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MORPHOLOGY OF PITS IN HARDWOOD FIBRES

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

J.F.C. MAGENDANS

II. BORDERED PITS AND FUNNEL PITS: FURTHER EVIDENCE OF CONVERGENT EVOLUTION

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PREFACE

Since a long time the need made itself felt of better knowledge, and of distinguishing characteristics of various types of pits, particularly those of the hardwood fibres. Plain definitions of these structures, in conformity with views concerning evolutionary development of xylary elements, are much-needed for nomenclature of wood fibres in plant physiological research and the study of taxonomy of hardwoods. It is my wish that the now presented data, figures, and diagrams and their interpretations may conclusively show the distinction between bordered pits and the so-called funnel pits. Better understanding of this difference, both types of pits not being homologous, will undoubtedly lead to a reduction of the difficulties in the study and teaching of wood anatomy.

I am very grateful to Mr W.L.H. van Veenendaal for his able technical assistance. Professor Dr M.T.M. Willemse, Dr A.A.M. van Lammeren and Dr R.W. den Outer helpfully reviewed the manuscripts.

J.F.C. Magendans. Wageningen, September 1998.

CONTENTS

INTRODUCTION

Nomenclature of axial xylary elements and interpretation of the morphology of pits are closely interconnected. The existing opinions about the relation between and nomenclature of xylem fibres are based on the so-called tracheid-fibre continuum of intermediate forms between bordered pits and simple pits. But these views contradict evolutionary evidence of bordered pits being the result of changes in the configuration of wall strengthening structures in the primitive conductive elements in the xylem of fossil plants and thus bordered pits would belong to the tracheary elements. Besides physiological phenomena point to the strict relation between libriform and parenchyma, both possessing simple pits.

The way of investigating the types of pits in xylem fibres has not been much convincing up to now. Controversy still exists about the assessment of bordered pits in the secondary xylem and the classifying of the non-perforate fibrous elements based on a *general* standard of pit measures. The conception of bordered pits as homologous to simple pits is unsatisfactory because of different morphology and size of both types of structure, and because intermediate forms have not been found. In addition much criticism is possible concerning the prevailing opinions of transitional forms between bordered and simple pits, and techniques of observation.

After scrutiny of fourteen hardwoods and one herb belonging to fourteen different families widely spread all over the plant world, which possess wood fibres with pits resembling small bordered pits, the difference in structure and dimension between bordered pits of tracheary elements and the pits of libriform fibres in each species has become more and more evident. The fact that bordered pits and the smaller pits of libriform fibres are not homologous cannot be disregarded any longer.

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

CONTENTS

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.

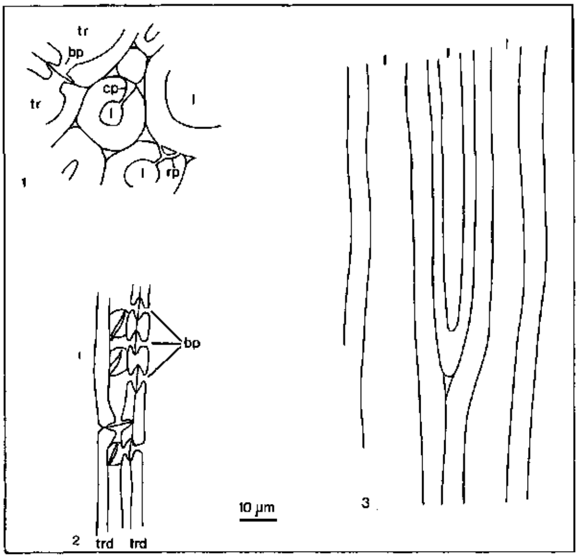
Dr R.W. den Outer recommended this tree with a type of wood considered by wood anatomists as problematical to judge the character of the fibrous imperforate elements in the ground tissue.The fibres of this tissue would show intermediates between tracheids and libriform fibres: fibre-tracheids (*sensu* 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 corresponding 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.

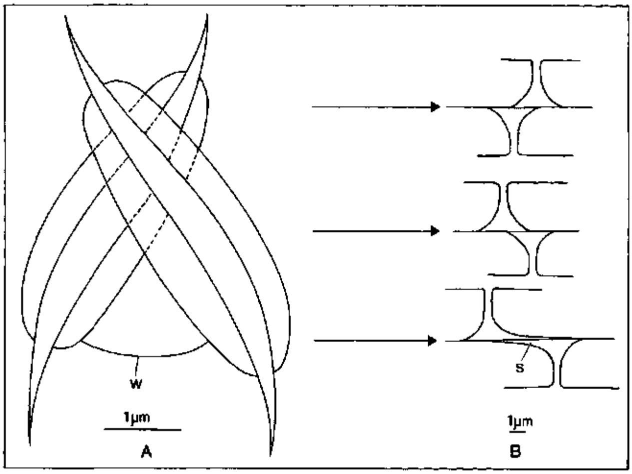


Fig. 4; Secondary xylem of *Alnus viridis*. A, details of radial surface view of funnel pit-pair in libriform fibre ; B, transections of this type of pit (smaller) at three levels. A regular lenticular pit cavity consisting of two identical complementary halves does not exist. The slit-formed spaces 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.

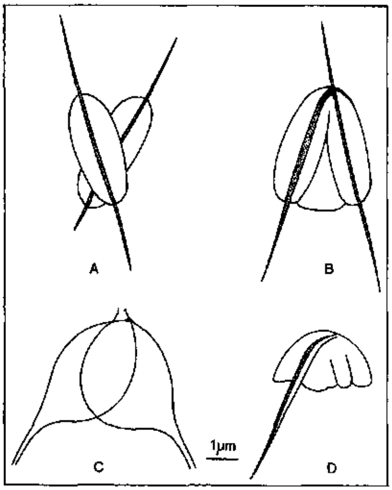


Fig. 5; Secondary xylem of *Alnus viridis*. Details of radial surface views of funnel pit-pairs in libriform fibres; A, B, these images resemble more or less Fig. 4; C, D, funnel pit-pairs depicted in an oblique way.

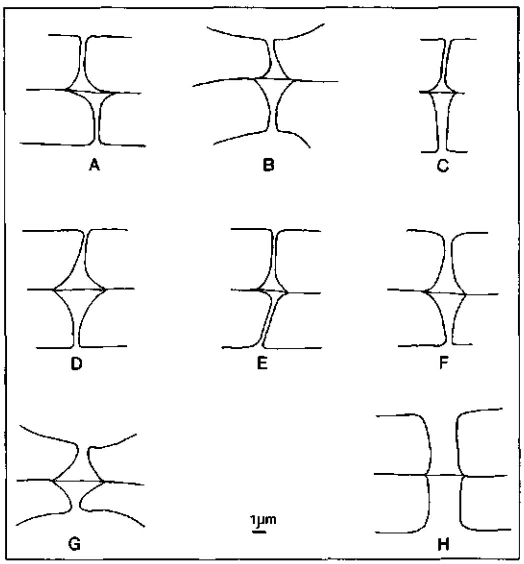


Fig. 6; Secondary xylem of *Alnus viridis*. A-G, transverse sections of funnel pit-pairs in libriform fibres; A, section probably below the centre, cp. Fig. 4; B, in the centre this pit-pair does not show uniformity, but a small degree of "blindness"; C-F, funnel pit-pairs are always more or less crooked: 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.

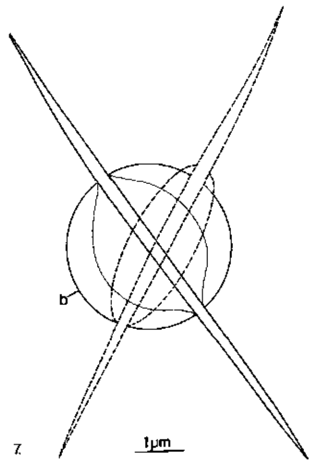


Fig. 7; Secondary xylem of *Alnus viridis.* Radial surface view of pit in common wall of tracheary element and a 'transitional element', in fact a libriform fibre, see text. This very uncommon pit-pair seems to show approximately congruence-co-ordination and a round border. The 'border' is much too small 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'.

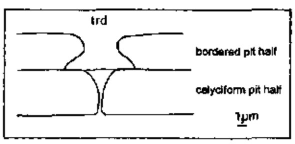
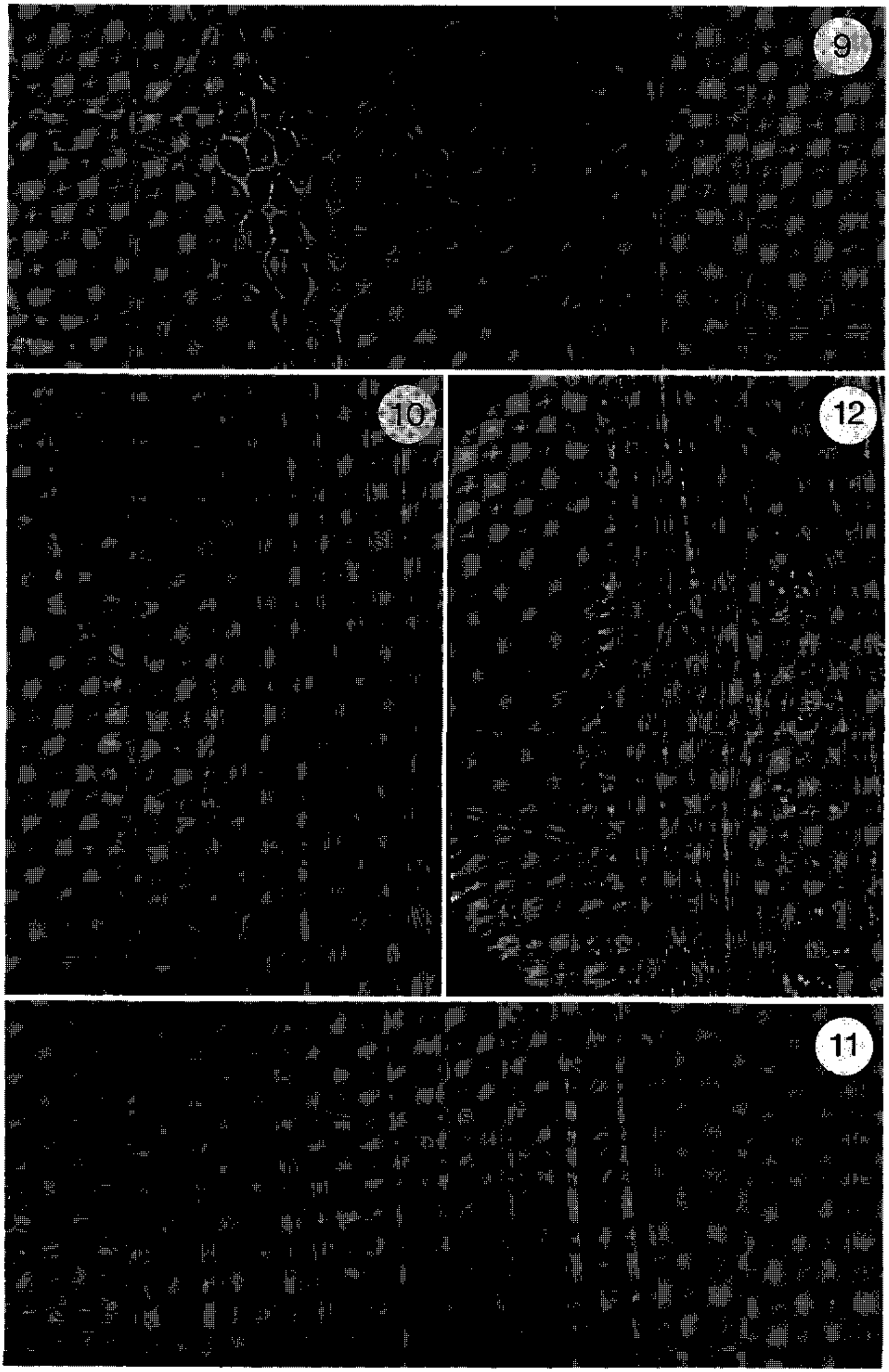


Fig. 8; Secondary xylem of *Alnus viridis.* Transection of pit-pair in common wall of tracheid (trd) and a so called 'transitional form' between tracheid and libriform fibre, in fact a libriform fibre (l), see text. Half-bordered and half-funnel pit-pair. Also a greater number of this type of pit-pairs 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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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.

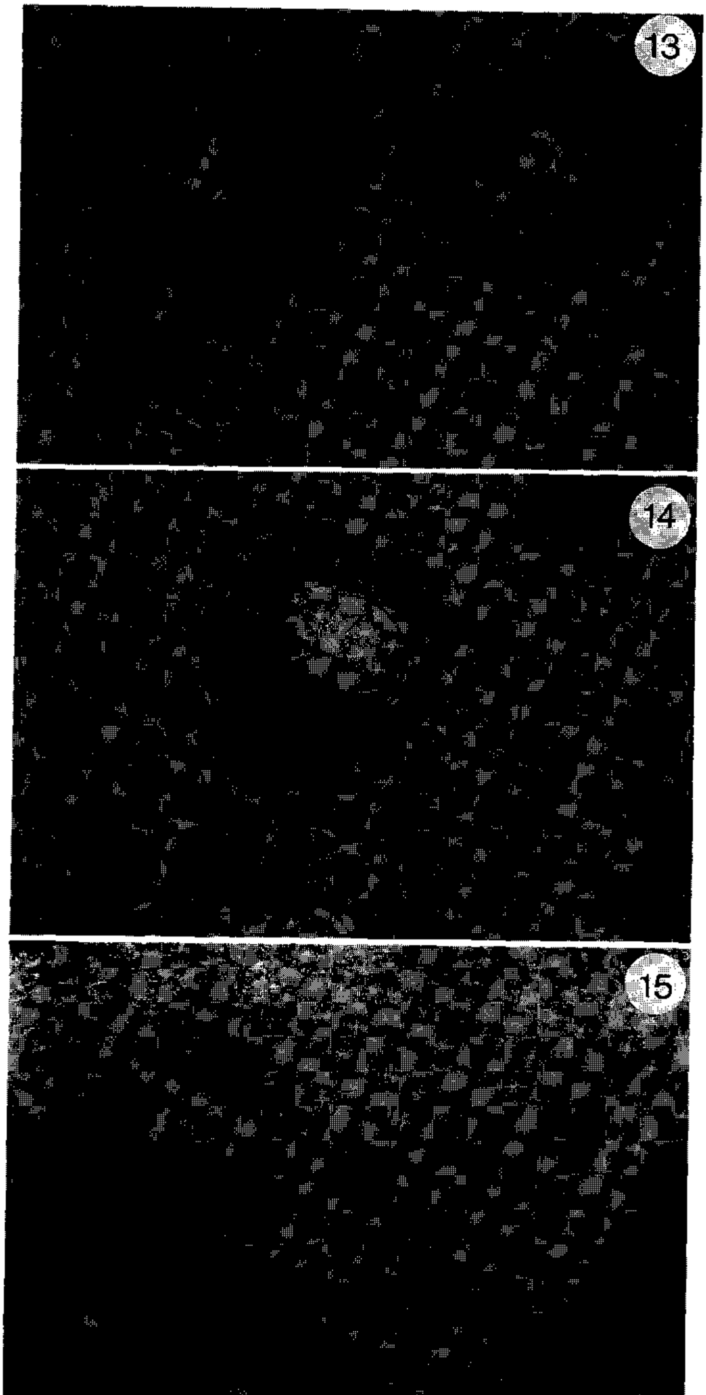
4.1. Physiological indications.

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.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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

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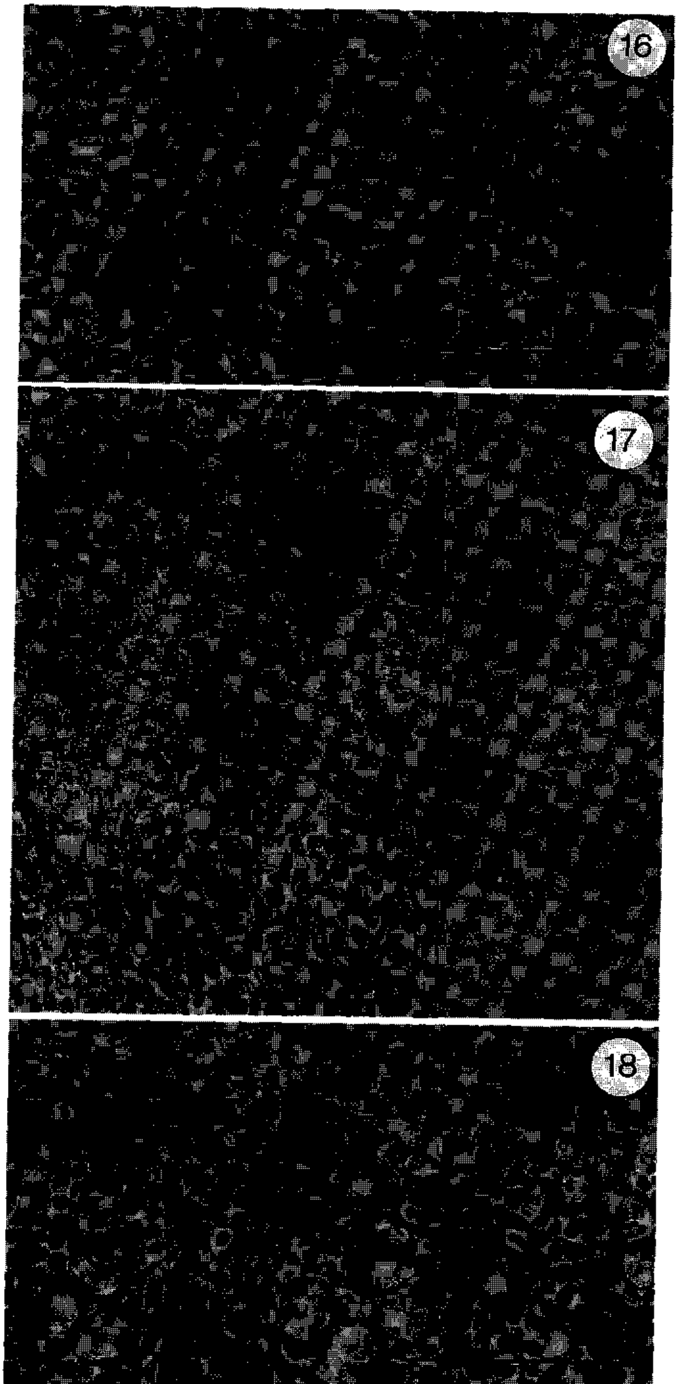
Fig. 16. Light micrograph of recently reactivated cambium of *Fraxinus excelsior*. The transection shows that the differentiation of the libriform fibres (l) lags far behind the differentiation of the large vessel (v). c, cambial initials.

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 μm.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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.

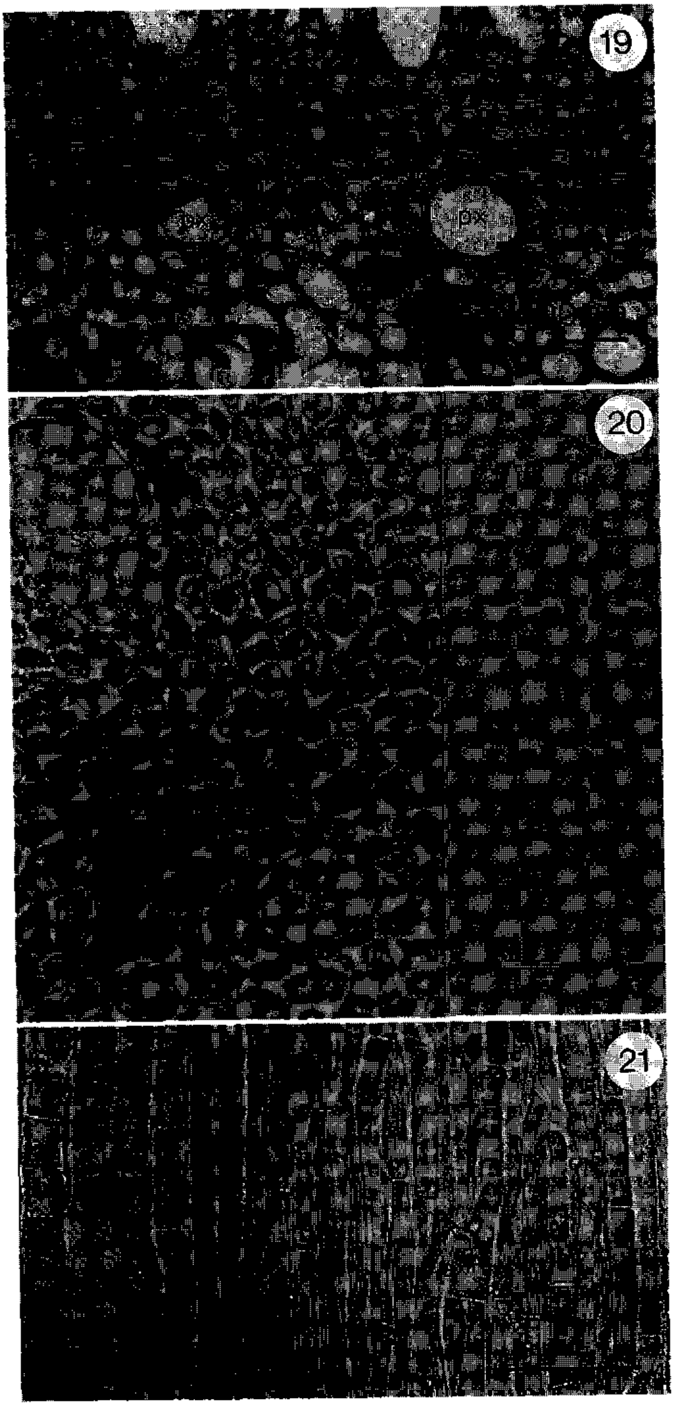
4.2. Morphological indications.

"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 μm.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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).

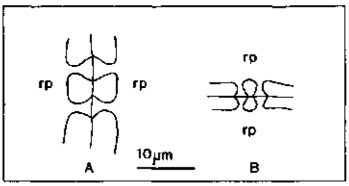

Fig. 22. *Alnus viridis*, radial section of secondary xylem. Camera lucida drawings of procumbent ray-parenchyma cells (rp) showing calyciform or funnel like pit-pairs in tangential (A) and transverse (B) walls.

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

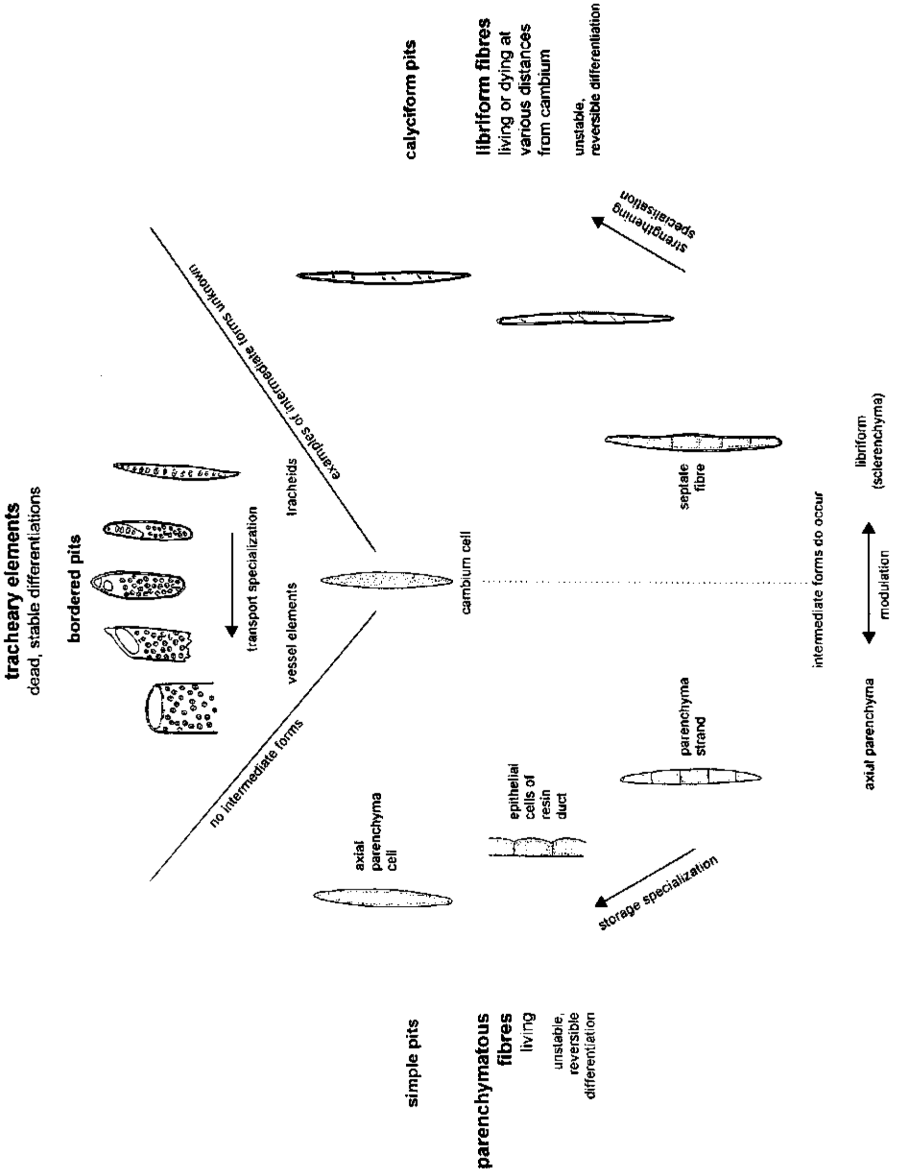

Fig. 23. Diagrammatic survey of important axial elements in secondary xylem. Two main categories are distinguished: a tracheary complex with a stable type of differentiation and with bordered pits, and a complex of fibrous elements with a modulation type of differentiation and with simple or funnel pits. 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

6. ACKNOWLEDGEMENTS

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II. BORDERED PITS AND FUNNEL PITS: FURTHER EVIDENCE OF CONVERGENT EVOLUTION

CONTENTS

SUMMARY

The structure of pits in axial tracheary elements and libriform fibres was investigated in detail by means of light microscopy, confocal laser scanning microscopy and scanning electron microscopy. As it has been reported that bordered pit structures can be observed in libriform fibres as well (e.g. VAN DER SCHOOT & VAN BEL, 1989) a selection of species has been made to compare pit structures in tracheary elements and libriform fibres to determine whether they form a continuum or discrete classes. Fourteen hardwoods and one herb belonging to fourteen different families, spread all over the plant world, are selected because their libriform fibres show funnel-shaped widenings of pit canals near the middle lamella (BAAS, 1986) in pits. Transectional and longitudinal measurements of bordered pits belonging to tracheary elements and the pits with funnel-shaped widenings of pit canals, the so called funnel pits belonging to libriform fibres (MAGENDANS, 1998), were compared by means of tests of significance within each species. Two different populations of pits were distinguished differing in morphology and size within every species. Definitions are proposed for these two types of pits: bordered pits and funnel pits.

1. INTRODUCTION

The views of BAILEY & TUPPER (1918) of main lines of specialization of tracheary elements and fibres as a tracheid-fibre continuum from fibres with pure bordered pits like those in the vessel walls up to fibres with simple pits, are still generally accepted. VAN DER SCHOOT & VAN BEL (1989) considered the fibrous elements in the secondary xylem of *Solanum lycopersicum* as a tracheid-fibre continuum as well. MAGENDANS (1998) demonstrated the bordered pits of tracheary elements and the funnel-shaped (BAAS, 1986) pits of libriform fibres in *Alnus viridis* and *Solanum lycopersicum* as being morphologically incomparable. Rather a different morphological origin of bordered pits (cp. HENES, 1959) and funnel pits appeared from that paper, with only rare, intermediate forms, in fact libriform fibres, at the borderline of tracheary and libriform tissues. The form and size of a pit in a certain element is influenced by its neighbouring element. In this paper more evidence is given for a convergent evolution of both types of pits using light, confocal laser scanning and scanning electron microscopical techniques. Measurements of the two different types of pits in fourteen hardwoods and one herb, belonging to fourteen different families, were statistically tested to evaluate size differences between the two groups of pits.

2. MATERIALS AND METHODS

Fourteen hardwoods and one herb of fourteen different families arranged in ten orders spread all over the plant world (KALKMAN, 1972) were selected for the study of pits in tracheary elements and libriform fibres. The examined species are listed below; those tagged with an asterisk have been studied from freshly fixed (FAA) material, the others from dried samples.

Species	Family	Order
Acer campestre L.	Aceraceae	Sapindales
Aesculus hippocastanum L. *	Hippocastanaceae	Sapindales
Alnus viridis (Chaix) DC. *	Betulaceae	Fagales
Anthocephalus cadamba (Roxb.) Miq.	Rubiaceae	Rubiales
Betula pendula Roth * and *Betula pubescens* Ehrh. *	Betulaceae	Fagales
Bruinsmia styracoides Boerl. et Koord.	Styracaceae	Ebenales
Corylus avellana L. *	Corylaceae	Fagales
Fraxinus excelsior L. *	Oleaceae	Oleales
Nyssa javanica (Blume) Wangerin	Nyssaceae	Umbelliflorae
Populus tremula L. *	Salicaceae	Salicales
Quercus acutissima Curruth.	Fagaceae	Fagales
Solanum lycopersicum L. cv. Moneymaker *	Solanaceae	Tubiflorae
Styrax obassia Siebold et Zucc. *	Styracaceae	Ebenales
Tilia cordata Mill. *	Tiliaceae	Malvales
Ulmus minor Mill.	Ulmaceae	Urticales

All these species possess a ground tissue of libriform fibres with funnel pits (MAGENDANS, 1998) on their walls. Only in *Quercus acutissima* tracheids (*sensu* CARLQUIST, 1986a) are present as well. Plant material was obtained from the greenhouse (*Solanum lycopersicum*) or from the wood collection of the Laboratory of Plant Cytology and Morphology, Wageningen University and Research Centre (Wlw; STERN, 1988). Wood of *Quercus acutissima* was obtained from Hamburg, Germany (RBHw). Scanning electron micrographs were made using Jeol SEMs 5200 or 6300 F. Confocal laser scanning microscopy was done with a Bio- Rad MRC 600 (transverse sections) using 1% toluidine blue in aqueous solution for colouring the sections and an excitation wavelength of 488 and 568 nm. Light microscopy was done with a Nikon Microphot - FXA (radial and transverse sections). In light microscopy oil immersion and 1500x magnifying optics were used. Camera lucida drawings were made with a Wild drawing tube (for size measurements). Of each species values of measurements of 20 bordered pits and 20 funnel pits in transverse and in longitudinal sections were compared. Tests of significance were by T - tests.

Abbreviations: LM, light microscopy; CLSM, confocal laser scanning microscopy; SEM, scanning electron microscopy.

3. DEFINITIONS AND TERMINOLOGY

The current definitions of parts of two types of pits in tracheary elements and libriform fibres in hardwoods need more precision. In agreement with interpretations of the microscopical images, the following characterizations can be given (cp. MAGENDANS, 1998).
Regarding bordered pits in hardwoods (Fig. 1, I, II).

Bordered pit-pair: a pit-pair in which the secondary walls overarch the pit membrane, thus forming a definite, mostly round, oval or rounded lenticular pit cavity with the complementary half; a rather definite boundary exists between cavity and pit canal. Are found in tracheary elements and usually occur in large numbers, in all walls.

Border: round, oval or rounded outline of the pit cavity of a bordered pit in face view.

Pit cavity: symmetrical lenticular space in a bordered pit-pair in the middle of which occurs the pit membrane, connected to the two cell lumina with definite, mostly slit-formed pit canals.

Regarding funnel-shaped (calyciform) pits in hardwoods (Figs. 1, III; 2, III; 3).

Funnel pit-pair: a pit-pair in which the two slit-formed pit canals widen gradually towards the middle lamella (calyciform). A definitely limited, true pit cavity, as in the bordered pit-pair, does not exist. The complementary halves do not fit exactly and are partly blind: the pit halves are not congruent, and the outer apertures of the complementary pit canals have more or less shifted positions in relation to each other along the middle lamella. In general funnel pits show a large variety of forms and dimensions in the same wood; this in contrast with bordered pits which are rather uniform.

Funnel pits are distinctly smaller than bordered pits in the same wood, irregularly spaced and relatively infrequent as compared to the numerous, larger bordered pits of tracheary elements. They are found in libriform fibres.

Funnel rims: irregular, often lobed outline of the funnel widenings of a funnel pit-pair near the middle lamella in face view. Probably sometimes hardly distinguishable from outwards bending buckle of pit canal near middle lamella (e.g. Figs 11 A,B).

Funnel widening: in face view ellipsoid space near the middle lamella formed by the gradually widening pit canal. Together, the complementary funnel widenings form a very irregular narrow space near the middle lamella.

4. HOW TO DETECT BORDERED PITS AND FUNNEL PITS

Bordered pit-pairs are well co-ordinated (Fig. 1, I, II), i.e. the cavity halves of the pits form each other's mirror image or each complementary half forms congruence-co-ordination (HENES, 1959). Only in the 'corners' of an element one cavity half of a pit-pair may be 'forced' to be somewhat distorted in relation to the other half, but the cavity halves of the pit-pair always remain co-ordinated. In transection the pit cavity always shows a symmetrical lenticular appearance (Fig. 2, I, B; II, B), independent of level of focus. Definite limits exist as boundaries between pit cavity and pit canals.

Funnel pit-pairs are not co-ordinated (Figs 1, III; 2, III; 3) and the complementary halves are partly blind (cp. MAGENDANS 1998, Fig. 4). The cavity near the middle lamella is not a distinctly lenticular space, but is actually composed of two slit-formed, near

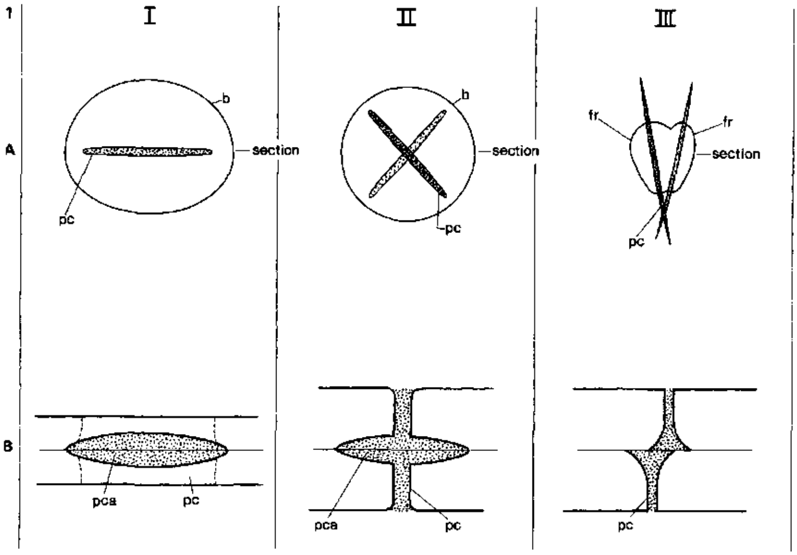
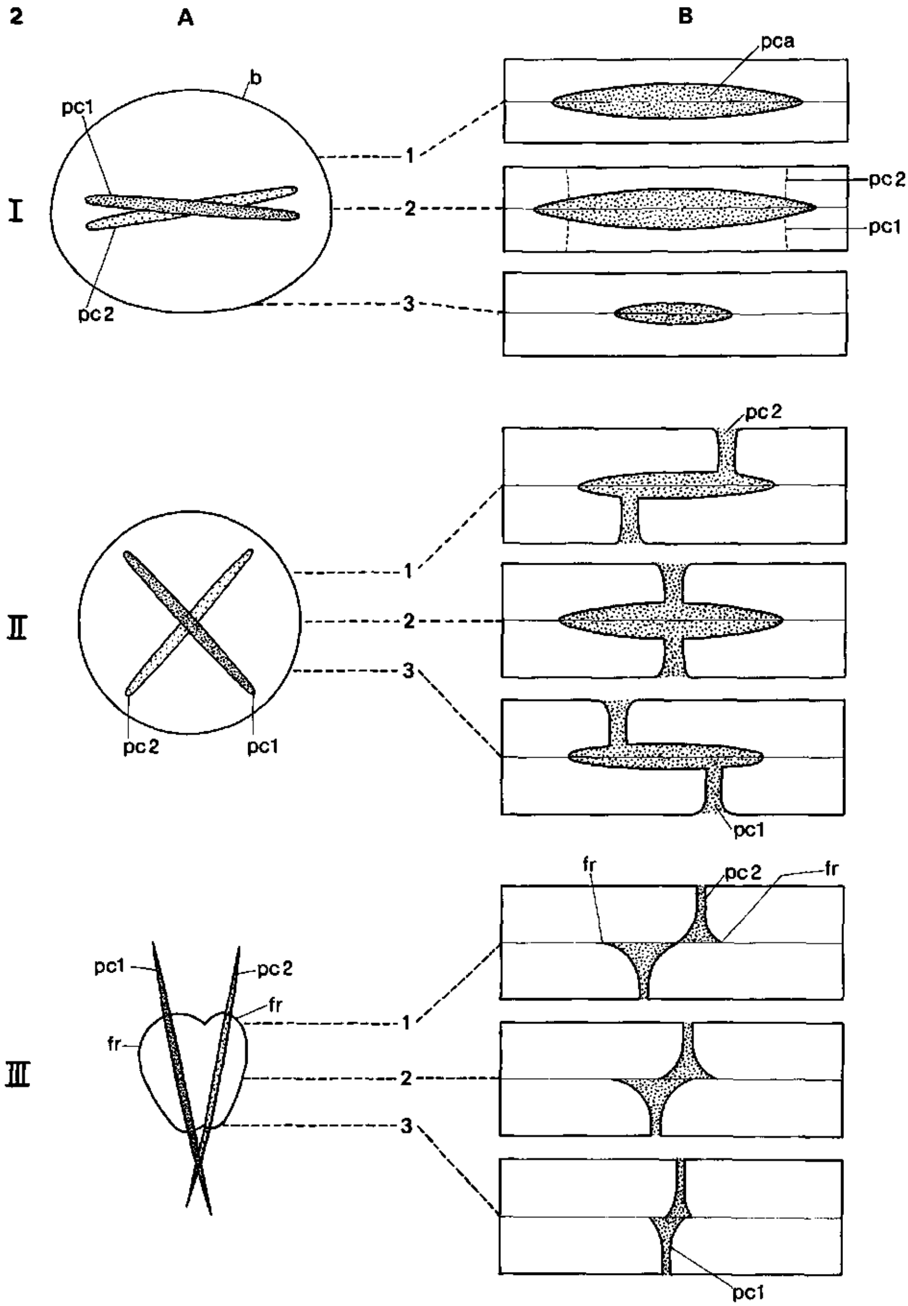


Fig. 1; Diagrams of pit types in xylem in face view (A) and transverse sections (B, at indicated levels in A). Bordered pit-pair (I) and bordered pit-pair with crossed, slit-formed pit canals (II) occurring in tracheary elements, viz. mainly in vessel walls (I) and principally in tracheid walls (II). Funnel pit-pair (III) shows pit canals gradually widening as two dissimilar calyces upside down to each other in libriform fibre walls. Pit cavity and pit canals have a dark appearance in microscopical images (dotted). b, border; fr, funnel rim; pc, pit canal (in I-B hardly visible); pca, pit cavity.

Fig. 2; Diagrams of a bordered pit in vessel wall (I), a bordered pit in tracheid wall (II) and a funnel pit in libriform fibre wall (III) in face view (A) and transverse sections (B, at indicated levels 1,2,3 in A). Depending on level of focus the bordered pit in the vessel wall shows a wide dark pit cavity (1), a slightly wider, dark cavity in the centre of the pit with canals hardly visible (2) and a smaller cavity (3). The cavity maintains a lenticular appearance. The bordered pit in the tracheid wall also shows a cavity with lenticular appearance, but the canals change position depending on level of focus. The funnel pit shows two separate calyces (1), or the slit-formed canals communicate with each other (2, 3). Upon changing optical section the complementary widened pit canals shift entirely in relation to each other along the middle lamella. Dotted: dark appearance in the microscopical image. pc1, slitlike pit canal in back wall of element in front; pc2, slitlike pit canal in front wall of rear element. Legends see also Fig. 1.

the middle lamella ellipsoid, spaces that show strongly variable positions to the complementary half. In fact in the funnel pit-pair a true pit cavity does not exist; we can only find two complementary pit canals not identical in shape. The funnel pits are often more or less crooked (MAGENDANS, 1998). Funnel pits are distinctly


2
A
B
b
pc1
pc2
pca
I
II
III
1
2
3
pc1
pc2
fr

smaller than bordered pits in the same wood; they are relatively scarce and irregularly arranged on the walls of libriform fibres in contrast with the numerous, larger and distinctly bordered pits of the tracheary elements in the mostly regular, alternate pitting on the vessel walls. Identification in transection is easiest taking into account the positional shifting of the two widened slit-formed canals in relation to each other when changing level of focus through the structure, the absence of a true pit cavity and the gradual widening of the pit canals in the direction of the middle lamella (Fig. 2, III, B). In face view the absence of an oval, round or rounded border as in bordered pits is most significant; only a small, lobed outline (funnel rims; Figs 2, III, A, fr; 3, fr) can be observed in the funnel pit-pair.

3

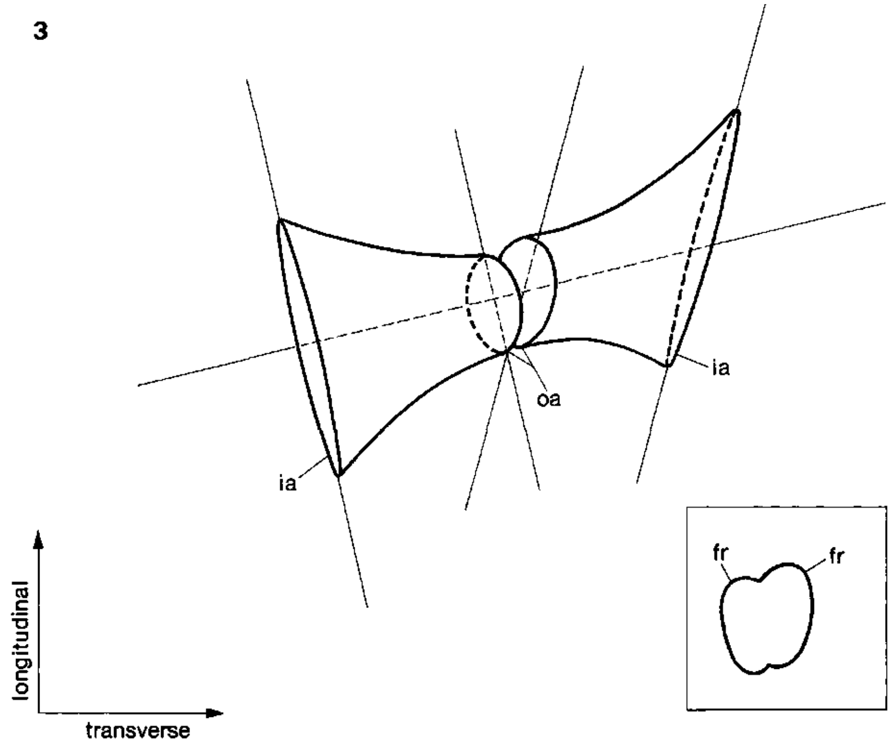


Fig. 3; Three-dimensional diagram of funnel pit showing widening slit-formed pit canals to the middle lamella into ellipsoid calyciform spaces. Outer apertures of pit canals, situated at the middle lamella,
not co-ordinated. ia, inner aperture; oa, outer apertures of pit canals. Insert: outline of outer apertures in face view, i.e. funnel rims (fr).

5. RESULTS

The microscopical structure of bordered pits and funnel pits is investigated in fourteen hardwoods and one herb. These xylem types have been selected because of the known presence of large pits, generally taken as bordered pits, in the fibres (e.g. BAAS, 1986; CARLQUIST, 1986a,b, 1988; FUJII, 1993; MOLL & JANSSONIUS, 1906-1936; REINDERS & REINDERS-GOUWENTAK, 1961 and VAN DER SCHOOT & VAN BEL, 1989) and as morphological intermediaries in the 'continuum' from tracheids with pure bordered pits like those on vessel walls to fibres with simple pits.

5.1. *Acer campestre* (Aceraceae) (Figs 4-6).

The occurrence of bordered pits (bp) is limited to the only tracheary elements present, the vessels (Fig. 6A), and funnel pits are found in libriform fibres. Figure 4 shows the scattered funnel pits (fp) in libriform fibres; these pits differ much in dimensions mutually. The slit-formed pit canal from left above to right beneath is highest in the wall complex, i.e. the micrograph shows a view of the rear walls of cut fibres. Figures 5 A,B show the poorly co-ordinated pit halves of funnel pits with gradually widening pit canals (fp). In addition Fig. 5C shows a blind funnel pit (bfp). The bordered pits on the front wall of the vessel in Fig. 6A show their pit cavities and borders. The wall must have been cut lengthwise near the middle lamella. The funnel pits are shown in Fig. 6B with the same magnification, demonstrating their much smaller size and different morphology. The average transverse and longitudinal dimension of the bordered pits (table 1) is much larger than that of the clear and on average big examples of the funnel pits. The differences are statistically significant.

Table 1. Average ± standard deviation of transverse and longitudinal diameters in face view in μm of 20 bordered pits in tracheary elements and 20 distinct examples of funnel pits in libriform fibres. Applying the T-test always shows significant ($P<0.005$) larger average transverse diameters of bordered pits than of funnel pits in every examined wood. Only *Betula pendula* shows a non-significant difference between bordered pits and funnel pits longitudinally. Merely clear images of larger funnel pits are considered; the average diameter of funnel pits is considerably smaller.

	bordered pits		funnel pits	
	transverse	longitudinal	transverse	longitudinal
Acer campestre	7.77 ±1.58	7.03 ±1.97	2.21 ±0.42	2.23 ±0.46
Alnus viridis	7.07 ±1.32	4.37 ±0.38	3.19 ±0.58	3.07 ±0.58
Anthocephalus cadamba	6.15 ±0.87	5.88 ±0.56	5.11 ±0.85	5.03 ±0.78
Aesculus hippocastanum	7.58 ±0.75	6.66 ±0.62	3.34 ±0.52	3.14 ±0.42
Betula pendula	3.68 ±0.41	3.10 ±0.39	2.84 ±0.42	3.13 ±0.58
Bruinsmia styracoides	11.56 ±1.10	8.93 ±1.30	5.28 ±0.65	5.32 ±0.63
Fraxinus excelsior	8.04 ±0.65	3.94 ±0.40	2.81 ±0.31	2.83 ±0.34
Nyssa javanica	13.02 ±1.94	6.99 ±0.36	5.65 ±0.74	6.17 ±0.81
Populus tremula	10.50 ±0.89	9.50 ±0.65	1.81 ±0.27	2.05 ±0.33
Quercus acutissima	6.73 ±1.30	5.49 ±0.82	1.75 ±0.23	1.63 ±0.27
Solanum lycopersicum	7.61 ±0.78	6.30 ±0.61	1.75 ±0.35	1.75 ±0.36
Styrax obassia	5.63 ±0.49	4.11 ±0.29	3.08 ±0.55	3.06 ±0.40
Tilia cordata	6.11 ±0.54	5.48 ±0.50	3.54 ±0.59	3.81 ±0.66
Ulmus minor	7.81 ±1.36	7.03 ±0.76	2.30 ±0.32	2.11 ±0.35

5.2. *Aesculus hippocastanum* (Hippocastanaceae) (Figs 7,8).

The occurrence of bordered pits (bp) is again limited to the only tracheary elements present: the vessels (Fig. 8B). Funnel pits are found in the libriform fibres (Figs 7, fp; 8A, fp) in a scattered fashion and differ much in dimensions mutually. The slit-formed pit canal from left above to right beneath (Fig. 7, fp) is highest in position in the wall complex, thus the micrograph shows a view of the rear walls of the cut fibres. Figure 8A shows the poorly co-ordinated pit halves of the funnel pit with gradually widening pit canals (fp). The average transverse and longitudinal dimension of the bordered pits (table 1) is much larger than that of the clear examples of the funnel pits. These differences are statistically significant.

5.3. *Alnus viridis* (Betulaceae) (Figs. 9-18) and *Corylus avellana* (Corylaceae) (Figs 19-24).

Bordered pits can only be found on the vessel walls (*Corylus*, Figs 19, 21, bp); the ground tissue of axial elements in these hardwoods consists again of libriform fibres (Figs 9, 10). Fig. 9 shows the characteristic images of funnel pits of *Alnus* in radial view and Figs 10A-D in transections (cp. Fig. 2, III, A). The funnel pit-pairs are always smaller than the bordered pits (Table 1, *Alnus*), scattered on the fibre walls and not well co-ordinated. SEM views in Figs 11-13 show the poor co-ordination of the funnel pit-pairs in more detail; the funnel widening is formed by a very irregular narrow space near the middle lamella and the pit canals are dissimilar (Figs 11B, 13). In Fig. 12 the funnel pit-pair between a larger transection of a libriform fibre (right) and the small transection of a fibre apex (left) is badly co-ordinated. The funnel pit-pairs in SEM views (Figs 14A,B; 15A,B) show very dissimilar pit-halves and very tortuous pit canals to the right. SEM views (Figs 16, 17) show again funnel pits with different pit canals in each pit, especially the right pit canal in Fig. 16 is very irregular. Figure 18A shows a SEM view of a funnel pit-pair (fp) in the common wall between two libriform fibres. The rear wall of the front fibre is visible with the inner aperture of the slit-formed pit canal in the front fibre. More outlines of the complex structure of the funnel pit-pair are visible in this micrograph, see Fig. 18B, caption. No combined outline of the boundaries of a (former) pit membrane or funnel rims (Fig. 2, I, II) can be indicated. Bordered pits in the wood of *Corylus* (Figs 19A, bp; 21A-

C, bp) have pit cavities with clear elliptical outlines; the funnel pits are characterized by being smaller, scattered on the fibre walls and by pit canals that clearly widen gradually towards the middle lamella (calyci-form) and are not co-ordinated within the pit pairs (Figs 19A-D, fp; 20 A, fp). Moreover funnel pit-halves are often blind (Figs 20A,B, blp). Figures 22A,B show radial fibre walls with scattered funnel pits that vary much in dimensions; in Fig. 22C a draft is made of the funnel pit in face view visible in Fig. 22A, fp (cp. Fig. 2, III, A). Figs 23A-C show tangential sections of libriform fibres (lf) with longitudinally and perpendicularly cut funnel pits (fp) on the radial walls. The image (fp) in Fig. 23A is interpreted in Fig. 23D. The edges of twist (e) in the slit-formed pit canals can also be observed in e.g. Figs 11B, 13. Finally Figs 24A,B show characteristic images of funnel pits (fp) on tangential fibre walls and on a radial fibre wall (arrow).

5.4. *Anthocephalus cadamba* (Rubiaceae). Figs 25-28.

MOLL & JANSSONIUS (1906-1936) described this hardwood having fibres that must be called tracheids (*sensu* CARLQUIST, 1986a) because of presence of bordered pits limited to the radial walls. But the fibres of this hardwood clearly show funnel pits: these are scattered, statistically smaller than the bordered pits on vessel walls (table 1, critical level $P < 0.005$, Fig. 27) and their morphology is completely similar to the characterizations given for funnel pits (Figs 25, 26). Moreover these pits often show a very bad co-ordination (Figs 25, 27, 28) and a well-defined pit cavity cannot be indicated. Figure 26A shows well co-ordinated bordered pits (bp), densely distributed on a common wall between two vessel elements (v); in Figs 26B-D the smaller, scattered funnel pits (fp) are visible that are poorly co-ordinated and sometimes blind (Fig. 26C, arrow). In Figs 25A-C (fp) the funnel rims can clearly be seen as belonging to two different outer apertures of the pit canals of the shown pit-pairs. Blind funnel pits are often found in this hardwood, blind bordered pits are never found on common vessel walls.

5.5. *Betula pendula* and *B. pubescens* (Betulaceae). Figs 29-31.

Measurements of bordered pits and funnel pits in *B. pendula* (table 1) show significantly larger bordered pits in transverse section (critical level $P < 0.005$). In longitudinal section, however, no significant difference was found, but it must be remembered that the measured funnel pits are larger than the average for reasons of more certain detection and measurement. Anyhow the population of bordered pits is different from that of funnel pits as the micrographs in Figs 29-31 show. Bordered pits in *B. pubescens* (Fig. 31, bp) show another morphology than the usual structure of funnel pits in this hardwood (Fig. 30A,B, fp). The latter are scattered and badly co-ordinated; the funnel rims are observed as belonging to two different outer apertures of the pit canals (*B. pendula*, Fig. 29B, fp; cp. Fig. 2, III, A).

5.6. *Bruinsmia styracoides* (Styracaceae). Figs 32-38.

Measurements of bordered pits and funnel pits in this hardwood (table 1) again show significant larger bordered pits in transverse and also in longitudinal sections. The differences are considerable. The bordered pits and funnel pits constitute again two different populations of structures without any indication of intermediate forms. In addition, looking at Figs 35A-C, it seems clear that the tendency of forming transitional structures between bordered pits and funnel pits is probably completely absent as well. The fibre wall does not show pits at all facing the multitude of bordered pits on the adjoining vessel wall. MOLL & JANSSONIUS (1906-1936) described the fibres of this hardwood as tracheids (*sensu* CARLQUIST, 1986a) and REINDERS & REINDERS-GOUWENTAK (1961) described these fibres as showing 'borders'. Figures 32A-C (fp) and 34A,B (fp), however, show only fibres with scattered funnel pits that are badly co-ordinated and much smaller than the pits-with-a-border of the vessels (Figs 33A,B, bp; 36A,B). Figure 37 shows details of Fig. 36B, bp; see caption. The phenomenon of the pit canals in bordered pits changing slit direction (Fig. 33A,B on the right) is possibly comparable to the twisted pit canals of thick-walled vessels to other tracheary elements in *Quercus acutissima*, and is reported for thick-walled vessels with multi-layered structure as well (KISHI et al. (1981) in: FUJII, 1993). Finally Figs 38A-D show funnel pits seen from the outside of fibres (A,B) and from the lumen of fibres (C,D). The slit-formed pit canals seem to widen regularly (calyci-form) to the middle lamella (A,B).

5.7. *Fraxinus excelsior* (Oleaceae). Figs 39,40.

Bordered pits on vessel walls are much larger than the funnel pits on the fibre walls; again the difference is significant, both in longitudinal and transverse section (table 1). Both types of pits constitute again two different populations of structures without transitional forms. The funnel pits in radial fibre walls (Figs 39A-C, fp) show the common images of this type of pit in face view; in transections the co-ordination is often bad (Figs 40 A,B) and completely dissimilar from the perfect co-ordination of the bordered pits in the common walls of vessels (Fig. 40C, bp). The pit cavities of the latter conform well to the given definition: definite, symmetrical, oval, lenticular with a rather definite limit as boundary between cavity and pit canal. The funnel widenings, however, form very irregular narrow spaces near the middle lamella caused by the gradual widening of the slit-formed pit canals towards the middle lamella and the shift of the pit halves along the middle lamella in relation to each other (Figs 40A,B, arrow, see caption).

5.8. *Nyssa javanica* (Nyssaceae). Figs 41-46.

Libriform fibres in this hardwood were called tracheids (*sensu* CARLQUIST, 1986a) with bordered pits by MOLL & JANSSONIUS (1906-1936). REINDERS and REINDERS-GOUWENTAK (1961) use the name bordered pits as well with regard to pits in these fibres. However, the real bordered pits on the vessel walls are much larger than the pits on the fibre walls and their morphology and distribution is different. Measurements (table 1) show bordered pits to be much larger than funnel pits, especially in transverse section. Bordered pits are closely packed together on the common walls of vessels, funnel pits very much scattered in the fibres. Bordered pits are about uniform in structure and size, funnel pits show much difference mutually both in shape and size. Figure 41 shows the funnel pits with vertically (partly) rather short, blunt and wide pit canals (arrows in B, C) and a very badly co-ordinated funnel pit (A, fp) with funnel rims of two outer apertures of pit canals clearly shifted in relation to each other. Fig. 42 E shows the rather big uniform bordered pits (bp) on the vessel walls as opposed to the small, scattered, often badly co-ordinated funnel pits (Figs 42C,D, fp). A rather high degree of asymmetry between complementary pit halves of funnel pits is shown in Figs 42A,B (fp) and in Figs 43-46: see captions.

Especially the funnel pit fp 1 in Fig. 43 and the right, apparently rather well co-ordinated funnel pit-pair at this level of focus in Fig. 44 (fp) show a high degree of asymmetry of the funnel widenings on both sides of the pit membrane (Fig. 44, pm). Funnel pit-pairs in Figs 45, 46 show much asymmetrical complementary pit halves as well, see captions.

5.9. *Populus tremula* (Salicaceae). Fig. 47.

Measurements of bordered pits and funnel pits in this hardwood (table 1) show the biggest differences between these two types of pits of all hardwoods mentioned in this table. These pits constitute two distinct categories of structure with different dimensions, distribution on the cell wall and morphology. No indication is found of the presence of transitional forms between the two types of pits. Figures 47A,C show images of funnel pits (fp) with pit canals gradually widening to the middle lamella (calyci-form). The common walls between vessels show clear bordered pits (Figs 47C,D, bp) with regular, lenticular pit cavities instead of the small irregular narrow spaces of the complementary funnel widenings in the funnel pits. Bordered pits are densely distributed, funnel pits scattered on the walls of resp. vessels and fibres.

5.10. *Quercus acutissima* (Fagaceae). Fig. 48.

FUJII (1993) showed images of wood elements of *Quercus acutissima* obtained by way of a resin casting method; a method that generally appears unsuited to reveal the shifted positions within the double structure of funnel widenings and funnel rims. In these images libriform fibres have 'scattered and small pits', shown especially in Figs 23, 30, 31 of that article. The funnel pits in these figures show variance in size and are badly co-ordinated (Fig. 30, the middle pit on the right). The results of measurements in table 1 of the present study are accordingly. The funnel pits are much smaller than the bordered pits. Figures 48A-C show the badly co-ordinated funnel pit-pairs as well (fp) and in Fig. 48D the much larger bordered pits (bp) on vessel walls (v) and tracheid (*sensu* CARLQUIST, 1986a) walls (tr) are evident. The large regular and lenticular pit cavities of the latter are conspicuous. No indication is found of the presence of transitional forms between bordered pits of tracheids and funnel pits in libriform fibres.

5.11. *Solanum lycopersicum* (Solanaceae). Figs 49-51.

VAN DER SCHOOT & VAN BEL (1989) considered the fibrous elements in the secondary xylem of *Solanum lycopersicum* as a tracheid-fibre continuum from fibres with pure bordered pits like those on the vessel walls up to fibres with simple pits. The elements found by the first author of this article in the tomato stem are described in MAGENDANS (1998). Axial elements are vessels (large and small), libriform fibres and paratracheal xylem parenchyma. Figure 49D shows larger and smaller vessels (v) with bordered pits (bp) on the common walls. Parenchyma cells (pa) show half bordered pit-pairs on the common walls with vessels, and on the common wall between the two parenchyma cells a funnel pit seems to be present (arrow). Figures 49 A,B show transections of libriform fibres with very clear images of badly co-ordinated (fp) and blind (bfp) funnel pits; and Fig. 49C demonstrates the variability of forms of funnel pits (fp) in libriform fibres, some resemble simple pits (arrow). Figures 50, 51 show also transections of libriform fibres with a badly co-ordinated funnel pit-pair (fp) and a blind pit (bfp). The size of bordered pits is much larger than that of funnel pits (table 1). Moreover no indications are found of the presence of transitional forms between bordered pits of vessels and funnel pits of libriform fibres. Our results indicate that there is more reason to accept a continuum of pit structures between funnel pits and simple pits (Fig. 49D, arrow: funnel pit in parenchyma). With the bordered pits as a separate category.

5.12. *Styrax obassia* (Styracaceae). Figs 52-55.

REINDERS and REINDERS-GOUWENTAK (1961) mention the secondary xylem of *Styrax* as an other example that offered difficulties to MOLL and JANSSONIUS (1906-1936) for determining the nature of the fibres. These fibres are by no means tracheary elements (*sensu* CARLQUIST, 1986a) as was their opinion, and REINDERS and REINDERS-GOUWENTAK (1961) speak of 'borders' with regard to pits of these fibres. Size, distribution and shape of pits in these fibres indicate the presence of funnel pits. Measurements (table 1) show statistically larger bordered pits and Figs 54, 55 (same magnification) demonstrate this difference well. Figures 52A-C show the characteristic shape of the funnel pits in face view (fp) with the lacking congruence of funnel rims in the pit-pairs, congruence that is always present in bordered pit-pairs. In Figs 53A-D the two types of pits can be compared well in transection; the bordered pits (Fig. 53D, bp) showing a much more regular appearance and a more densely distribution on vessel walls than funnel pits (A-C, fp) on fibre walls. Finally the two types of pits are compared in Figs 54, 55, see captions.

5.13. *Tilia cordata* (Tiliaceae). Figs 56, 57.

Tilia shows characteristic images of funnel pits as well (Figs 56A-D). The funnel rims of the pit-pairs can be observed separately, indicating a situation of non-co-ordination, i.e. the outer apertures of the pit canals of complementary pit halves are shifted in relation to each other to a varying degree (B,C, fp; D, fp below). These pits show a big diversity of dimensions too; for measurement (table 1) only clear images of larger funnel pits are considered, the smaller ones (A, above, D, fp, above) were excluded. This means that the values of average funnel pit diameters in table 1 are too high and therefore the difference with bordered pits much more significant than indicated in the table. In Figs 57A-D the different shapes of funnel pits (A-C, fp) and bordered pits (D, bp) are illustrated. The funnel pits are poorly co-ordinated; the bordered pits larger, with rather uniform, regular pit cavities, densely distributed and well co-ordinated.
The bordered pits of *Tilia* are much larger than the funnel pits and the distribution and shape are different too. Then it may be stated that the group of bordered pits constitutes a separate category as distinguished from funnel and simple pits.

5.14 . *Ulmus minor* (Ulmaceae). Fig. 58.

Measurements (table 1) and micrographs (Figs 58A-D) show the much larger size of bordered pits in relation to funnel pits. The shape of funnel pits seems to vary, dependent on the wall thickness of libriform fibres (cp. Figs A and D), but the gradual widening of the pit canals to the middle lamella is evident (Fig. B, fp). The co-ordination in funnel pits is again poor (Fig. C, fp, bfp), while the congruence of bordered pit halves is conspicuous (Figs E, F). In brief, the observations confirm again the idea of two different populations of structures: bordered pits and funnel pits, without indications of the existence of transitional forms.

LEGENDS TO FIGURES 4-58

Figs 4-6; *Acer campestre.*
Fig. 4. LM showing radial section of libriform fibres with many funnel pits (fp) of varying dimensions scattered on the radial walls. The slit-formed pit canal from left above to right below is highest in position within the wall complex. Cp. Fig. 2, III.

Fig. 5; CLSM showing transverse sections of libriform fibres. A, funnel pit-pair (fp) with non-co-ordinated complementary pit halves. B, idem. C, funnel pit-pair (fp) showing gradually widening pit canals. bfp, blind funnel pit half.

Fig. 6; SEM showing bordered pits (A, bp) on radial vessel wall with araucarioid arrangement, and funnel pits (B, fp) on radial fibre wall. The border b is mostly oval. The funnel pits are much smaller and scattered on the fibre wall. A,B same magnification

Figs 7,8; *Aesculus hippocastanum.*
Fig. 7; LM showing radial section of libriform fibres with funnel pits scattered on the radial walls. The slit-formed pit canal from left above to right below is highest in position within the wall complex. Cp. Fig. 2, III.

Figs 8A, B; CLSM showing transverse sections. A, libriform fibres; a funnel pit-pair (fp) with badly co-ordinated complementary pit halves, each widening gradually to the middle lamella, i.e. no distinct limit exists as boundary between canal and funnel widening. B, vessels (v) and libriform fibres (lf); the large bordered pits (bp) on the common wall of two vessels are densely distributed and of uniform size. No pits are found on the common walls between vessels and libriform fibres.

Figs 9-18; *Alnus viridis.*
Fig. 9; LM showing radial section of libriform fibres; funnel pits (fp) with their characteristic appearance are scattered.

Figs 10A-D; CLSM of transverse sections of libriform fibres showing few scattered, poorly co-ordinated funnel pits (fp). r, ray; v, vessel.

Figs 11-17; SEM of transverse sections of libriform fibres.
Fig.11A; Three funnel pits (fp1-3) with funnel widenings formed by a very irregular narrow space near the middle lamella in each case. The pit halves are far from equiform as in bordered pits. B; sketch of fp3, showing asymmetrical pit canals. e, edge of twist in pit canal (cp. Fig. 23D).

Fig. 12; Badly co-ordinated funnel pit halves (fp). Note the presence of one funnel pit half on the wall of the intruded tip of a fibre.

Fig. 13; A funnel pit is visible with tortuous pit canals. The funnel widening consists of very unequal parts, these parts being very asymmetrical.

Fig. 14A; Funnel pit in common wall parts with two very dissimilar pit halves. B; Draft of same funnel pit; the pit canal to the right is very tortuous.

Fig. 15A; Funnel pit with very dissimilar, tortuous pit canals. B; idem, greater magnification.

Figs 16, 17; Funnel pits of which in particular Fig. 16 demonstrates dissimilar, tortuous complementary pit canals, resulting in very asymmetrical pit halves.

Fig. 18A; SEM of funnel pit-pair in radial wall in face view, seen from lumen of libriform fibre. B; Draft of funnel pit in A. Interpretations of the visible outlines of structure are: 1, slit-formed pit canal narrowing gradually to the middle lamella; 2, parts of outer aperture of pit canal in rear wall of front fibre; 3, part of outer aperture of pit canal in front wall of back fibre; 4, parts of outline of slit-formed pit canal in front wall of back fibre. Pit membrane is absent.

Figs 19-24; LM of *Corylus avellana*.
Figs 19A-D; Transverse sections. A, parts of three vessels (v) with large bordered pits (bp) densely distributed on their common walls. The ground tissue of the wood consists of libriform fibres with much smaller and scattered funnel pits (fp). The lower funnel pit can be seen to be poorly co-ordinated unlike all bordered pits. B, clear image of funnel pit (fp) in transverse section of libriform fibres; pit halves are not completely similar, co-ordination is not perfect. C, id., pit halves not co-ordinated. D, id., poorly co-ordinated pit halves of the left funnel pit (fp). In all funnel pits of Fig. 19 the complementary slit-formed pit canals can be seen to widen gradually to the middle lamella (calyci-form) unlike pit canals and pit cavities of bordered pits. r, ray.

Figs 20A, B; Transverse sections of libriform fibres and rays. Five scattered funnel pits (fp) are found of which two are blind (blp), i.e. without complementary half. Two funnel pits (e.g. A, fp) are badly co-ordinated. r, ray.

Figs 21A-C; Tangential sections with perpendicularly cut radial common walls of vessels (v) with densely distributed bordered pits (bp). A, many uniform bordered pits in unbroken row. B, bordered pits in face view as well (right) on tangential vessel wall. C, structure of bordered pits (bp) is clearly shown: these structures are completely different from those of funnel pits. lf, libriform; ps, parenchyma strand; r, ray.

Figs 22A, B; Radial sections showing libriform fibres with scattered funnel pits (fp) which vary in dimensions: rather small (A, left above) and larger (A, B, fp). C, draft of funnel pit (fp) in A (cp. Fig. 2, III, A). fr, funnel rims; ml, middle lamella; pc, slitlike pit canal on rear wall of front fibre; ps, parenchyma strand.

Figs 23A-D; Tangential sections (A-C) showing libriform fibres with funnel pits (fp) in radial wall and perpendicularly cut to the middle lamella. Interpretation of structure outlines of the image in A (fp) is presented in draft D. e, edge of twist in pit canal (cp. e.g. Figs 12 B, 14); fw, funnel widenings; lf, libriform fibre; pc, slitlike pit canal; r, ray.

Figs 24A, B; Tangential sections of libriform fibres showing funnel pits (fp) on tangential fibre walls and on a radial wall (arrow). r, ray.

Figs 25-28; *Anthocephalus cadamba*.
Figs 25A-C; LM showing funnel pits (fp) in face view on radial walls of libriform

fibres. Funnel rims can clearly be observed as belonging to two different outer apertures of pit canals of the pit-pair (cp. Figs 2, III, A; 28; 29).

Figs 26A-D; CLSM of transverse sections of vessels (A) and libriform fibres (B-D). Vessels (v) show many bordered pits (bp) densely distributed on the common wall; pit cavities are distinct; transverse, flat, slit-formed pit canals are less clear (cp. Fig. 2, I, A). On fibre walls smaller, scattered funnel pits are present that have mostly asymmetrical pit halves (fp) or are blind (C, arrow).

Figs 27, 28; SEM of transverse sections of libriform fibres.
Fig. 27; Badly co-ordinated and partly blind funnel pit-pair. A pit cavity does not exists.
Fig. 28; Funnel pit-pair showing, at least in this transection, much similarity to blind pits. It seems as if complementary pit halves have been shoved away from each other.

Figs 29-31; *Betula pendula* (Fig. 29) and *B. pubescens* (Figs 30, 31).
Figs 29A-C; LM showing funnel pits (fp) on radial walls of libriform fibres. Funnel rims can be observed as belonging to different outer apertures of both pit canals, especially in B (fp) (cp. Fig. 2, III, A).

Figs 30A, B; CLSM of transverse sections of libriform fibres with scattered funnel pits (fp) showing badly co-ordinated pit halves.

Fig. 31; SEM of radial section. Many closely packed bordered pits (bp) are shown on radial vessel wall (nearly hexagonal configuration).

Figs 32-38; *Bruinsmia styracoides*.
Figs 32A-C; LM of radial sections showing scattered funnel pits (fp) in face view on radial walls of libriform. Funnel rims (fr) can clearly be observed as belonging to different outer apertures of both pit canals, especially in B.

Figs 33-35; CLSM of transverse sections.
Figs 33A, B; Different parts of common vessel walls with densely distributed bordered pits (bp). Right pit halves in A and B show edges of twist in all pit canals; these slit-formed canals show two changes of direction (cp. Figs 36B, 37). v, vessel.

Figs 34A, B; Same libriform fibres with same funnel pit (fp). These micrographs show different levels of focusing, demonstrating poor co-ordination of the pit-pair.

Figs 35A-C; Same libriform fibre (lf) and adjoining vessel (v) in transverse section. Common wall between both elements shows only halves of bordered pit-pairs in vessel wall (arrows) in each level of focus. Complementary halves in the fibre wall are lacking at each level (B, C, different levels of focusing)

Figs 36-38; SEM of radial sections.
Figs 36A, B; Densely packed, vestured, bordered pit halves on radial vessel walls observed from the middle lamella. B, pit canals, e.g. in bordered pit half bp, show two changes of direction with two edges of twist (e) in between, cp. Figs 33, 37. oa, outer aperture.

Fig. 37; Bordered pit half bp in Fig. 36B. Edges (e) indicate more clearly points of changes of direction of slit-formed pit canal. oa, outer aperture.

Figs 38A-D; Funnel pits on radial fibre walls. A, B, observed from middle lamella with one half of funnel rims (one outer aperture); inner aperture slit-formed; C, D, observed from fibre lumen; ia, inner aperture.

Figs 39,40; *Fraxinus excelsior.*
Figs 39A-C; LM of radial sections showing funnel pits (fp) in face view on radial walls of libriform fibres. Funnel rims are visible in e.g. C (fp). In A (arrow): longitudinal section of a funnel pit on a tangential wall.

Figs 40A-C; CLSM of transverse sections. A, B, clear images of scattered and badly co-ordinated funnel pits (fp) in libriform fibres (cp. Fig. 2, III, B) or hardly co-ordinated at all (B, arrow). C, vessels (v) of which the common wall shows 6 very clear images of closely packed and uniform bordered pits (bp) in an almost straight line. bph, half-bordered pit-pairs to parenchyma cells (pa).

Figs 41-46; *Nyssa javanica.*
Figs 41A-C; LM of radial sections showing scattered funnel pits (fp) in face view on radial libriform fibre walls. A, clear funnel rims in badly co-ordinated funnel pit (fp). B, C, very conspicuous, vertically rather short, blunt and wide parts of the pit canals (arrow).

Figs 42A-E; CLSM of transverse sections. A, B, funnel pits (fp) in libriform fibre walls that show a high degree of asymmetry, cp. Figs 44, 46. C, D, badly co-ordinated funnel pits (fp) in libriform fibre walls; in D with pit membrane still present. E, uniform bordered pits (bp) on common vessel wall that show a densely distribution and a much higher degree of symmetry. v, vessel.

Figs 43-46; SEM of transverse sections of libriform fibres with funnel pits.
Fig. 43; fp1, this funnel pit-pair may be co-ordinated to some extent, but then the degree of asymmetry is very high; fp2, this funnel pit is probably blind; fp3, very asymmetrical pit-pair.

Fig. 44; Left pit-pair (fp), has been grazed but seems to show much asymmetry; right pit-pair (fp), seems well co-ordinated at this level, but shows on both sides of the pit membrane (pm) a high degree of asymmetry.

Fig. 45; Badly co-ordinated pit-pair (arrow: probable boundary of funnel widening of lower pit half); moreover much asymmetrical pit halves.

Fig. 46; Seemingly rather co-ordinated pit-pair at this level, but with a considerable degree of asymmetry.

Fig. 47; *Populus tremula.*
Figs 47A-D; CLSM of transverse sections. A-C, libriform fibres showing small, scattered funnel pits (fp) with pit canals widening to the middle lamella (calyciform). C, D, densely distributed bordered pits (bp) on the common vessel walls; bordered pit-pairs with conspicuous, large, regular and lenticular pit cavities. v, vessel.

Fig. 48; *Quercus acutissima.*
Figs 48A-D; CLSM of transverse sections. A-C, widely scattered and some badly co-ordinated funnel pits (fp) in libriform fibres; D, densely distributed bordered pits (bp) between vessel (v) and tracheids (tr) and tracheids mutually. Pit cavities of bordered pit-pairs regular and lenticular. r, ray.

Figs 49-51; *Solanum lycopersicum.*
Figs 49A-D; CLSM of transverse sections. A, B, clear images of a hardly co-ordinated funnel pit (fp) and a blind funnel pit (bfp) in libriform fibres; C, small, scattered asymmetrical funnel pits (fp) and a funnel pit with similarity to a simple pit (arrow); D, large, densely distributed bordered pits (bp) on vessel walls (v); the pit (arrow) on the common wall of two parenchyma cells (pa) seems to be a funnel pit.

Figs 50, 51; SEM of transverse sections of libriform fibres with a badly co-ordinated funnel pit (Fig. 50, fp; Fig. 51A same, in detail) and a blind pit (Fig. 51B, bfp).

Figs 52-55; *Styrax obassia.*
Figs 52A-C; LM of radial sections showing scattered funnel pits (fp) in face view on radial libriform fibre walls. Outlines of funnel rims are clearly visible (A, fp). pa, axial parenchyma.

Figs 53A-D; CLSM of transverse sections. A-C, scattered and badly co-ordinated funnel pits (fp) in libriform fibres; other funnel pits may be blind (B, bfp); D, densely distributed bordered pits (bp) on common walls of vessels (v); pit cavities regular and lenticular.

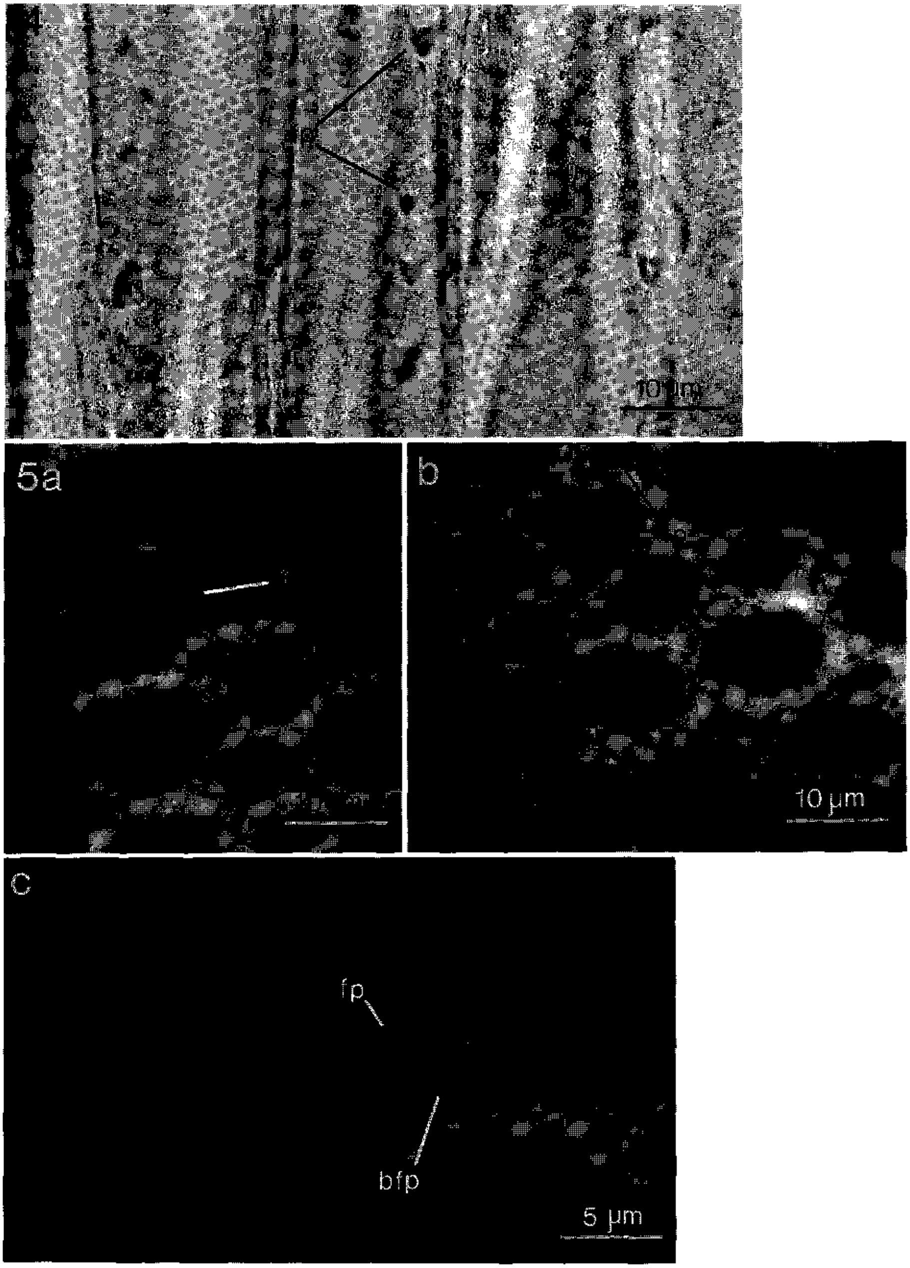
Fig. 54; SEM of radial sections. Bordered pits on vessel wall (A) and funnel pits on fibre wall (B), both shown with same magnification from middle lamellae. Shape of pit cavities narrowing to pit canals (bordered pits) or narrowing of funnel widenings (funnel pits) to inner apertures is difficult to assess (cp. Fig. 53: D versus A).

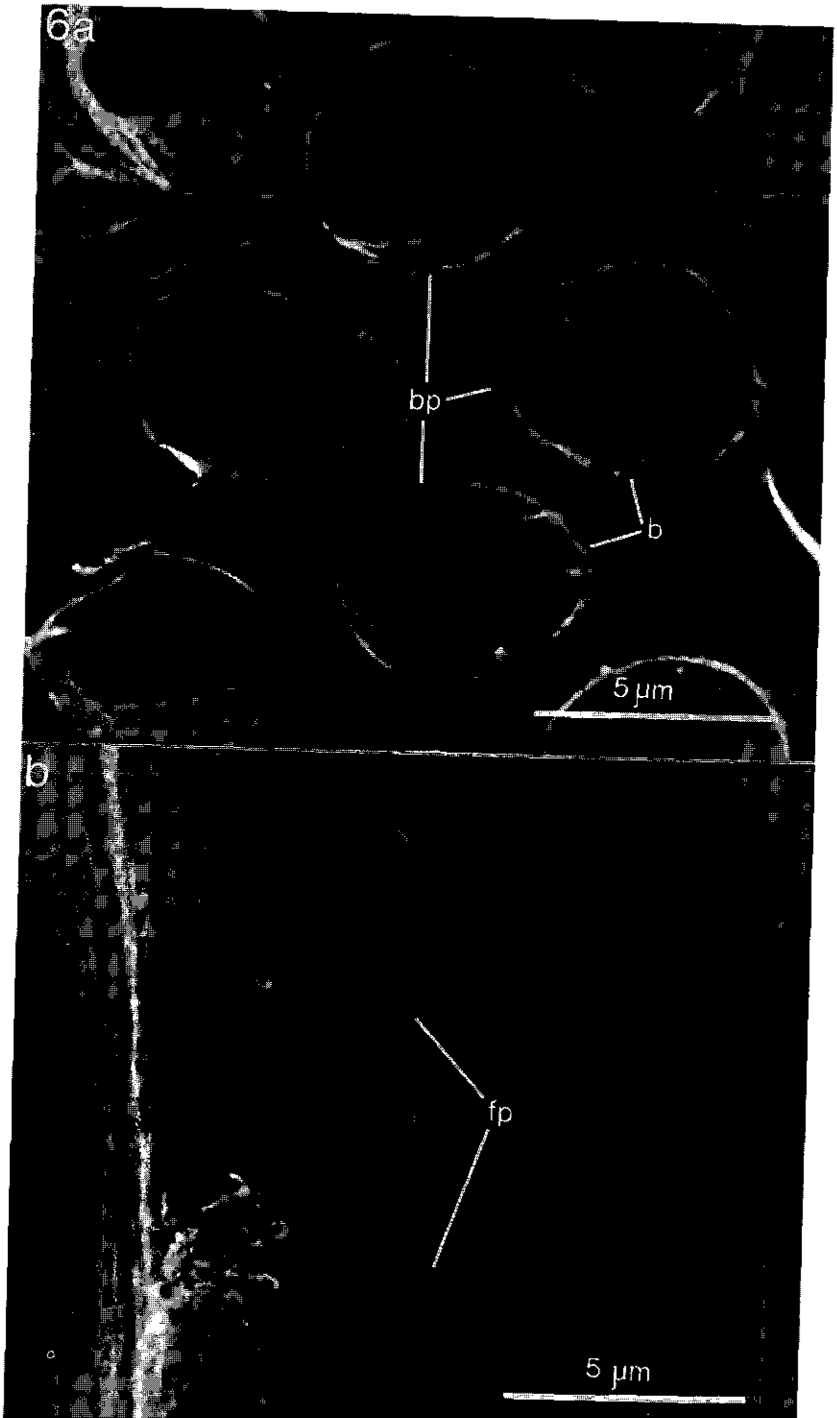
Fig. 55; SEM of radial sections. Funnel pit half on fibre wall shown from middle lamella (fp, left) and funnel pits (inner apertures) on wall of another fibre shown from lumen (fp, right). Same magnification as Fig. 54. fr, funnel rim.

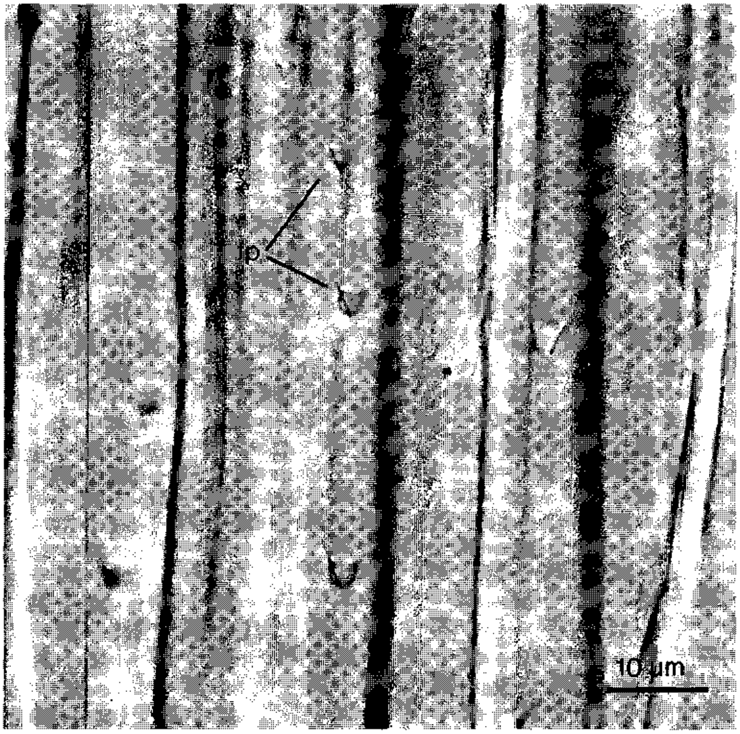
Figs 56, 57; *Tilia cordata.*
Figs 56A-D; LM of radial sections showing scattered funnel pits (fp) on radial libriform fibre walls. Conspicuous diversity of dimensions of funnel pits (A, fp and D, fp). Outlines of badly co-ordinated funnel rims are well visible in B, C (fp) and D (fp, below).

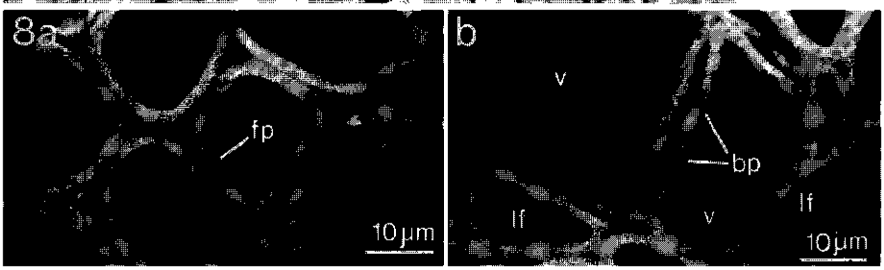
Figs 57A-D; CLSM of transverse sections. A-C, libriform fibres with poorly co-ordinated funnel pits (fp), some are blind (bfp). D, densely distributed, larger bordered pits (bp) on common wall of vessels (v).

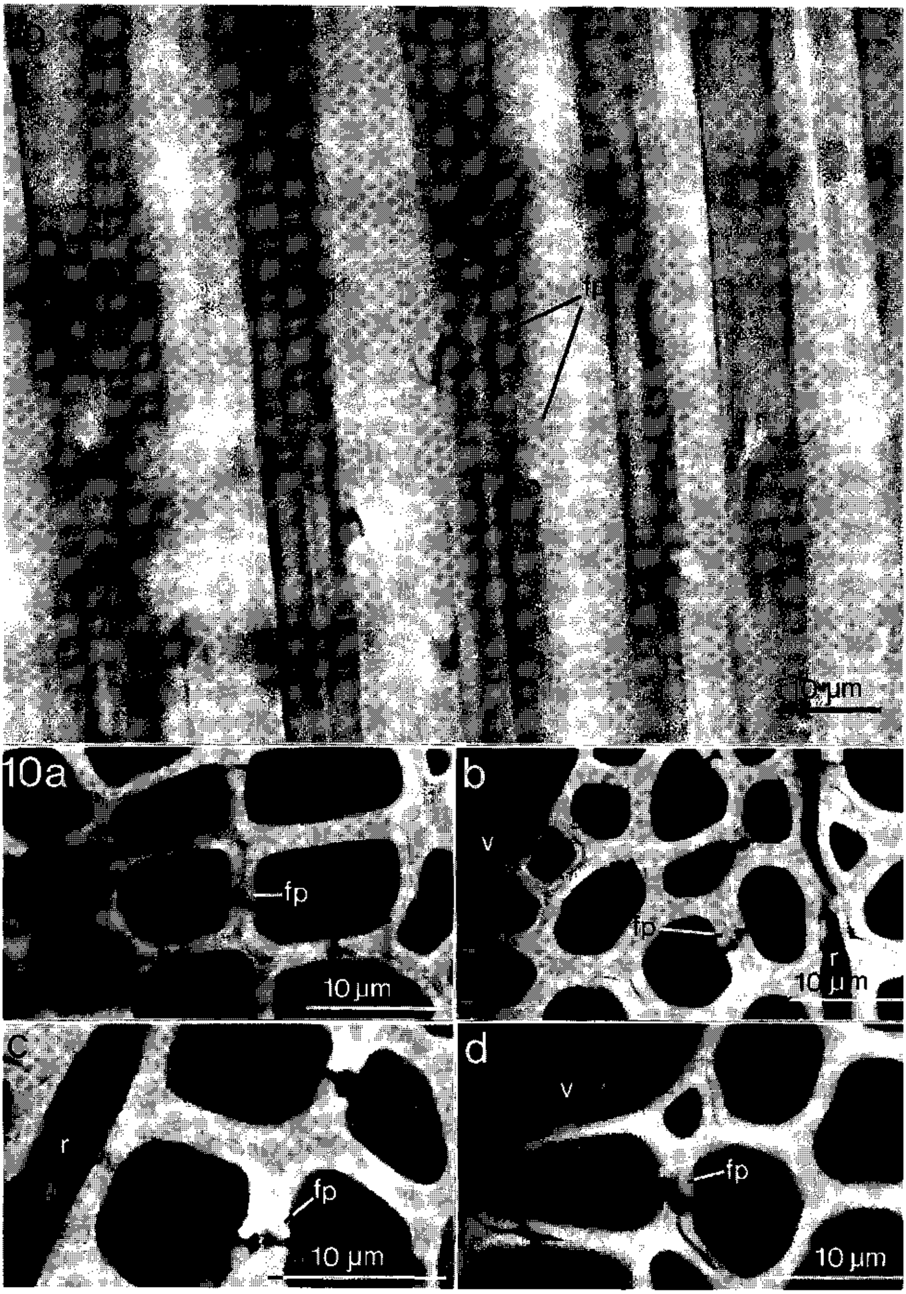
Fig. 58. *Ulmus minor.*
Figs 58A-F; CLSM of transverse sections. A-D, scattered funnel pits (fp) in libriform fibres with various wall thicknesses: varying shapes of funnel pits and some are blind (C, bfp); E, F, densely distributed, large bordered pits (bp) on common walls of vessels (v) with large, regular, oval pit cavities.

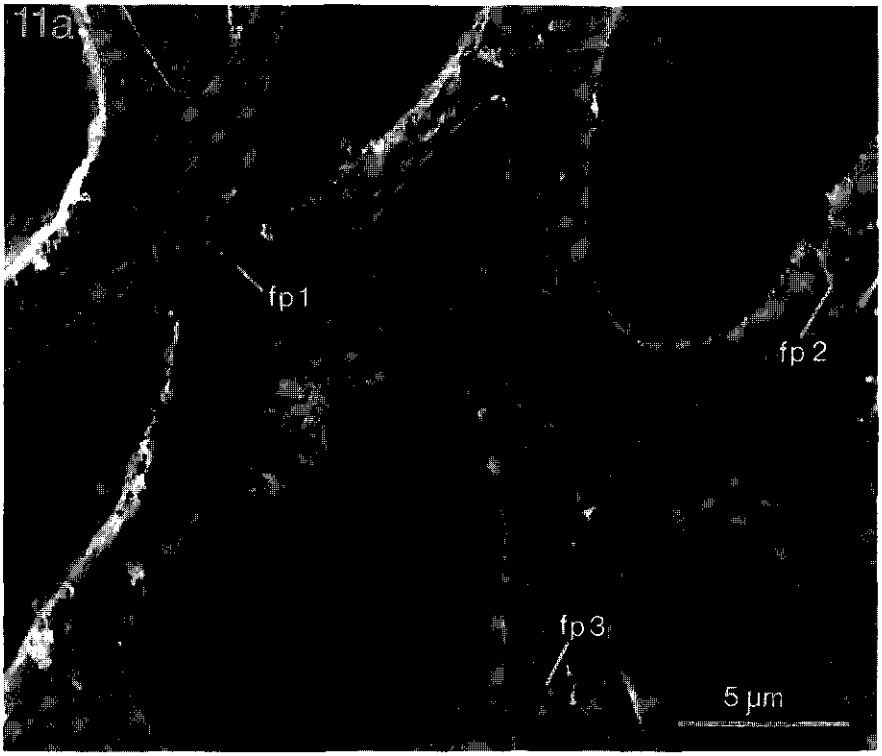

10 µm
5a
b
10 µm
c
fp
bfp
5 µm

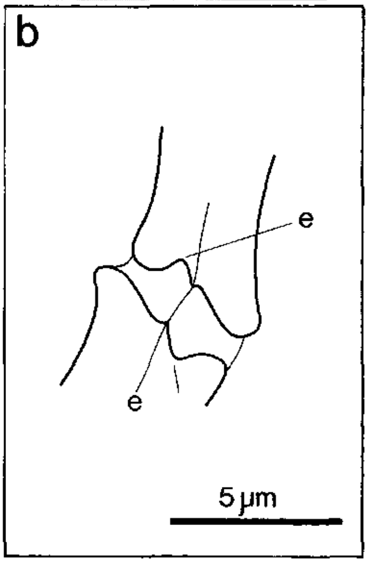

6a
bp
b
5 µm
b
fp
5 µm

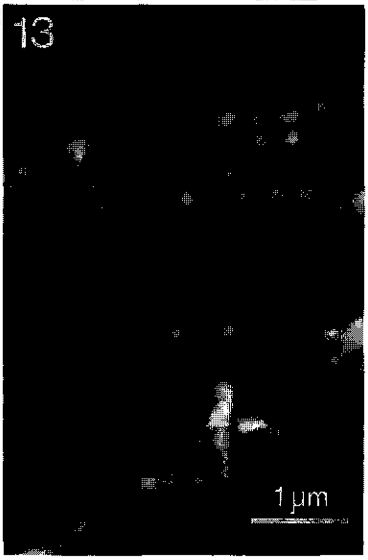

p
10 µm

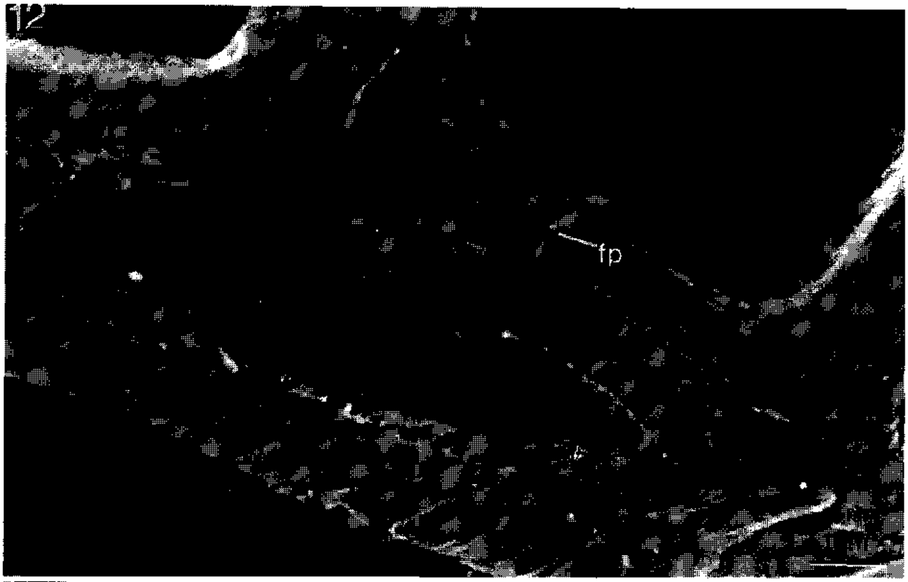

8a
fp
10 µm
b
v
bp
lf
v
lf
10 µm

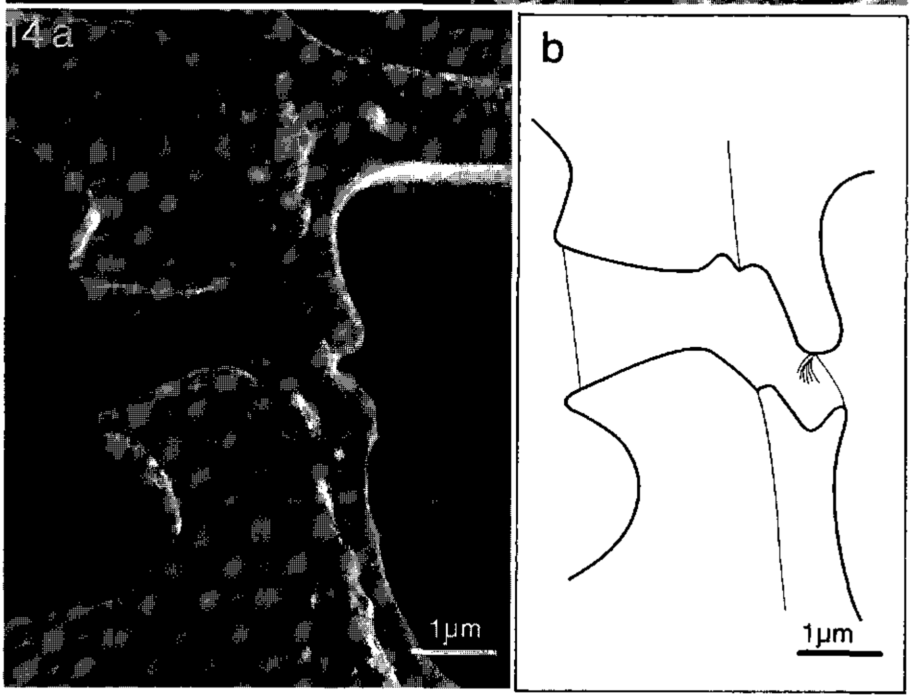

9
fp
10 µm
10a
fp
10 µm
b
v
fp
r
10 µm
c
r
fp
10 µm
d
v
fp
10 µm

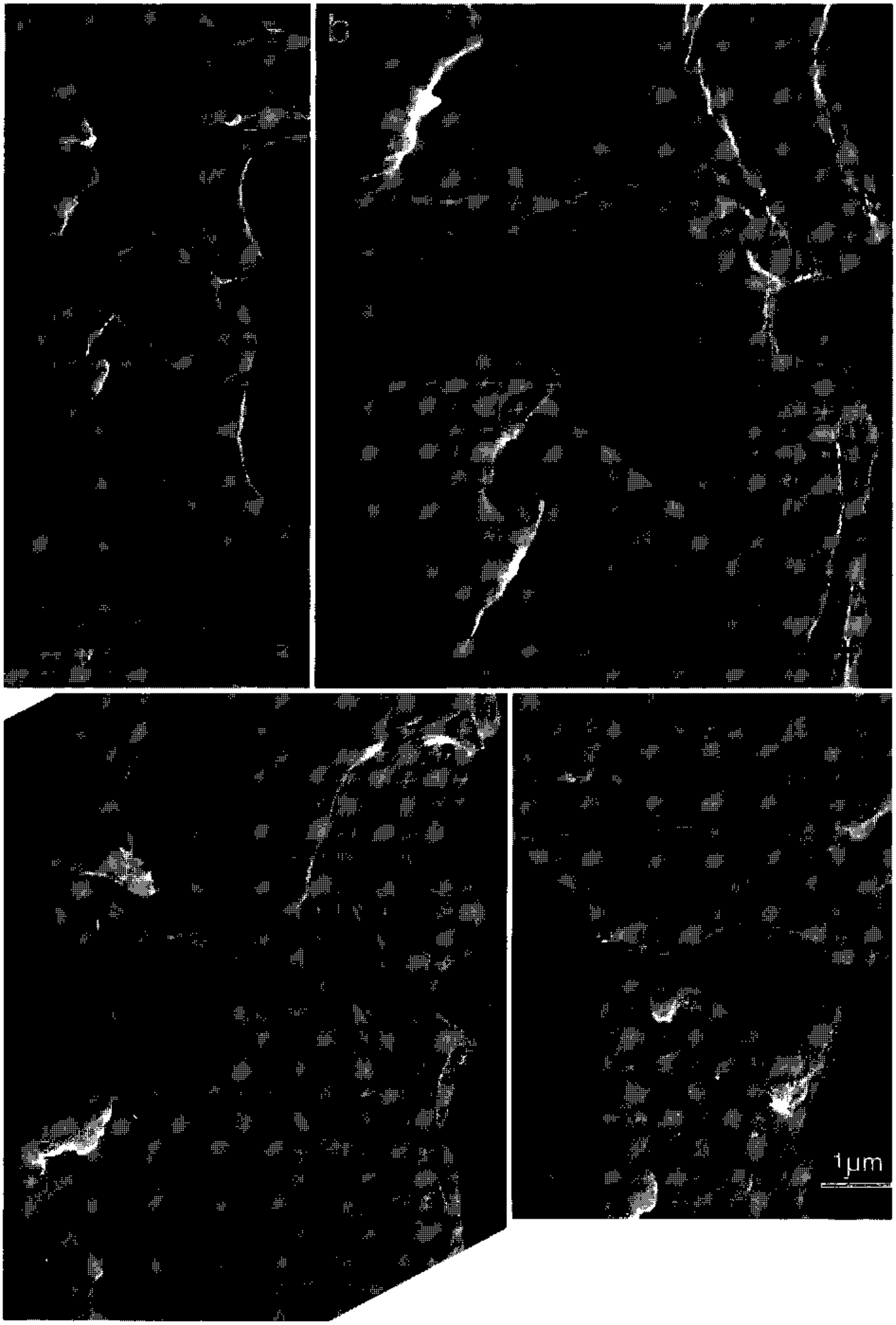

11a
fp 1
fp 2
fp 3
5 µm

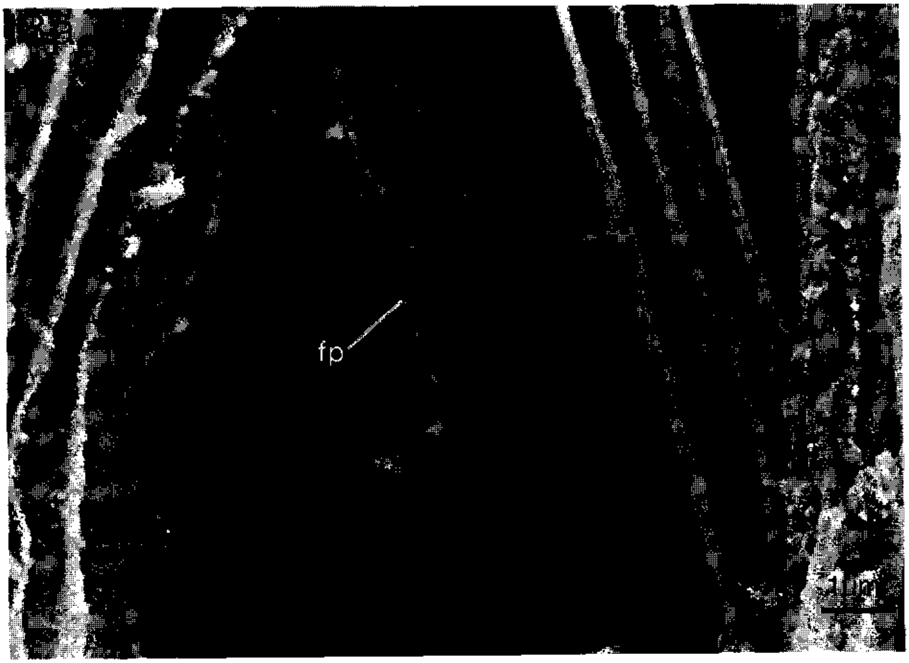

b
e
e
5 µm

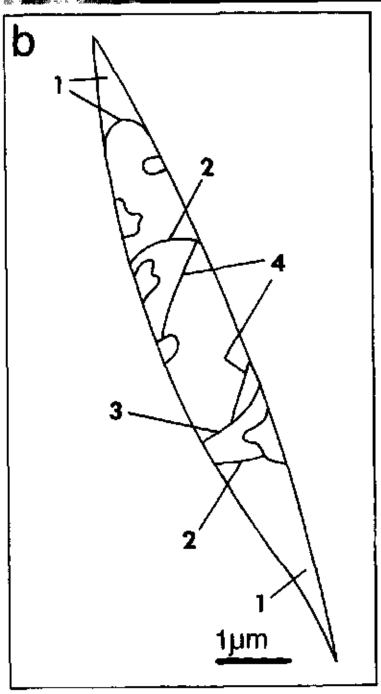

13
1 µm

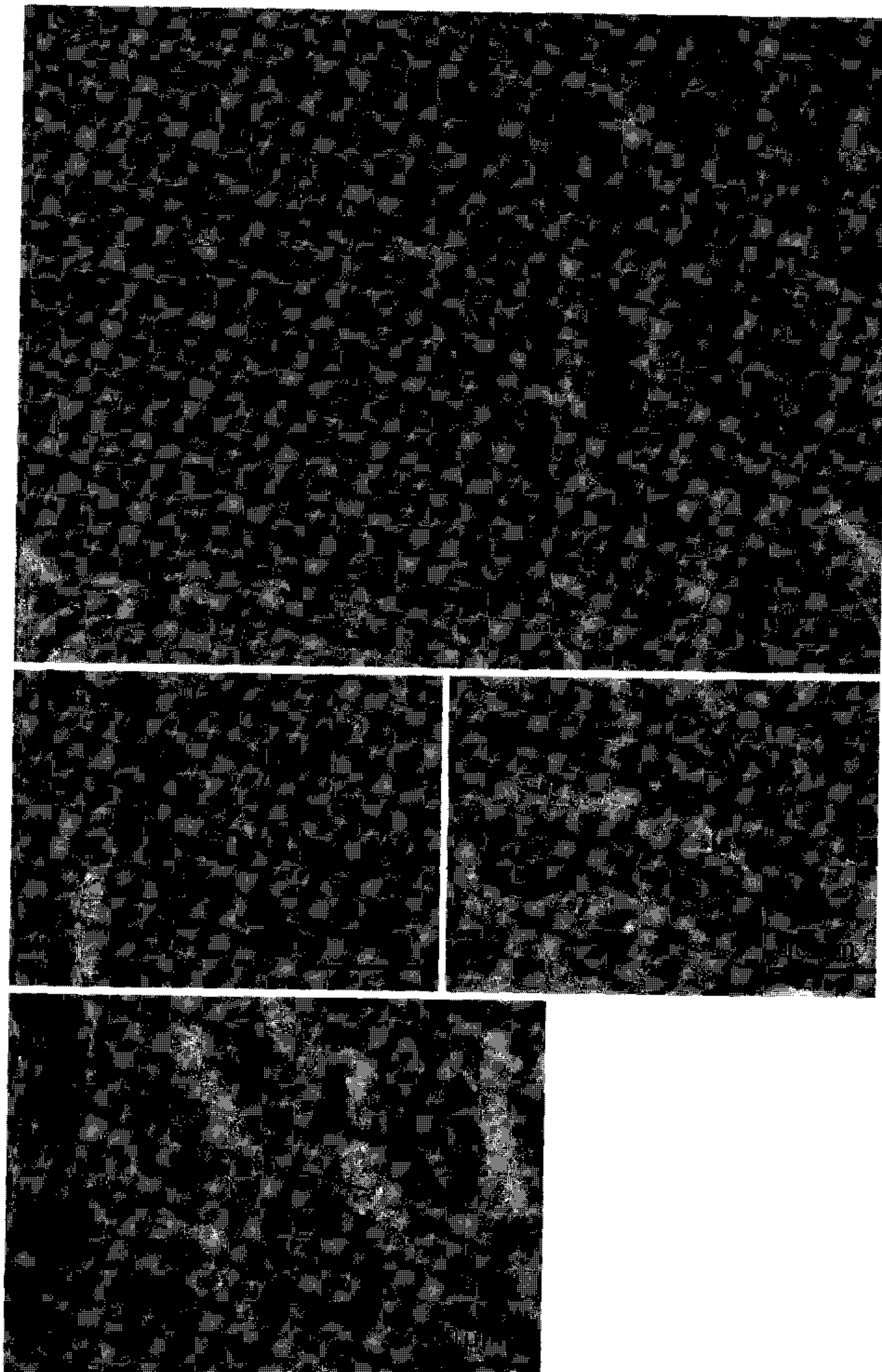

12
fp

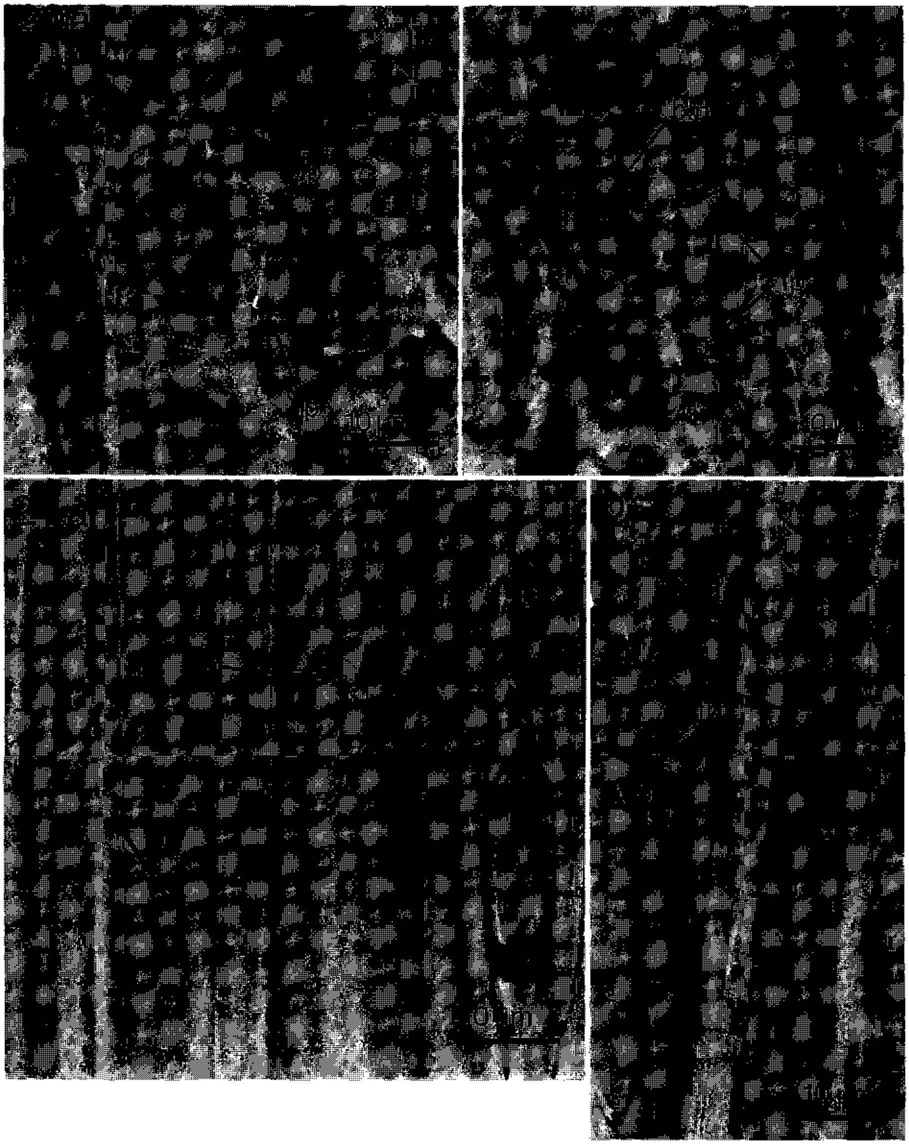

14 a
1µm
b
1µm

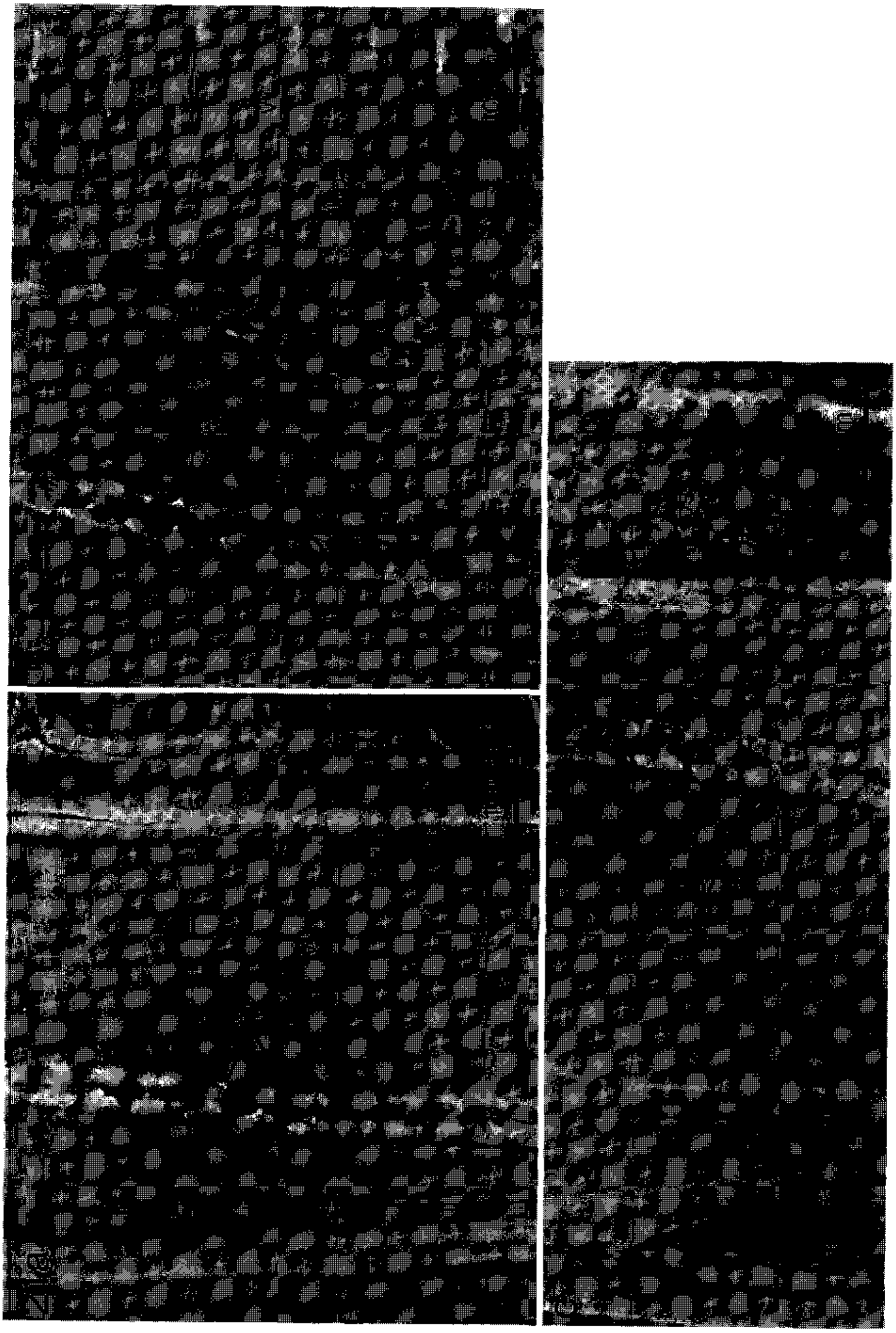

b
1µm

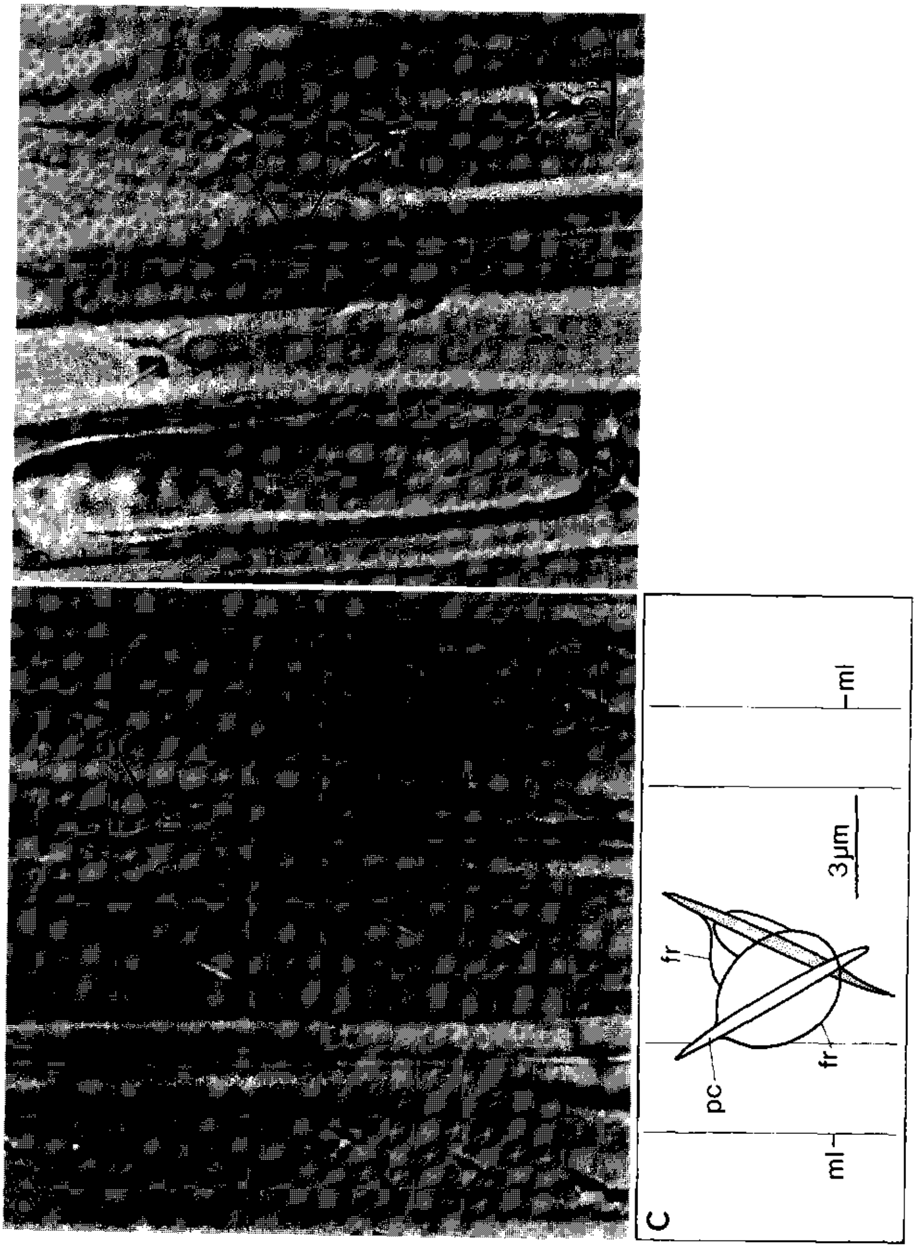

fp
1µm

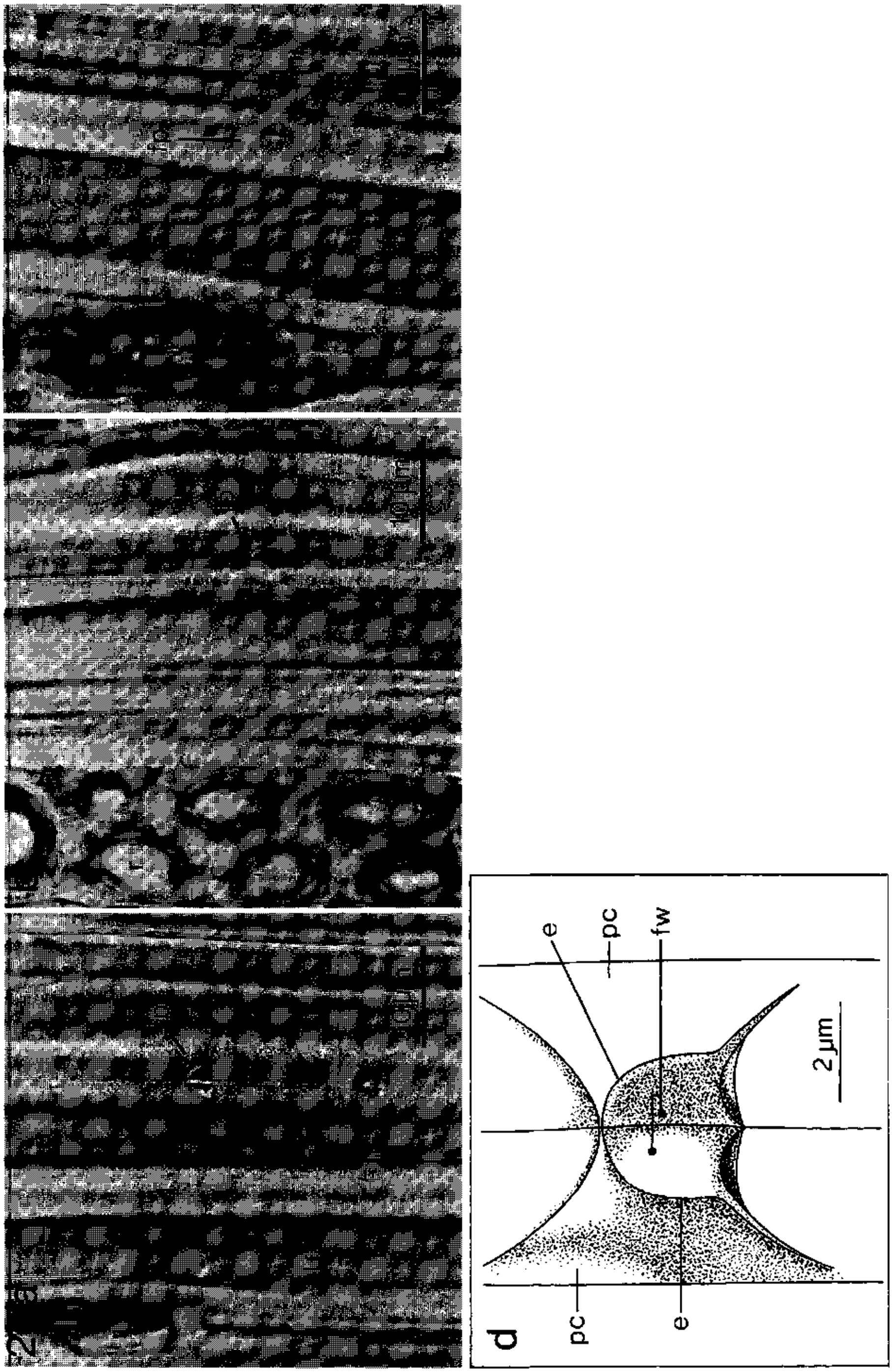

b
1
2
4
3
2
1
1µm

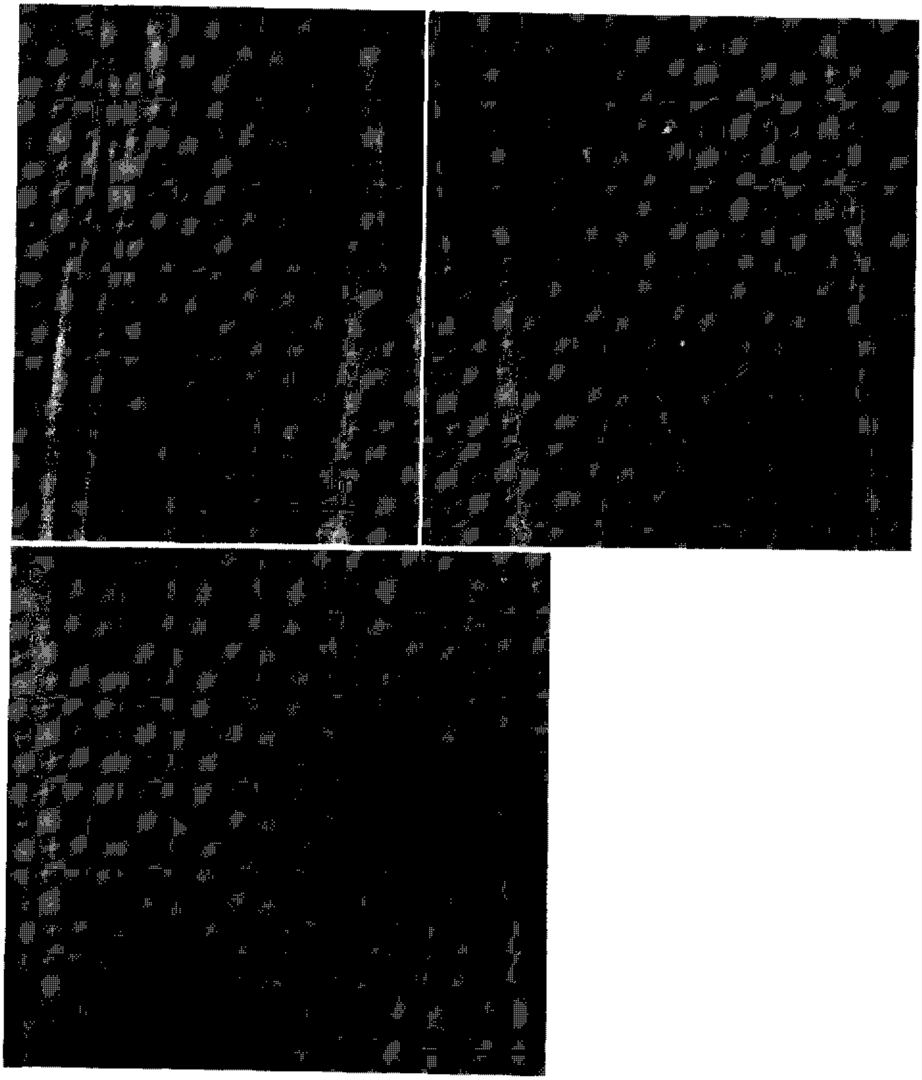


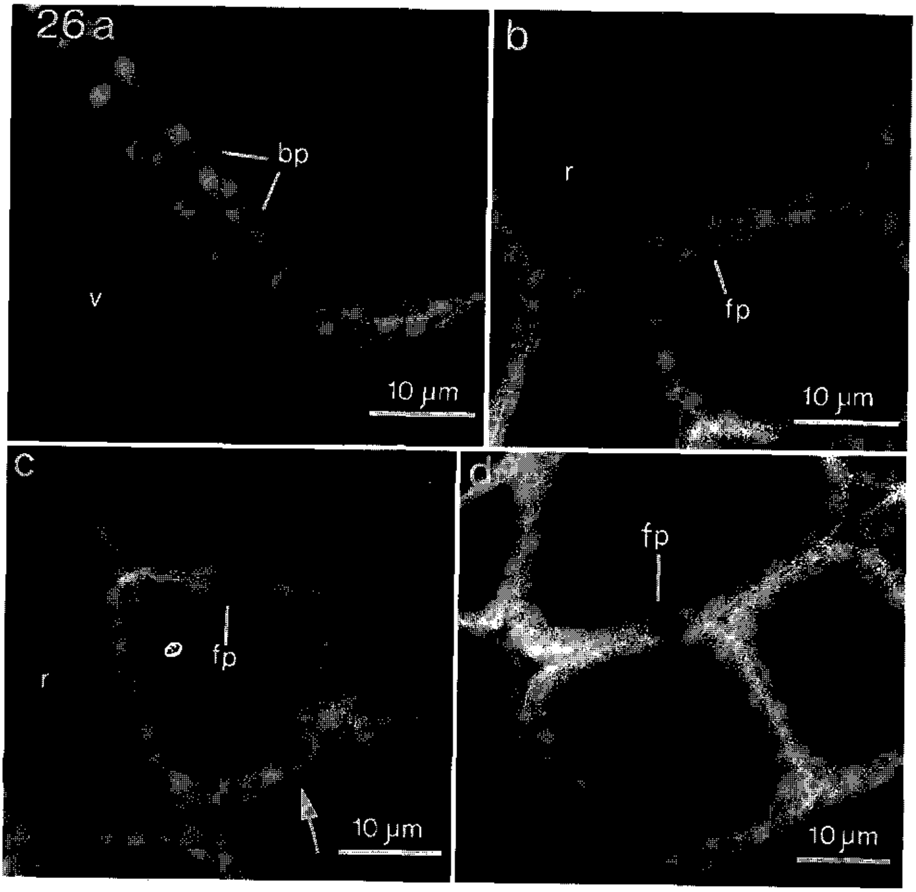


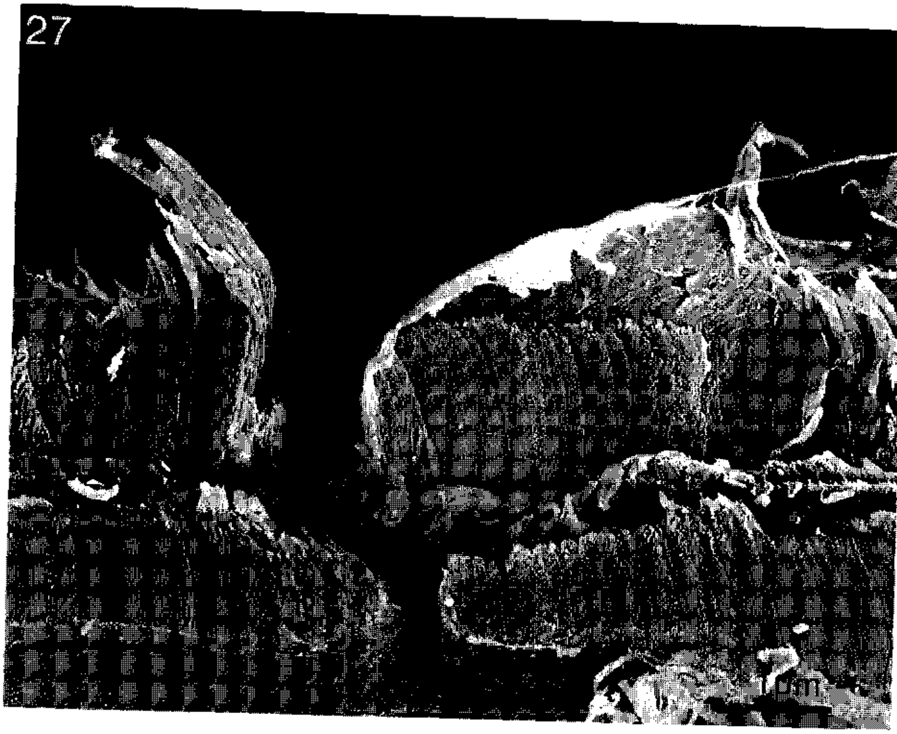



C
ml
pc
fr
fr
3µm
ml

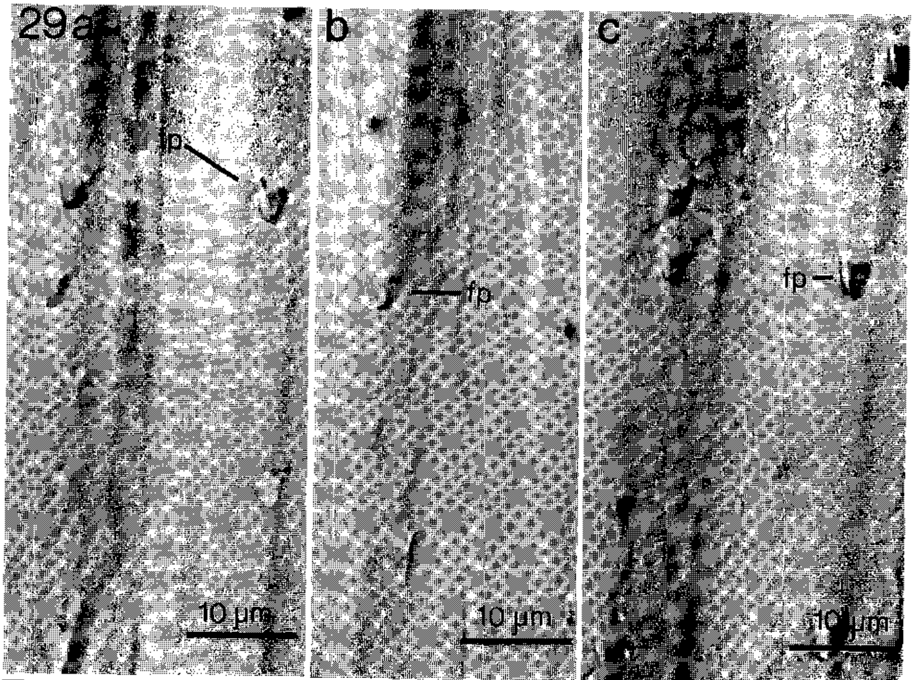

d
pc
e
pc
fw
e
2 µm

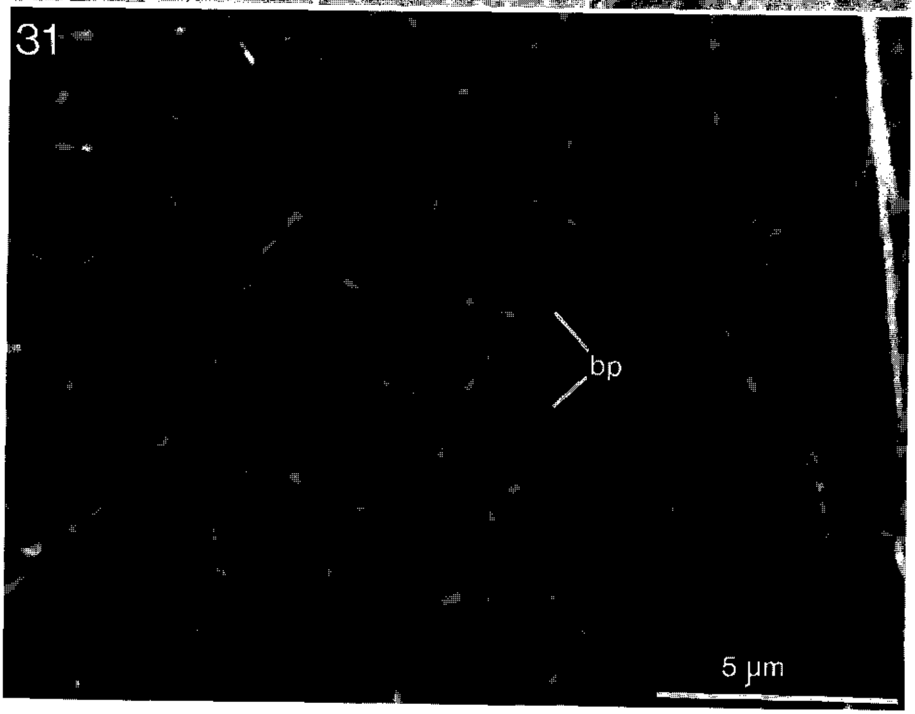


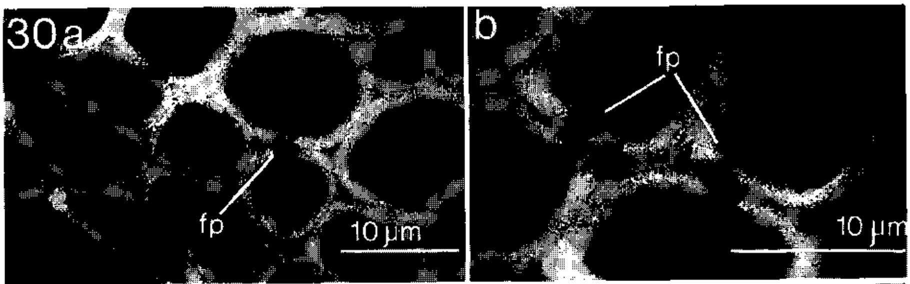

26a
bp
v
10 µm
b
r
fp
10 µm
c
fp
r
10 µm
d
fp
10 µm

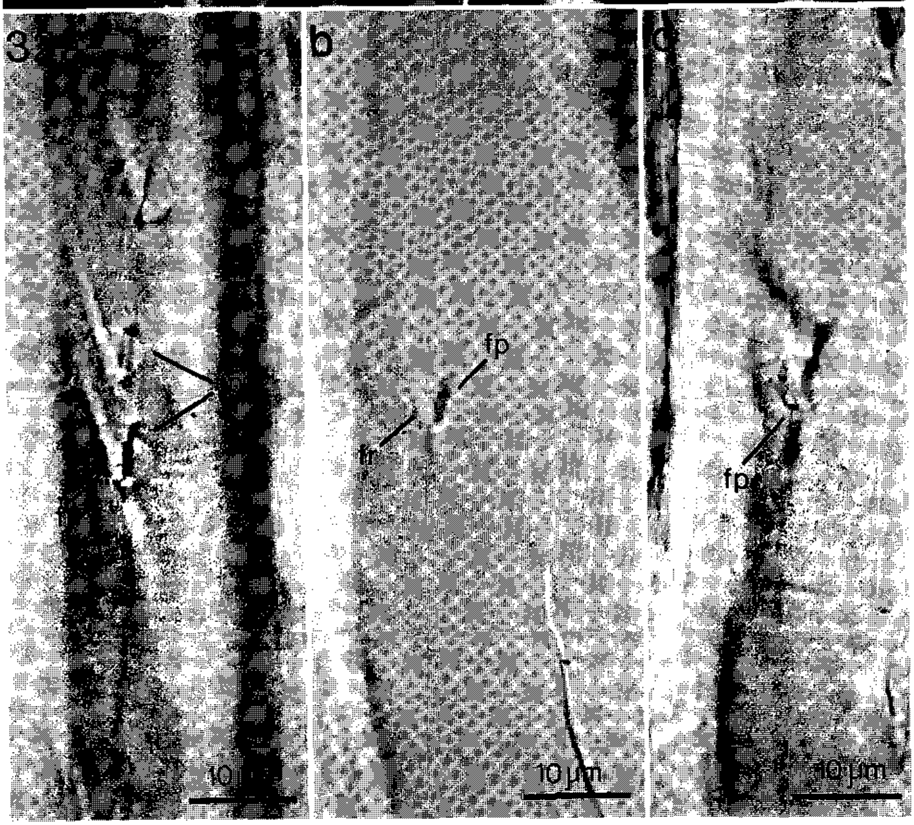

27
1µm

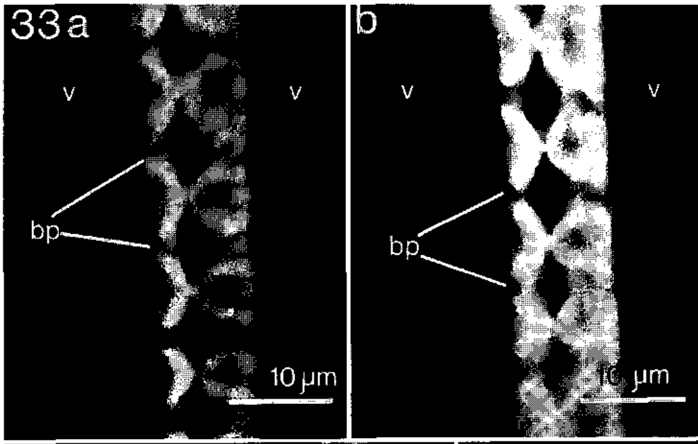

28
1µm

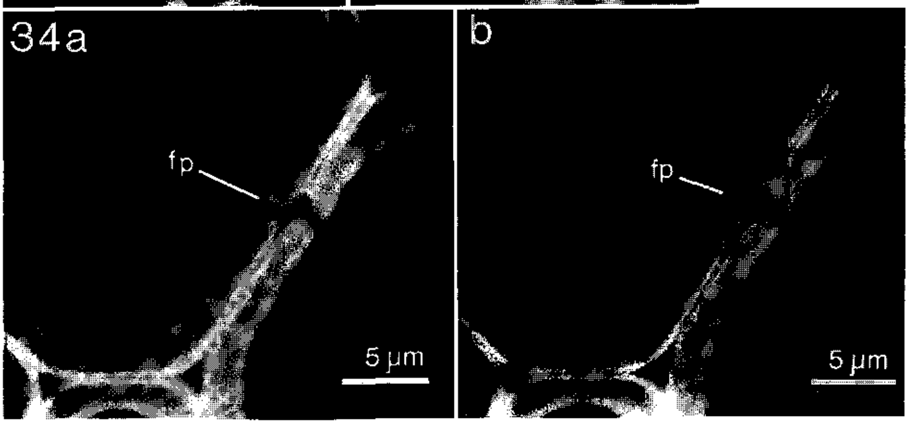

29a
fp
10 µm
b
fp
10 µm
c
fp
10 µm

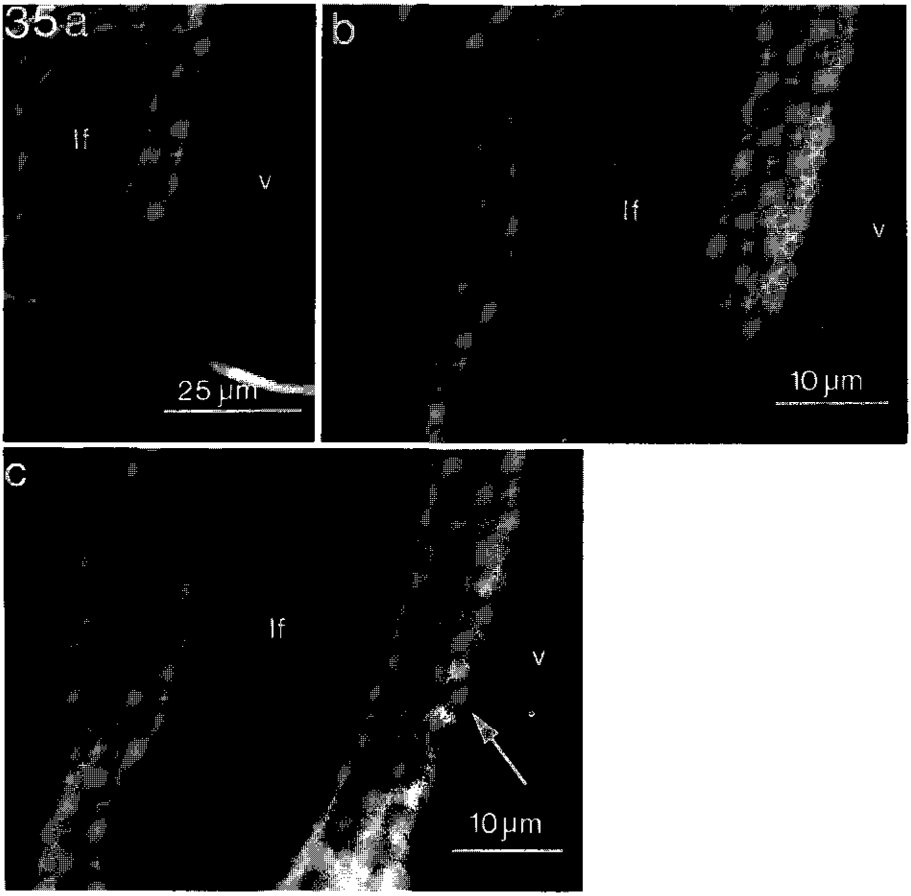

31
bp
5 µm

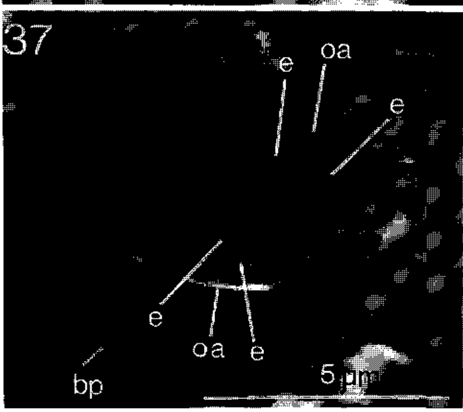

30a
fp
10 µm
b
fp
10 µm

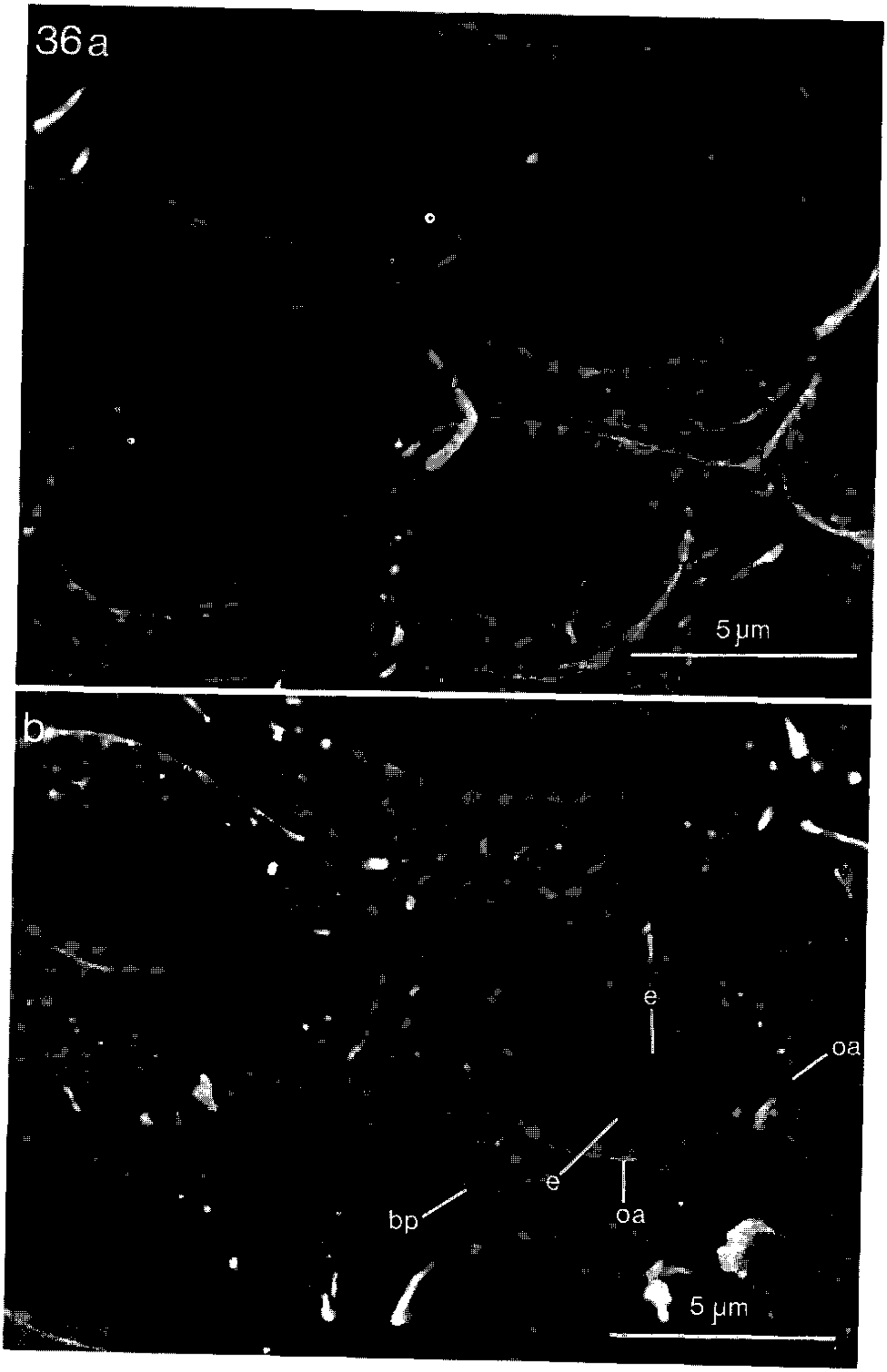

b
fp
fr
10 µm
c
fp
10 µm

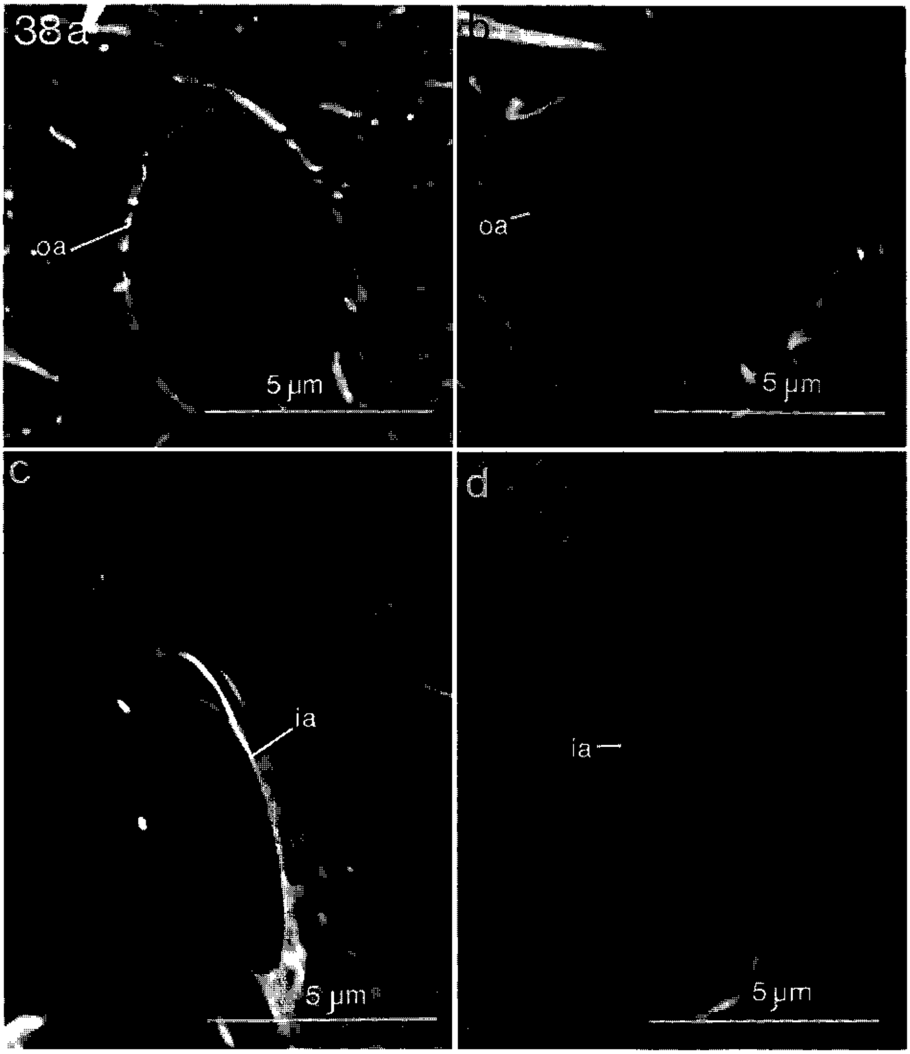

33a
b
v
v
v
v
bp
bp
10 µm
10 µm


34a
b
fp
fp
5 µm
5 µm

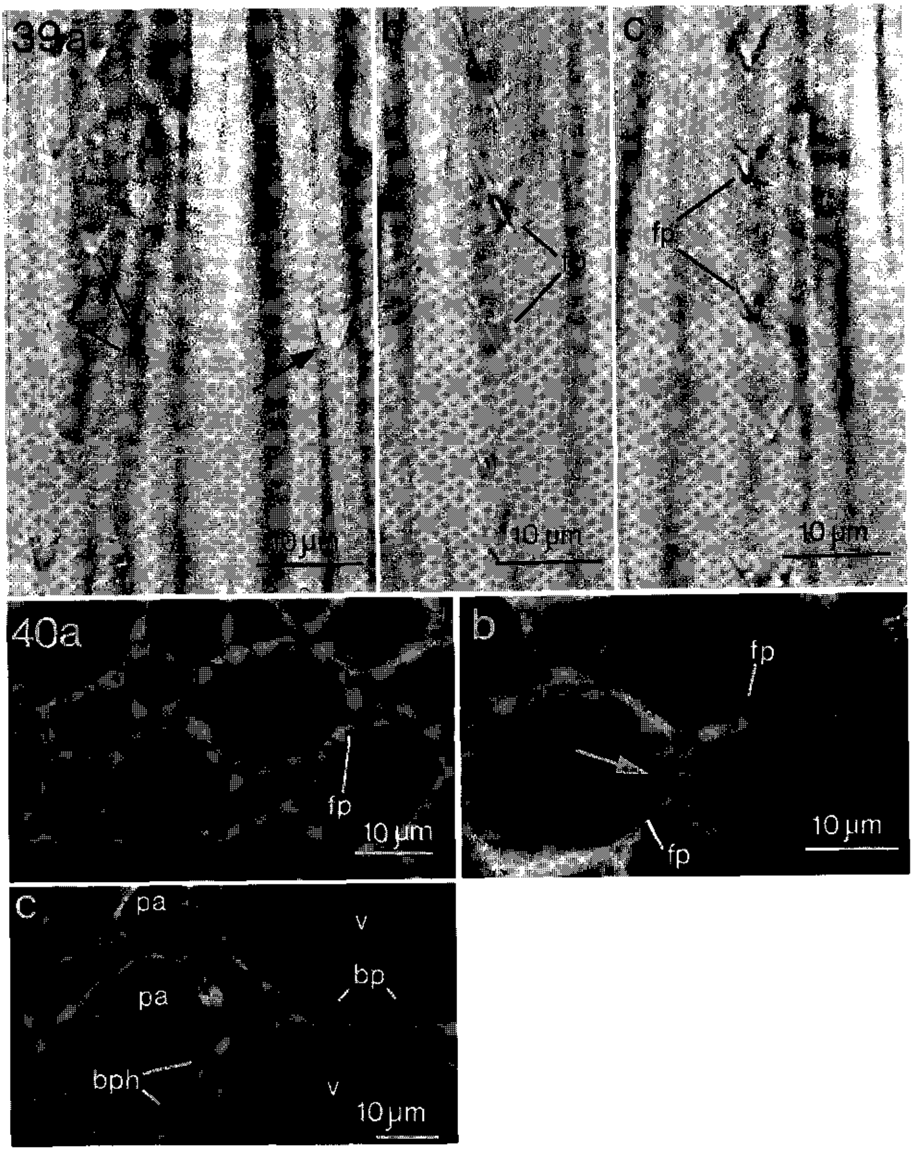

35a
lf
v
25 µm
b
lf
v
10 µm
c
lf
v
10 µm

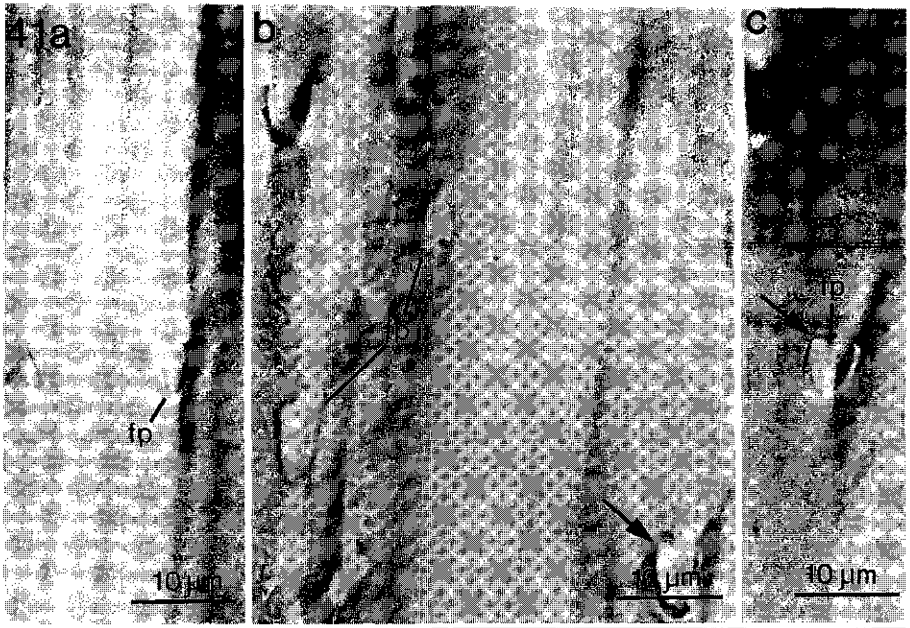

37
e
oa
e
e
oa
e
bp
5 µm

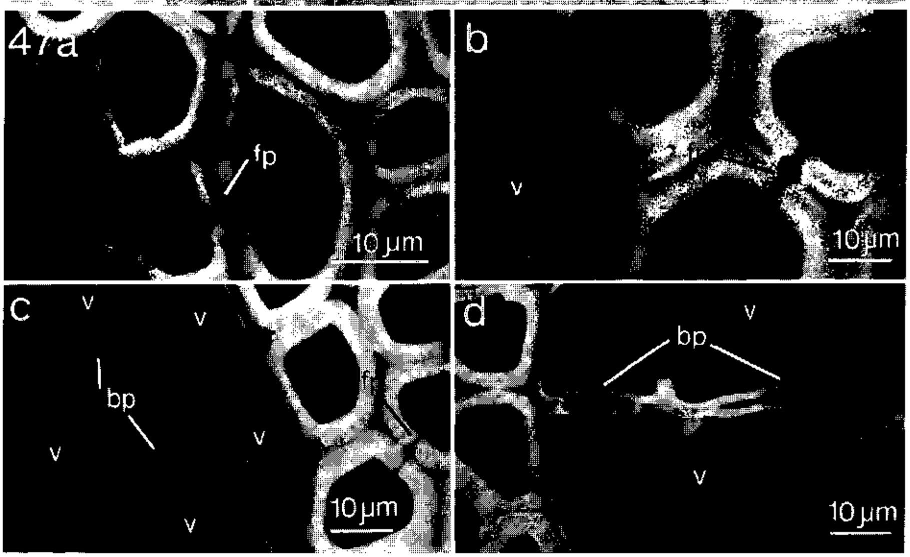

36a
5 µm
b
e
oa
e
oa
bp
5 µm

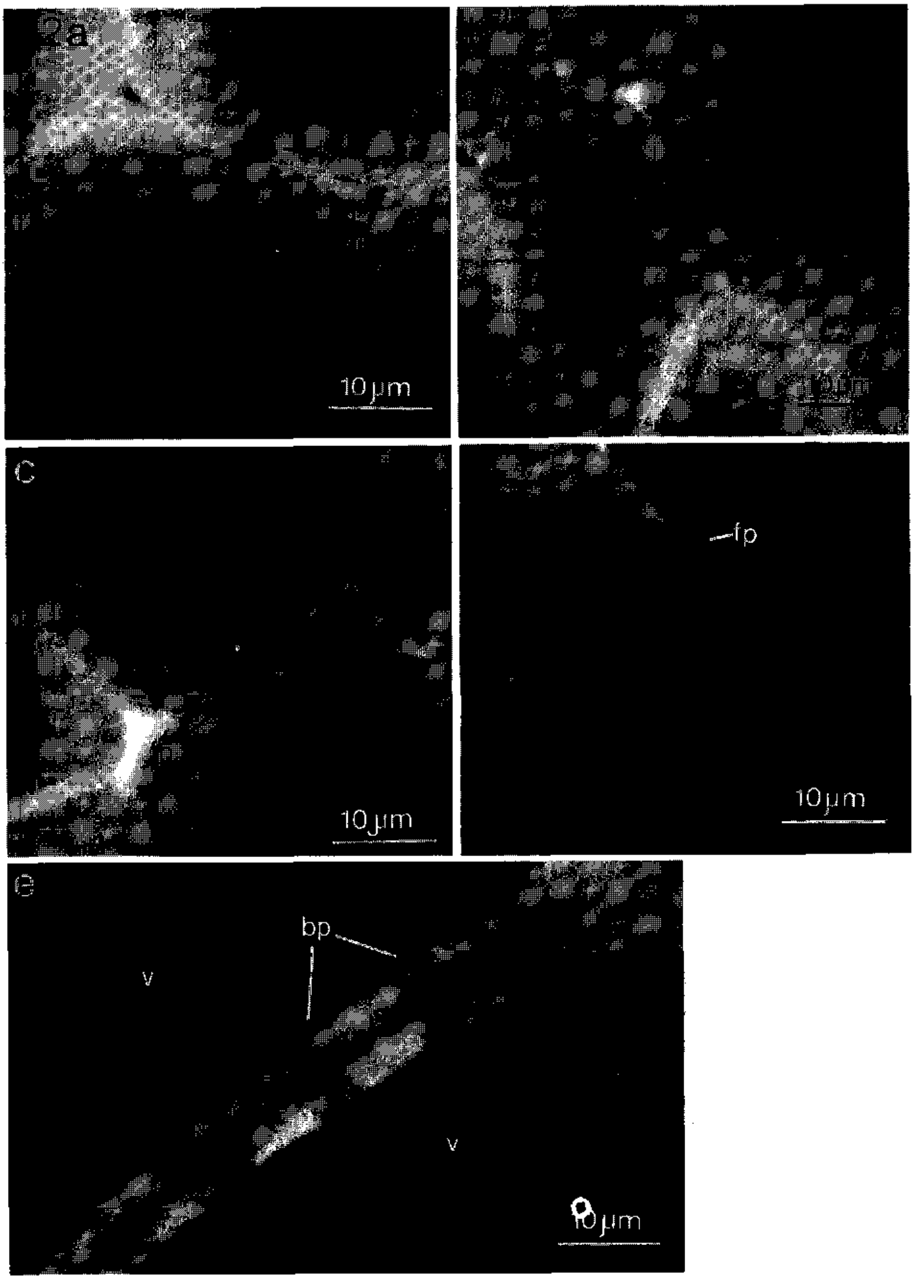


38a
oa
5 µm
b
oa
5 µm
c
ia
5 µm
d
ia
5 µm

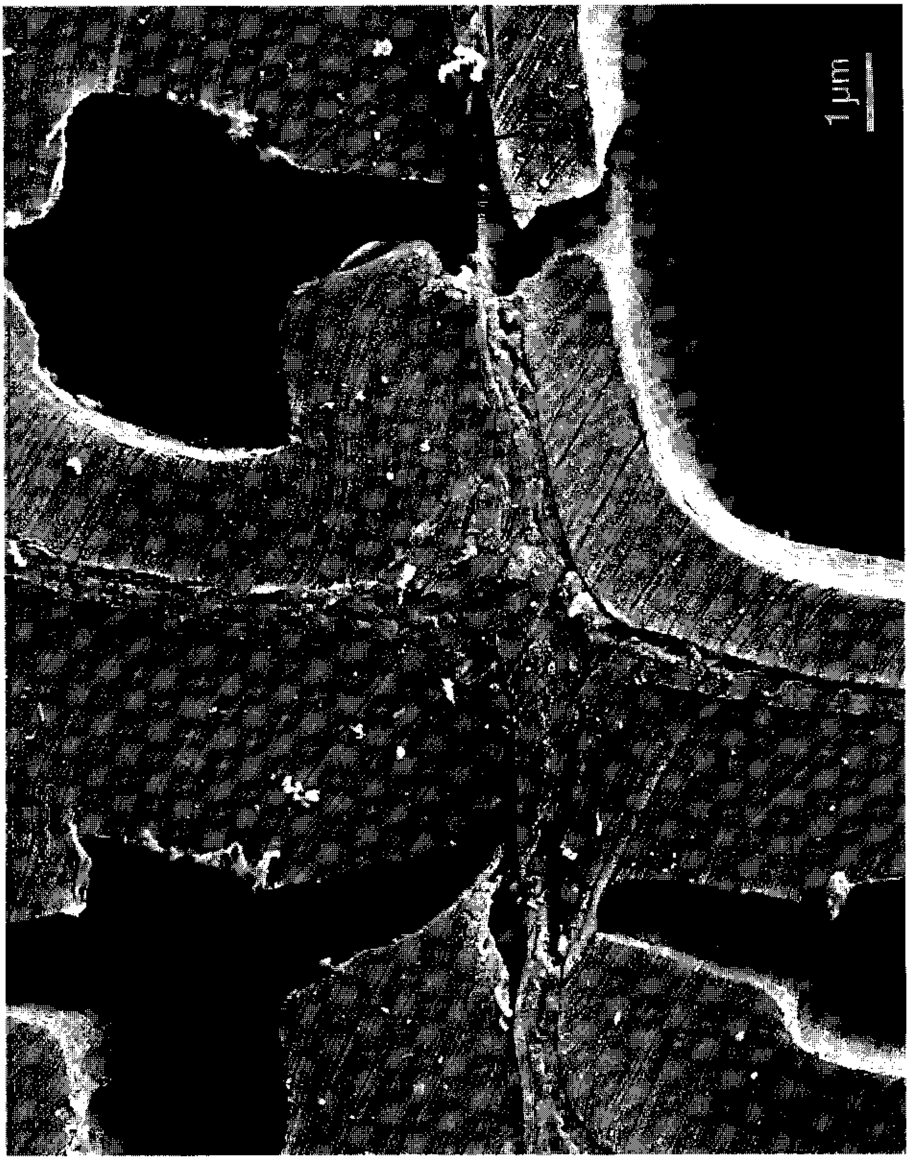

39a
b
c
fp
fp
10 µm
10 µm
10 µm
40a
fp
10 µm
b
fp
fp
10 µm
c
pa
pa
v
bp
bph
v
10 µm

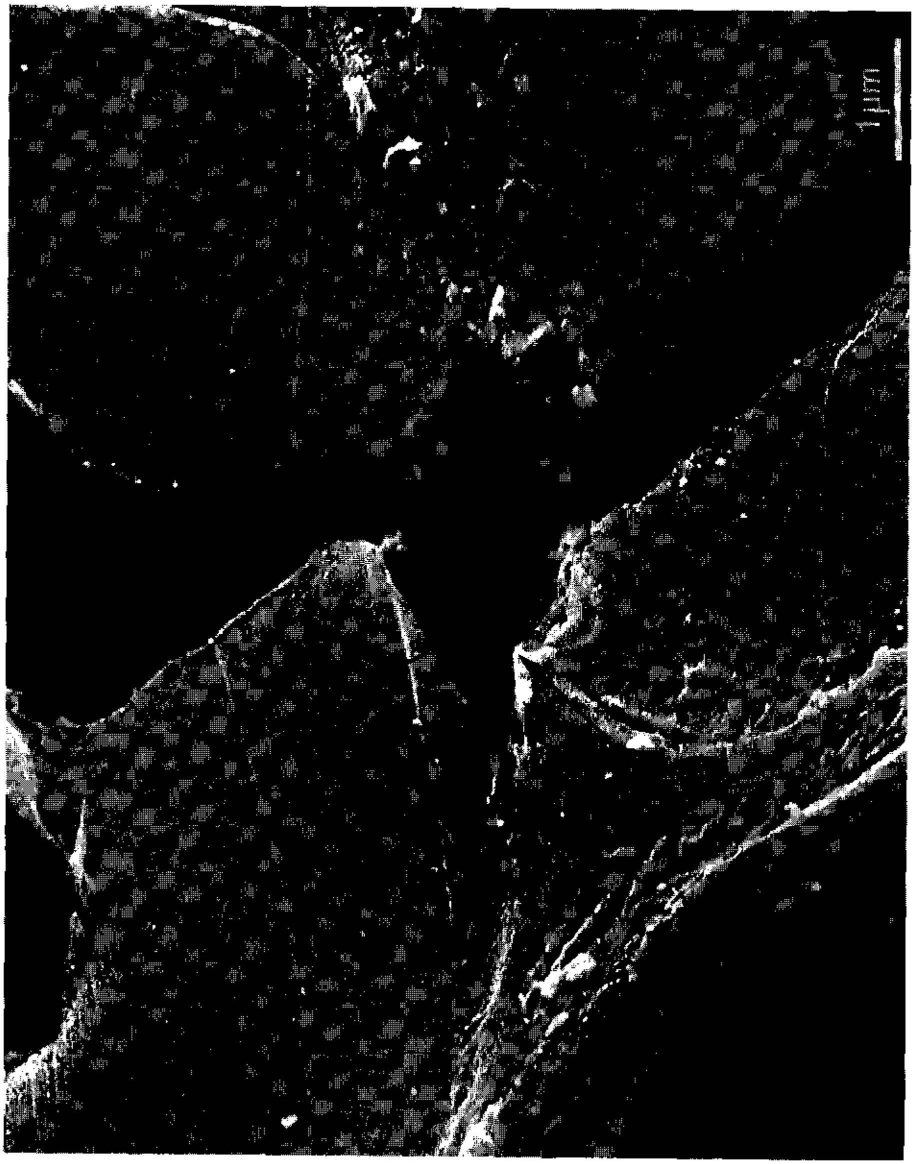

41a
fp
10 µm
b
c
fp
10 µm

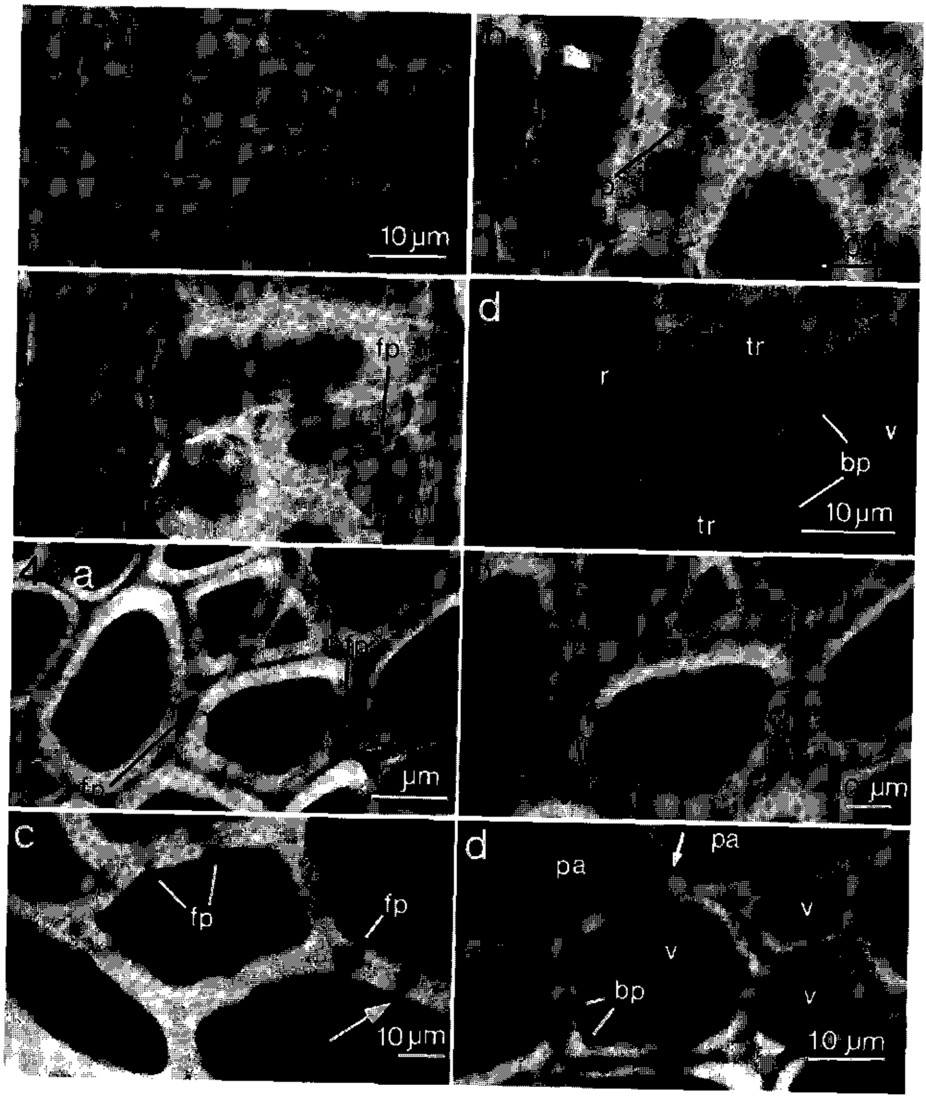

47a
fp
10 µm
b
v
10 µm
c
v
bp
10 µm
d
bp
v
10 µm


2a
10 µm
c
10 µm
fp
10 µm
e
bp
v
v
10 µm


43

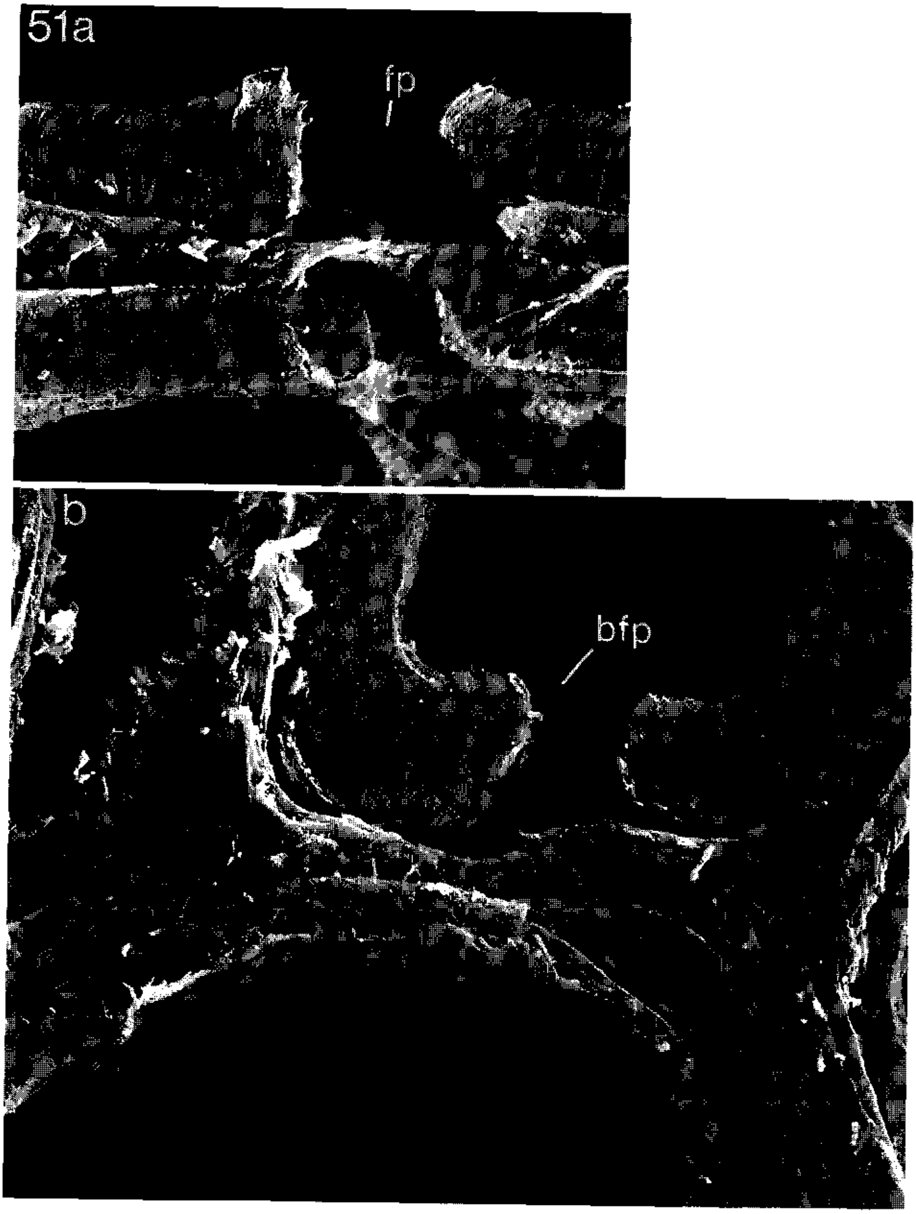

1 µm

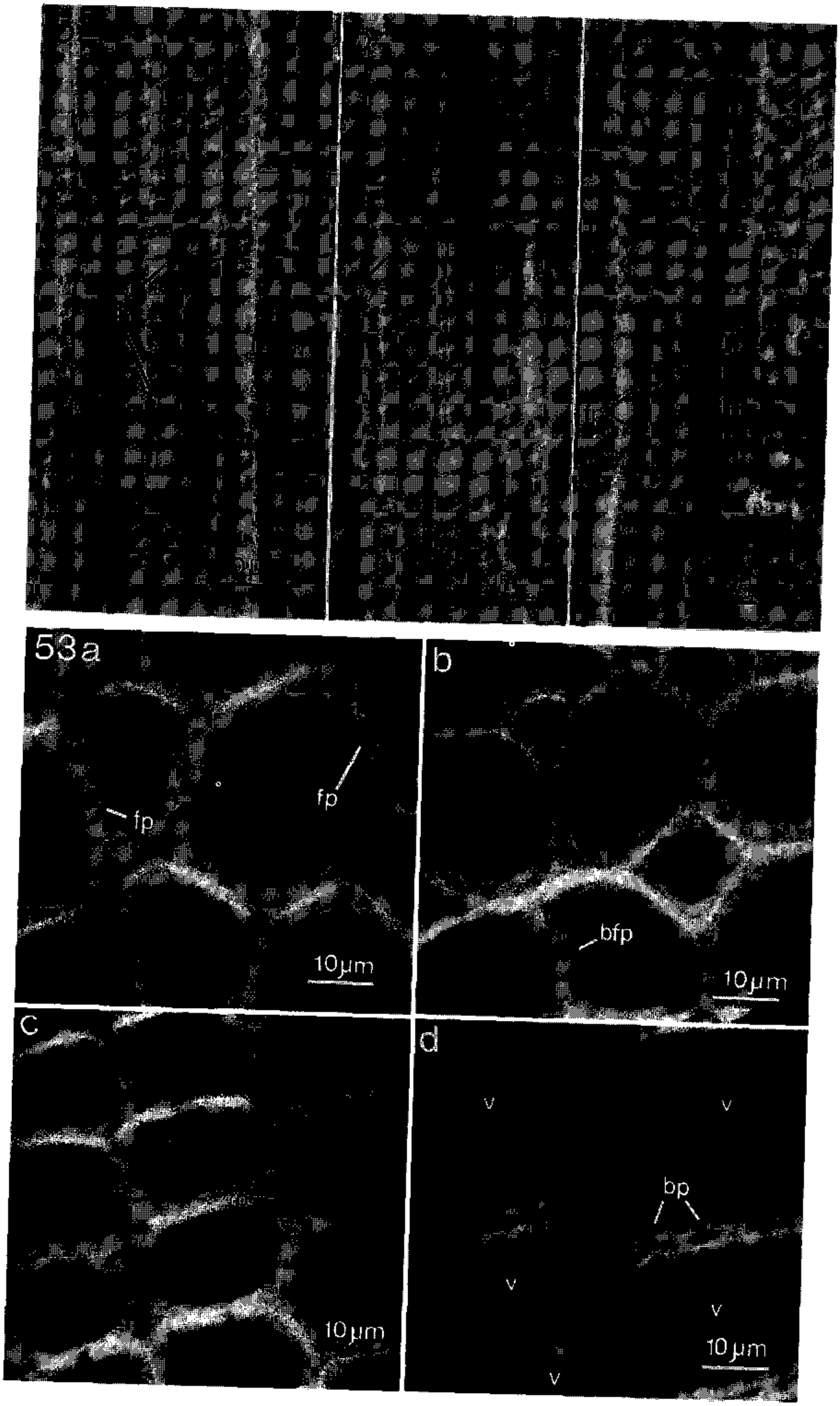


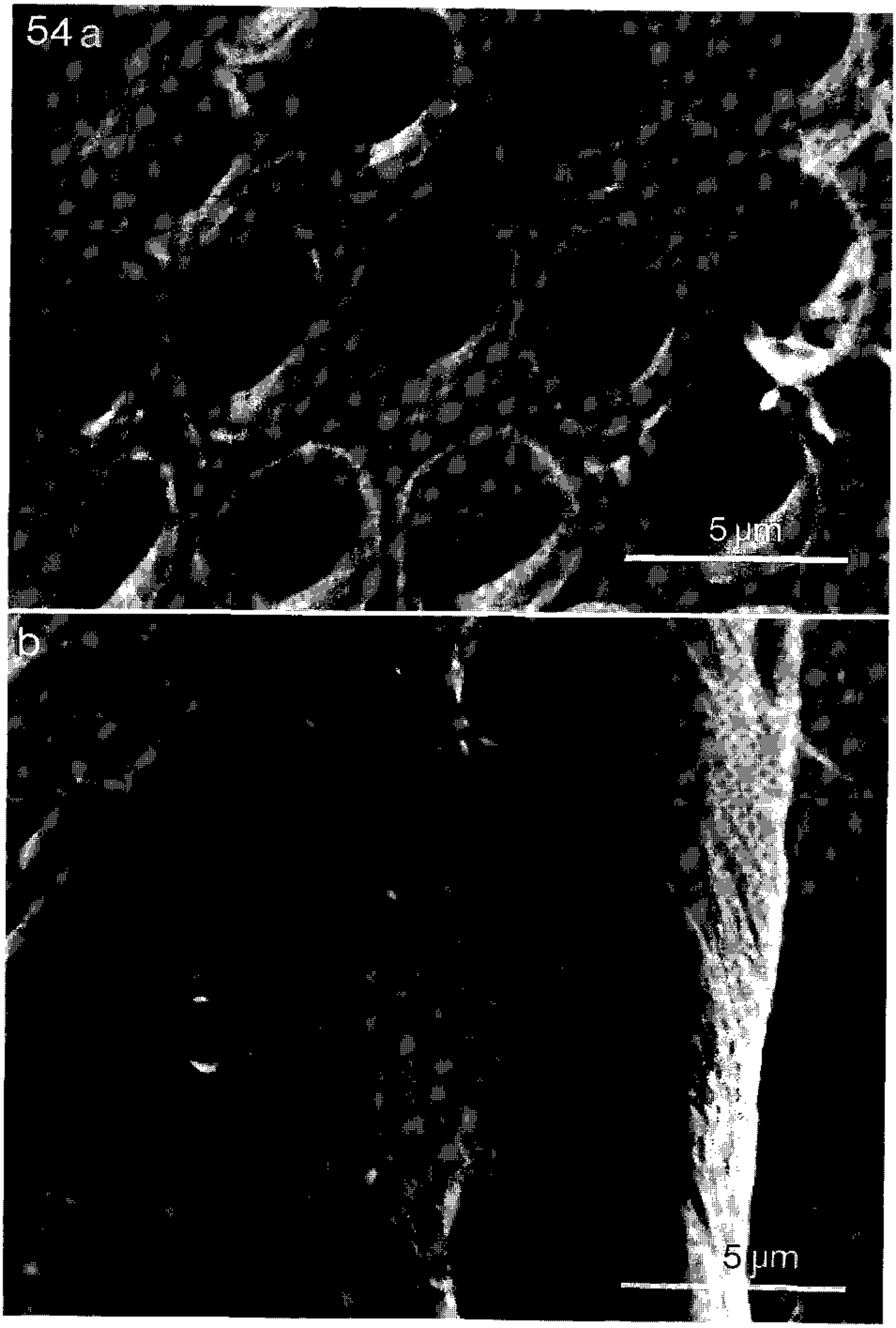


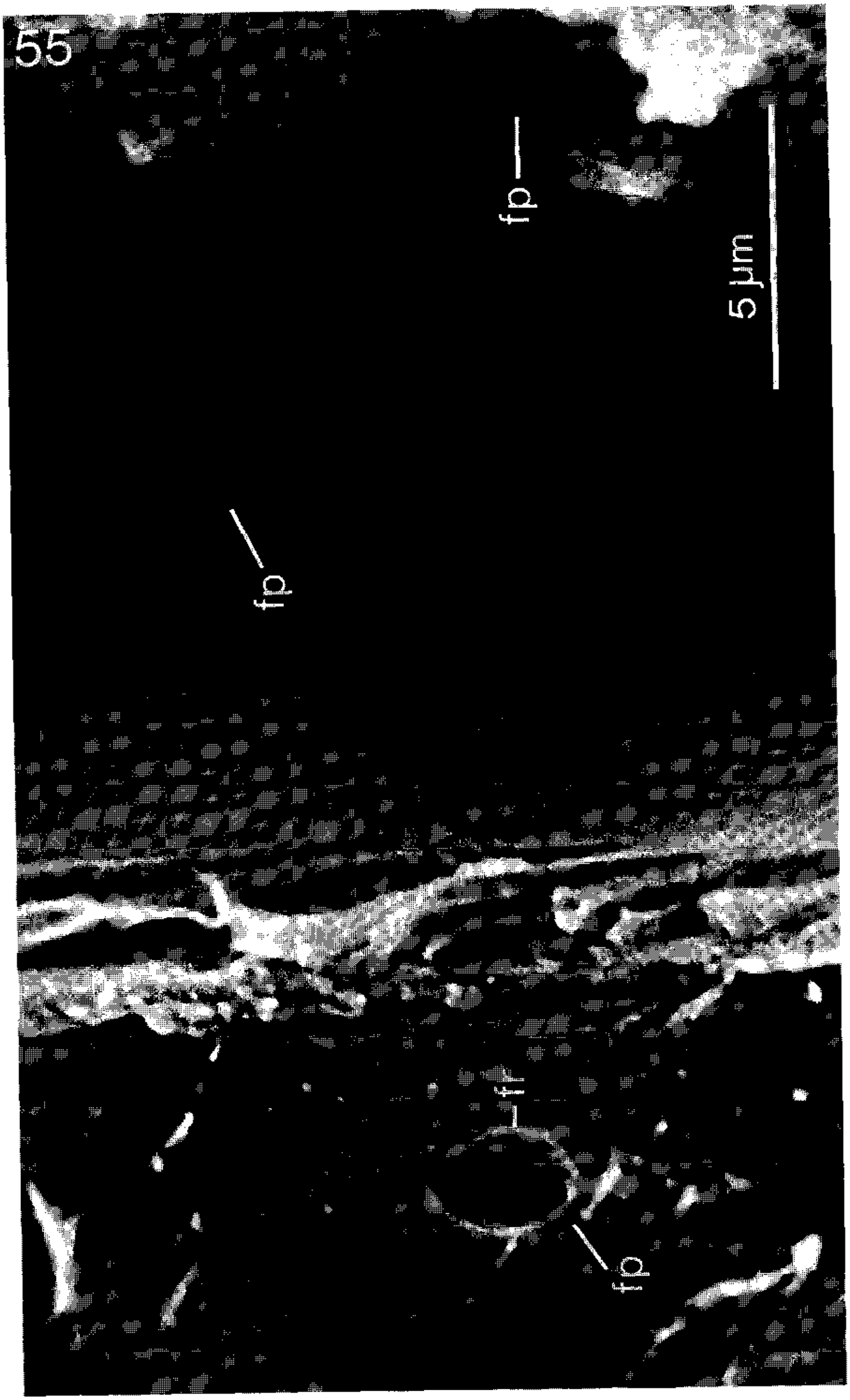
10 µm
d
tr
r
v
bp
10 µm
tr
a
fp
µm
µm
c
fp
fp
10 µm
d
pa
pa
v
v
bp
v
10 µm

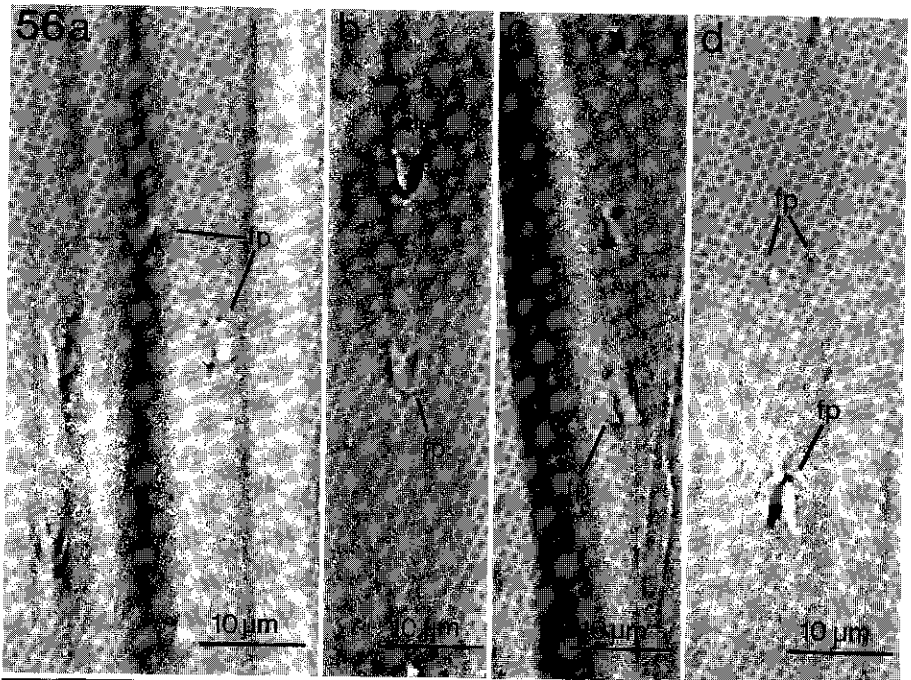

1 µm
tp

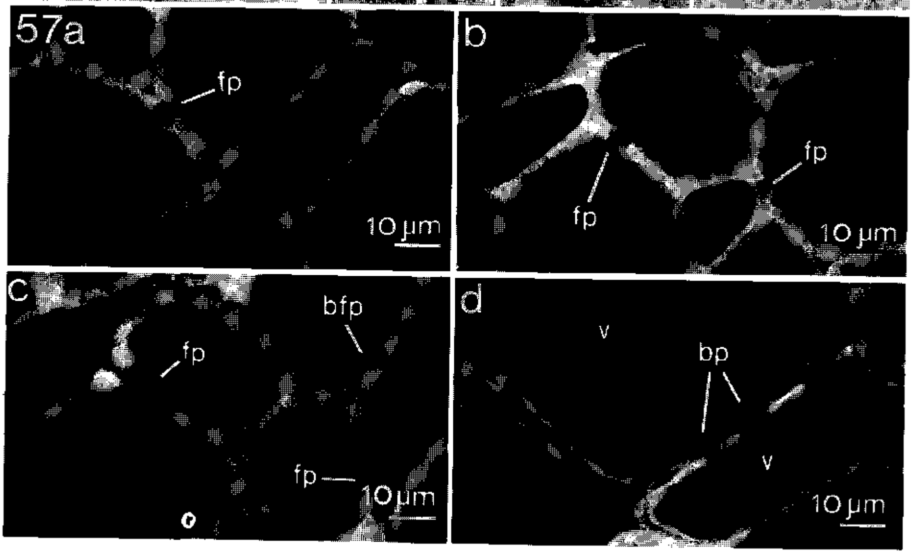

51a
fp
b
bfp

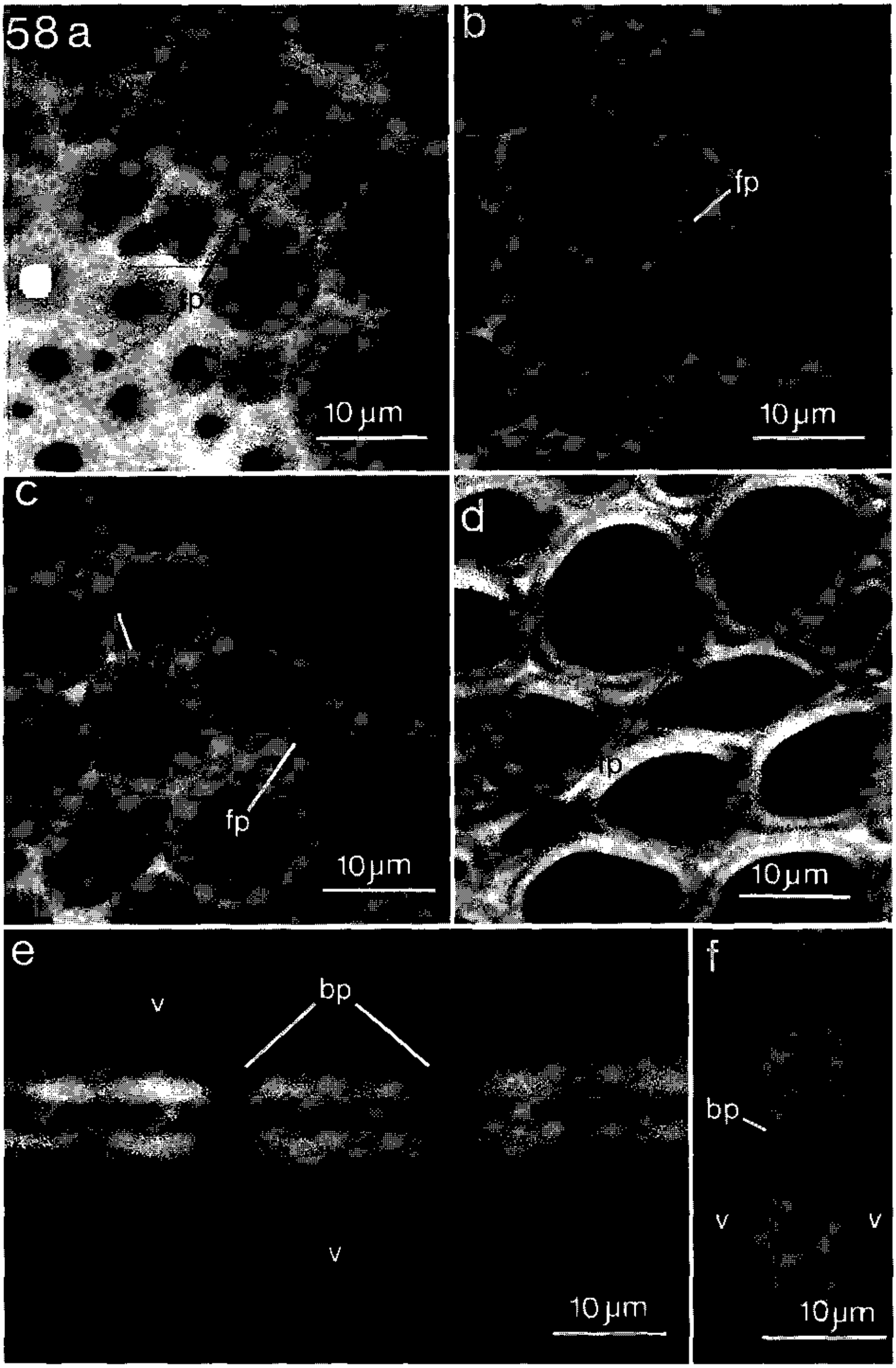

53a
fp
fp
10µm
b
bfp
10µm
c
10µm
d
v
v
bp
v
v
v
10µm


54 a
5 µm
b
5 µm


55
fp
5 µm
fp
fr
fp


56a
fp
b
fp
c
d
fp
fp
10 µm


57a
fp
10 µm
b
fp
fp
10 µm
c
fp
bfp
fp
10µm
d
v
bp
v
10 µm


58 a
fp
10 µm
b
fp
10 µm
c
fp
10µm
d
fp
10µm
e
v
bp
v
10 µm
f
bp
v
v
10µm

6. DISCUSSION

6.1. Evaluation of experimental approach.

Based on the results it appears that there are two categories of pits with different dimensions, shapes and distribution. The bordered pits are restricted to the tracheary elements, the funnel pits are restricted to the libriform fibres.

Examples of hardwoods in which the individual identification of tracheary fibres and libriform fibres, if both present, would be problematical, appear to be scarce. Even the ground tissue fibres in *Alnus viridis* and *Solanum lycopersicum* (MAGENDANS, 1998) are not difficult to identify as libriform (*sensu* CARLQUIST, 1986a). Three experimental approaches were done, i.e. LM, CLSM and SEM. CLSM and SEM gave images that were equivalent in information to the pictures obtained with LM applying oil immersion. In addition light microscopy, with the help of oil immersion, is sufficient for reliable identification of funnel pits. Figures 22A (fp), C; 24A (fp); 25A-C; 32B (fp) are examples of good images in face view and Figs 19A-D (fp) of transverse sections. Although it was mentioned that scanning electron microscopy 'aids very little in pit border detection' (CARLQUIST, 1988), it has been tried with two different types of SEM to produce good images of funnel pits; the best results are shown in Figs 14A; 15A, B; 27; 44; 45; 50; 51. Damage to the tissue produced by preparatory procedures, however, prevents the occurrence of perfect images. To obtain a 3-D impression of bordered and funnel pits with transmission electron microscopy (TEM) is much too elaborate. Confocal laser scanning microscopy gives few extra information on the structure of pits in transverse sections. The best results, shown in Figs 8A (fp); 30A, B (fp); 34A, B; 42C, D (fp) and 49A, B (fp), of which the last mentioned are the best, do confirm the images of the light micrographs.

The characteristics of the structure of bordered pits are well known. A central, oval, symmetrical, lenticular pit cavity is connected by mostly slit-formed pit canals to each lumen of the two tracheary elements in the common wall of which the bordered pit occurs. Bordered pits always show a densely distribution (araucarioid arrangement, hexagonal configuration, HENES, 1959) on the walls of tracheary elements. The characteristics of funnel pits are also shown to be rather constant within the range of diversity that is inherent in this category of structures. The complementary slit-formed pit canals in the common fibre walls do certainly not lead into the complementary parts of a lenticular cavity. The complementary pit canals end in the outer apertures of the canals that are situated at the middle lamella. As another important feature must always be considered the more or less shifted positions of the outer apertures of complementary pit canals in relation to each other along the middle lamella (e.g. Figs 22A (fp), C; 25A-C (fp); 32A,B (fp) (LM); Figs 49A, B (fp) (CLSM) and Fig. 27 (SEM)). These shifted positions result in a very irregular space near the middle lamella constituted by the two widened parts of complementary pit canals: funnel widenings. This situation of not being 'co-ordinated' gives the funnel pits their characteristic image in face view and offers difficulties in measuring these pits. In practice the width of the two outer apertures together is measured.

Further characteristics are the smaller size of funnel pits in a certain hardwood, the much greater diversity of dimensions of funnel pits compared to bordered pits and the degree of being spread on the fibre walls. The frequent occurrence of blind funnel pits in common walls between libriform fibres may also be mentioned. Blind bordered pits in common walls between axial tracheary elements, on the other hand, have never been observed. In face view borders of bordered pits are round or oval; the outlines of the funnel rims have different forms (Figs 1A, 2A). Keeping in mind these characteristics of both categories of wall structures it will not be difficult to determine the nature of a given fibrous element in a certain hardwood. Surely there is no reason to assume the existence of a morphological continuum between bordered pits and funnel pits. Transitional forms have never been discovered. More indications, on the other hand, are found of a morphological continuum between funnel pits and simple pits (e.g. Figs 49 C,D, arrow).

The results of measurement of both categories of pits, transverse and longitudinally, as summarized in table 1 do not evoke doubts about the conclusion that bordered pits and funnel pits are categories of structures with different dimensions. The more so when considering the fact that only the larger, clear examples of funnel pits and the width of the two outer apertures together have been measured. The average dimension of funnel pits is much smaller. And situations as in Figs 11A, B (*Alnus*) evoking the danger of confusing the edges of twist of pit canals with the outer apertures of these pit canals in face view, will not be frequent.

Finally we may come to the conclusion that bordered pits and funnel pits are morphologically different structures.

6.2. Nomenclature, evolution and ontogeny.

CARLQUIST (1988) shows a picture (Fig. 4.5.4) of extra-xylary fibres of *Austrobaileya scandens* . The caption says that these fibres belong to the pith and are called tracheary elements by the author. It is clear from the picture that these fibres are not tracheary and may belong to the sclerenchymatous tissue of the pith, and have pits that resemble very much the funnel pits of libriform. But CARLQUIST did not give any suggestion for a name of these pits, in spite of the fact that these pits show a completely different structure in comparison with bordered pits (Figs 4.5.2,3) of the tracheary elements of the xylem in *Austrobaileya scandens.* Bordered pits and funnel pits may be considered as morphologically different (MAGENDANS, 1998). Statistical comparison of transverse and longitudinal measurements of bordered and funnel pits has been carried out within the types of hardwood individually. Comparison of these measurements between different types of hardwood in search of intermediate forms, is irrelevant. The analysis of measurements of pits showed the existence of two different populations of pits in every type of hardwood. Together with the morphological dissimilarity of the two groups of pits and the different evolutionary development of bordered pits (HENES, 1959) we may come to the conclusion that the two groups are not homologous. In that case new terminology is inevitable.

The description of BAAS (1986) of structures with funnel-shaped widenings (calyciform model) may be chosen as basis for nomenclature. Then these structures can be called funnel pits in short. A pit cavity comparable with those discus-formed, lenticular spaces in bordered pits, does definitively not exist in funnel pits. Two slit-formed pit canals, gradually widening towards the middle lamella, can be observed with strongly variable positions to each other with an unavoidable percentage of blindness. An in face view appearing lobed outline resembles only very little a border. It is better to avoid the designation 'border' and use the concept funnel rims, albeit a bit too irregular for the normal significance of this word (cp. MAGENDANS, 1998, Figs 4, 5). The definition of the bordered pit in which 'the secondary wall overarches over the pit cavity' (ESAU, 1965), or 'a pit in which the secondary wall overarches the pit membrane' (ESAU, 1977) is not sufficient and cannot be maintained. A definite, symmetrical, lenticular or discus-formed, albeit ellipsoid sometimes, pit cavity belongs to this definition. This pit cavity is definitely bounded by the pit canals.

A fundamental morphological difference between bordered pits and funnel pits has not been recognized up to now. Wood anatomists are convinced of the occurrence of intermediary forms between bordered pits and simple pits. In my opinion their problem is that they cannot really show that these forms do exist. Evidently the degree of convergent evolution of the non-homologous structures has been sufficient for wood anatomists to disregard the parallel adaptations of both so very different structures. A well co-ordinated pit cavity is the central structure of the bordered pit-pair as relict of the space between the wall strengthening structures in the primitive conductive elements in xylem of fossil plants (HENES, 1959). This cavity is connected with the lumen of an adjacent element through a small opening, outer aperture, of a slit-formed canal with various forms and directions. A funnel pit-pair is only composed of two not co-ordinated, complementary simple pit halves with widening slitlike pit canals towards the middle lamella. The widenings of the pit canals are ellipsoid in face view and the axes of the ellipses form an acute angle (Fig. 3). The parallel adaptation consists of a resulting larger surface of pit membrane as in bordered pits. Simple pits in thicker cell walls of libriform fibres therefore often obtained about the same external features as bordered pits in face view. But on closer investigation funnel pits and bordered pits are morphologically very different structures. Transitional forms are rare and, if seemingly present, understandable in consequence of the influence of an adjacent element at the borderline between tracheary and non-tracheary tissues (MAGENDANS, 1998), as the structure of the bordered side of a half-bordered pit-pair is also strongly influenced by the complementary half.

Finally, the libriform fibres in the investigated hardwoods showed funnel pits with irregular shapes and varying sizes. In ontogeny the complementary halves of funnel pits seem to keep contact with each other with much difficulty because of strong (intrusive) growth of the fibres. A degree of blindness and the great variability of form and distortion of the funnel pits point to the problem of remaining 'complementary' of the pit halves during ontogeny. The phenomenon funnel pit is probably a consequence of (intrusive) growth of xylary fibres and also of extra-xylary fibres

(BAAS, 1986; CARLQUIST, 1988). The complementary pit halves of a calyciform-like pit-pair in the walls of ray parenchyma cells (CARLQUIST, 1988; MAGENDANS, 1998) are always well co-ordinated, but may be considered as examples of parallel adaptations as well. Those 'adaptive ray pits', likewise belonging to the category of simple pits, will probably have differentiated as a result of extra transport needs in the rays in the absence of intrusive growth.

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SUMMARY

This publication consists of two articles. In the first article (MAGENDANS, 1998) the structure of pits in nonperforate xylary fibres of two special cases of dispute, *Alnus viridis* (Chaix) DC., and *Solanum lycopersicum* L. cv. Moneymaker (VAN DER SCHOOT & VAN BEL, 1989), has been studied. Much attention has been paid to the question of the so-called intermediate forms, basis of the general view of xylem evolution. It appeared that the ground tissue fibres of both *Alnus viridis* and *Solanum lycopersicum* reveal a type of pits of which the pit canals widen gradually towards the middle lamella and in which a definite lenticular, co-ordinated pit cavity is lacking, furthermore the complementary halves of the pit are by no means mirror images as in bordered pits. These pits were called 'funnel-shaped' by BAAS (1986) and are nearly always partly blind. These 'funnel pits' are distinctly smaller than bordered pits in each hardwood and consist of only two complementary pit canals not identical in shape. The funnel pits showed a large variety of forms in the same wood unlike bordered pits which are rather uniform. Funnel pits are irregularly spaced and relatively infrequent.
Intermediate forms between tracheary elements and libriform fibres and consequently between bordered pits and funnel pits seem to be very rare. These forms of intermediary pits can only be found in adjacent wall parts between tracheary element and wood fibre. These intermediate forms of pits constitute combinations of complementary halves of bordered and funnel pits. So, real intermediate forms between tracheary elements and libriform fibres do not exist. In addition physiological phenomena are mentioned, indicating a different type of differentiation of tracheary elements and wood fibres or parenchymatous fibres. The differentiation into tracheary elements is stable: the modifying factors (MOHR & SCHOPFER, 1993) will only be operative a short time. The differentiation into the other axial xylary elements, parenchyma and libriform, is reversible and not stable. Xylary axial parenchyma remains alive, at least much longer than the other axial elements and so generally do the libriform fibres. 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.

The morphology of bordered pits and funnel pits turned out to be different in fourteen examined hardwoods and one herb of fourteen

different families spread all over the plant world (MAGENDANS & VAN VEENENDAAL, 1998). Moreover it was possible to offer definitions of both types of pits and their components, as the characteristics of both types appeared to be rather constant in all examined families. Bordered pits are well co-ordinated and the central structure, pit cavity, always shows a lenticular appearance in transverse section, independent of level of focus. Definite limits exist as boundaries between pit cavity and pit canals. Funnel pit-pairs are not co-ordinated and the complementary halves are partly blind. A true pit cavity does not exist, only two complementary pit canals are present which are not identical in shape. Certain identification of funnel pits appeared to be possible with light microscopy using oil immersion. Nevertheless confocal laser scanning microscopy (CLSM) and different types of scanning electron microscopy (SEM) were used as well to produce good images of funnel pits. Damage to the tissue by preparatory procedures, however, often prevents the occurrence of perfect images with SEM. The characteristics of funnel pits are shown to be rather constant within the range of diversity that is inherent in this category of structures. The complementary slit-formed pit canals in the common fibre walls do certainly not lead into the complementary parts of a lenticular cavity. As another important feature must always be considered the more or less shifted positions of the outer apertures of complementary pit canals in relation to each other along the middle lamella. These shifted positions result in a very irregular space near the middle lamella: funnel widenings. This situation of not being 'co-ordinated' gives the funnel pits their characteristic image in face view. Measurements of both categories of pits show that funnel pits are always smaller than bordered pits. Funnel pits show a scattered distribution on the fibre walls and great diversity of dimension among them. Funnel pits are often blind; blind bordered pits are never observed. Together these characteristics allow the detection of both types of pits and the determination of the nature of a given fibrous element in a certain hardwood. The conviction in the existence of a morphological continuum between bordered pits and funnel pits can therefore not be affirmed. The analyses of axial and transverse measurements of pits showed the existence of two different populations of pits in every type of hardwood. Together with the morphological dissimilarity of the two groups of pits and the different evolutionary development of bordered pits (HENES, 1959) we must conclude that the two groups are not homologous and new terminology is proposed.

The morphology of funnel pits suggests that a problem exists of pit halves remaining 'complementary' during ontogeny. The phenomenon funnel pit is probably a consequence of (intrusive) growth of xylary fibres and also of extra-xylary fibres (BAAS, 1986; CARLQUIST, 1988).