show many libriform fibres as a solid ground tissue around the pitted vessels (MAGENDANS, 1991). After these four cell layers the cambium suddenly forms only axial parenchyma with the same distribution of pitted vessels in this parenchymatous ground tissue. When the flowering stem of radish reaches about 10 cm the cambium suddenly produces libriform fibres again as ground tissue. Thus the same cambial cells are able to form only parenchyma strands or only libriform fibres as ground tissue, perhaps with the availability of assimilates as modifying factor. The number of vessels does not change per unit tissue area, only the total number of vessels increases as the number of leaves is growing. When the radish plant becomes taller, a more solid stem basis is required. More examples of this kind of substitution of fibres into parenchymatous tissue or vice versa are known from the literature (e.g. CARLQUIST, 1988).

The order of differentiation in the cambial zone into tracheary elements and the other axial elements points to a closer relation between tracheae and tracheids than to the relation between tracheae and libriform fibres.

In Figs 13,14 of *Solanum lycopersicum*, the aggregates of tracheary elements are shown to differentiate much earlier than the living fibres. In Fig. 16 the cambium of *Fraxinus excelsior* formed a new vessel after recommencement of the cambial activity; the differentiation of fibres lags far behind. *Ricinus communis* is also a well known example (REINDERS & PRAKKEN, 1964) and VILLALBA (1985) describes this phenomenon in the cambial zone

 Fig. 16. Light micrograph of recently reactivated cambium of *Fraxinus excelsior*. The transection shows that the differentiation of the libriform fibres (l) lags far behind the differentiation of the large vessel (v). c, cambial initials.

Figs 17, 18. Light micrographs of transections of cambial zone of resp. *Malus sylvestris* and *Fagus sylvatica*. The ground tissue of the xylem consists of tracheids, differentiating simultaneously with the vessels. Scale bar 100 μ m.



of *Prosopis flexuosa* DC.: the vessels differentiate much earlier than the libriform fibres. In *Malus sylvestris* (Fig. 17) and *Fagus sylvatica* (Fig. 18) on the other hand the ground tissue of the xylem consists of tracheids and differentiates simultaneously with the vessels. The tracheids die soon after differentiation.

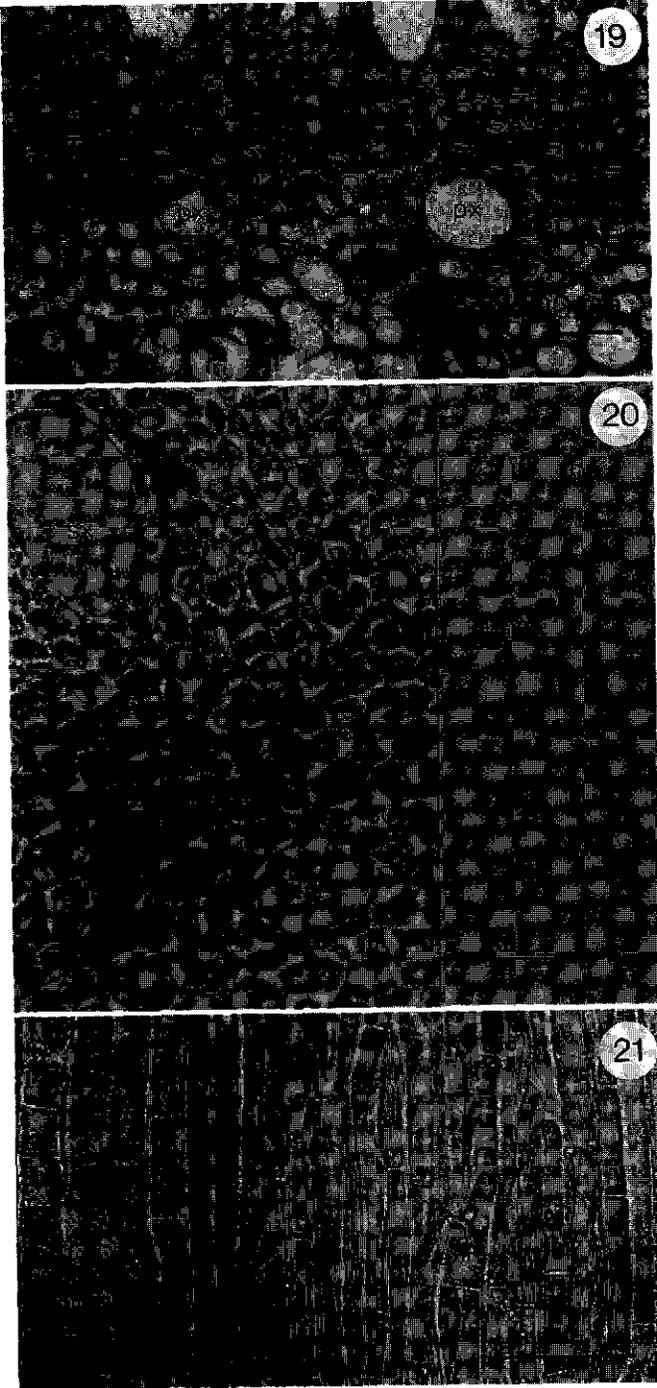
4.2. Morphological indications.

"The vascular tissues are commonly surrounded by parenchyma and are associated with sclerenchyma. A considerable proportion of (this) sclerenchyma arises from the same meristem as the vascular tissues do and is therefore treated as part of the vascular system" (ESAU, 1965a). "Parenchyma and sclerenchyma are not sharply delimited from one another" (ESAU, 1965b). In Figs 19, 20 transverse sections of a stem of *Vitis vinifera* are shown. In Fig. 19 the pith, primary xylem (px) and secondary xylem (sx) can be distinguished. Sclerenchyma fibres compose the ground tissue in the primary xylem, libriform fibres in the secondary xylem (Fig. 20). In Fig. 21 a radial section is shown of the same tissues. In the primary xylem the sclerenchyma fibres are septate; the libriform fibres in the abutting secondary xylem are septate in much the same way, and both "types" of fibres are living and have simple pits. Few arguments can be invented to endow these fibres with principally different names. More of these considerations will be presented in the discussion.

5. DISCUSSION

BAAS(1986), BAILEY & TUPPER (1918), CARLQUIST (1986a,b; 1988), ESAU (1965b, 1977), JEFFREY (1917), METCALFE & CHALK (1950), REINDERS (1935), VAN DER SCHOOT & VAN BEL (1989), TAKHTAJAN (1991) and TIPPO (1938) all agree with the opinion of a morphological continuum from tracheids to libriform fibres. This view is based on the fact that these authors observed a continuous series of intermediate forms between bordered pits and simple pits of the non perforate fibres in wood. Besides, these authors agreed with the ideas of BAILEY & TUPPER (1918)

Figs 19, 20, 21. Light micrographs of transections (19, 20) and a radial section (21) of a branch of *Vitis vinifera*. See text. l, libriform; px, primary xylem; sc, sclerenchyma; sx, secondary xylem. Scale bar 100 μ m.



that the principally strengthening elements, the libriform fibres, were the last stage of evolution of these fibres from the long tracheids in the most primitive woods. My objections to these views are of three kinds. 1. The morphological continuum from tracheids to libriform fibres cannot be demonstrated and surely does not exist at all, certainly not in one individual plant. Actually there exists a borderline in front of which non-bordered pit structures occur and at the back of which, after a fundamental change of structure, real bordered pits appear in every individual wood species. 2. It is improbable that the strengthening, fibrous elements, present next to the hydroids of mosses or in the xylem of ferns (BIERHORST, 1971; LORCH, 1931; NIKLAS, 1990), e.g. present as thick-walled stereids, intermixed with the moss hydroids (HÉBANT, 1970), would disappear and later in evolution be invented again on such a broad scale and at about the same places. The strengthening fibres are thought to have developed from the long primitive tracheids. Characters once obtained in evolution do not easily disappear again (CARLQUIST, 1988). The process of evolution of these tracheary elements was rather slow, circa 100 million years and sophisticated (HENES, 1959). Will it be probable then that soon a 'contra-evolution' started through which these developed tracheary fibres evolved back again into strengthening fibres of the same shape and at the same places where in the lower plants sclerenchyma (= libriform) is still present? Apart from that, TAKHTAJAN (1991) argues that during evolution the portion of the axial parenchyma in wood increases. So possibilities for a 'modulation type' of differentiation (MOHR & SCHOPFER, 1993) from this parenchyma into sclerenchyma were abundant. 3. Physiological phenomena support the view of ESAU (1965b) that parenchyma and sclerenchyma are not sharply delimited from one another just like parenchyma and libriform (KURODA & SHIMAJI, 1985). After wounding the cambium of *Populus euramericana* these authors found that the regenerating cambial cells produced three different types of differentiations: a) tracheary elements, b) a series of elements consisting of all transitional forms between parenchyma and libriform and c) products of ray initials that do not intermingle with a) and b). CARLQUIST (1988) mentions examples of living fibres morphologically having evolved so as to be relatively parenchyma-like too.

The methods used by VAN DER SCHOOT & VAN BEL (1989) to observe the imperforate fibrous elements in *Solanum lycoper-*

sicum are inadequate; in macerated material the exact positions of the elements in relation to other elements in the tissue cannot be determined. Rare transitional forms as anomalies of elements situated along the border of different types of tissues cannot be identified with this method. The method proposed by BAAS (1986), observing fibre-ray pits, does disregard the anatomical features that occur in the complementary wall parts when many, very large simple pits are positioned next to each other as always happens in the cross-fields. This proposal is rightly criticized by CARLQUIST (1986b). REINDERS (in REINDERS & PRAKKEN, 1964, fig. 126) observed large simple pits in a wide vessel of the early wood of *Quercus*, but this observation is wrong because of the relative small degree of border development in such large half-bordered pit-pairs and the large increase of wall thickness in the ray parenchyma cells between the pit membranes. So the ontogenetic aspects are not considered. The fact that BAAS (1986) discovered bordered pits in phloem fibres and other extra-xylary fibres and that CARLQUIST (1988, p.341) mentioned bordered pits in the tangential walls of ray cells in a large number of woods is remarkable. In my opinion a morphologist would never compare the real bordered pits in the tracheary ray cells of *Pinus*, which are exact, smaller copies of the bordered pits in the tracheids (with a torus!), with the calyciform-like pits in the tangential (and transverse!) walls of ray parenchyma cells of for example *Alnus viridis* (Fig. 22).

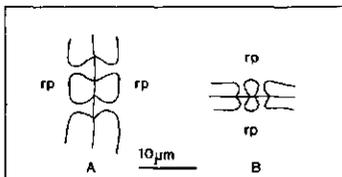


Fig. 22. *Alnus viridis*, radial section of secondary xylem. Camera lucida drawings of procumbent ray-parenchyma cells (rp) showing calyciform or funnel like pit-pairs in tangential (A) and transverse (B) walls.

The proposal of BAAS (1986) of using certain descriptive conventions, the 2 µm or 3 µm limit of the diameter of 'borders', can at the most be of use for taxonomists as are length and width of leaves, in spite of the enormous variability of sizes and practical difficulties mentioned already by CARLQUIST (1986b). These limits have certainly not a sound morphological basis. Bordered pits are highly precise evolved structures (HENES, 1959), originally compound (EDWARDS, 1992, Figs 7,8) evolved during circa 100 million years in the primitive conductive elements in the xylem of fossil plants. This evolution of the bordered pit in the xylem has no

direct relation to the model of a simple pit and its homologues which are much older in the plant world. The funnel pits could be measured separately (*sensu* BAAS, 1986) by taxonomists but the practical difficulties are great (cp. Fig. 4).

In my opinion the many examples of substitution of libriform by parenchyma, i.e. the conversion of the entire fibrous background of a wood into a quasi-parenchyma system, as temporary in *Raphanus sativus* (MAGENDANS, 1991), in globular cacti and many *Crassulaceae* (the phenomenon called parenchymatization, CARLQUIST, 1988) are resp. proof and indication for the 'modulation type' of differentiation (MOHR & SCHOPFER, 1993) into the parenchyma-libriform complex.

The phenomenon of the differentiation of a barrier-zone of parenchymatous tissue not far from the cambium as a reaction to the infection of *Verticillium* in *Fraxinus* (SCHROEIJERS, 1990) is also a temporary replacement of libriform fibres via transitional forms into parenchyma. When the infection is over, conversion to libriform fibres takes place again. Fibre di- (tri-, *Connaraceae*, Dr R.W. den Outer, personal communication) morphism leads to formation of parenchyma bands in wood and every degree of intermediacy is shown (CARLQUIST, 1988). Libriform fibres show their pits mainly restricted to the radial walls, as parenchymatous fibres do (e.g. VILLALBA, 1985). These instances and others are indications of the equivalency of the parenchyma-libriform complex (Fig. 23). The tracheary complex is not involved in these conversions and remains a totally independent transport and often water storage unit. The parenchyma-libriform complex forms a real continuum as does the tracheary complex; the conception of the morphological 'continuum' from tracheids to libriform fibres in the literature is improbable and inconsistent and moreover morphologically and also physiologically incorrect.

In conclusion an alternative is presented for the "diagrammatic illustration of average size and structure of tracheary elements in the mature wood of Coniferae and various groups of Dicotyledoneae" as published by BAILEY & TUPPER (1918, Fig. 6). Fig. 23 shows a diagrammatic survey of the most important axial elements in the secondary xylem. Two main categories are distinguished: tracheary elements and the complex of fibres consisting of parenchyma and libriform fibres. The dead tracheary elements represent 'stable' differentiations (MOHR & SCHOPFER, 1993) and show great specialization in transport capacity. All tracheary elements have real

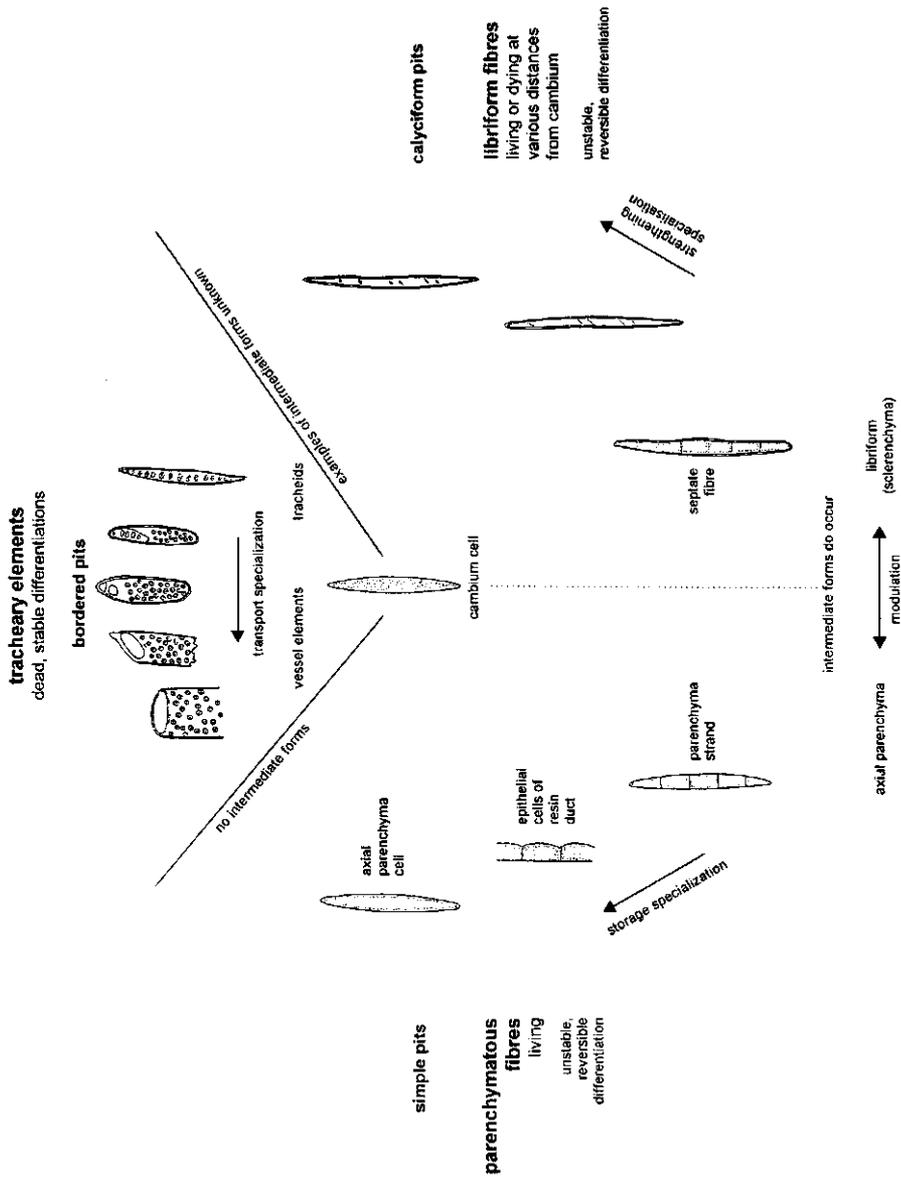


Fig. 23. Diagrammatic survey of important axial elements in secondary xylem. Two main categories are distinguished: a tracheary complex with a stable type of differentiation and with bordered pits, and a complex of fibrous elements with a modulation type of differentiation and with simple or funnel pits. Thus no sharp borderline can be distinguished between parenchymatous fibres and libriform fibres.

bordered pits and die soon after differentiation. The complex of parenchyma and fibres consists of living parenchymatous elements, including epithelial cells, and is often septate. This group of parenchymatous elements shows numerous transitional forms to the group of libriform fibres. These fibres are living at first but often die at various distances from the cambium. As the parenchymatous elements, these fibrous elements show unstable, reversible differentiations, called modulations by MOHR & SCHOPFER (1993), and have simple or funnel pits in the walls. Intermediate forms do not occur between vessels and parenchyma. Between libriform fibres and less specialized tracheary elements however, rarely 'transitional' elements can be found but exclusively as exceptions on the borderline and as a real abnormality (i.e. element with different caliciform or funnel pits).

This diagrammatic survey of the most important axial elements of the secondary xylem can also be presented as in table 1.

Table 1. Survey of the most important axial elements in the secondary xylem.

Tracheae Tracheids	Tracheary elements (complex) bordered pits	Dead in functional state near cambium
Libriform fibres Parenchyma	Fibrous elements (complex) simple pits or funnel pits	Alive or dying at varying distances from cambium

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