

Donald Kaplan's Legacy: Influencing Teaching and Research

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Tracheids in an early vascular plant: a tale of two branches

DIANNE EDWARDS^{1*}, CHENG-SEN LI^{2,3} and JOHN A. RAVEN⁴

¹*School of Earth, Ocean and Planetary Sciences, Cardiff University, Main Building, Park Place, Cardiff CF10 3YE, UK*

²*Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China*

³*Beijing Museum of Natural History, Beijing 100050, China*

⁴*Plant Research Unit, University of Dundee at SCRI, Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DQ, UK*

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Permineralized xylem strands in an otherwise coalified pseudomonopodially branching axis from the Lower Devonian of Røragen, Norway, allow the description of the architecture of the presumed tracheids using scanning electron microscopy, and a discussion on the roles of the various types of pitting in the functioning of the water-conducting cells. Tracheid construction differs in the main axis and lateral branch. The former has G-type tracheids in which close-set annular secondary thickenings are connected by a further microperforated secondary layer lining the imperforate presumed primary wall. Tracheids in the lateral branch possess bordered pits that may be circular, elliptical or scalariform, with rare examples of reticulate pitting. The secondary wall structures of the tracheids are discussed in relation to their major roles, namely conduction, mechanical strength and safety (i.e. prevention of implosion and embolism) and to different needs in different parts of the plant. It is suggested that in the main axis, tracheids are adapted for longitudinal transport of water with their abundant (presumed) lignification providing mechanical strength and resistance to embolism. In the lateral branch, by contrast, they are apparently adapted for rapid lateral transport at the expense of their structural and safety roles. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, 150, 115–130.

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INTRODUCTION

Halle's 1916 account of the Lower Devonian plants from Røragen, Norway, was the first comprehensive account of early vascular plants from Europe. The series of pioneering papers by Dawson on Gaspé plants of similar age (for summary see Dawson, 1888) was followed by a number of preliminary observations on assemblages from Belgium, France, Germany (see Halle, 1916) and Norway (Nathorst in Goldschmidt, 1913; Nathorst, 1914), the latter encouraging Halle to

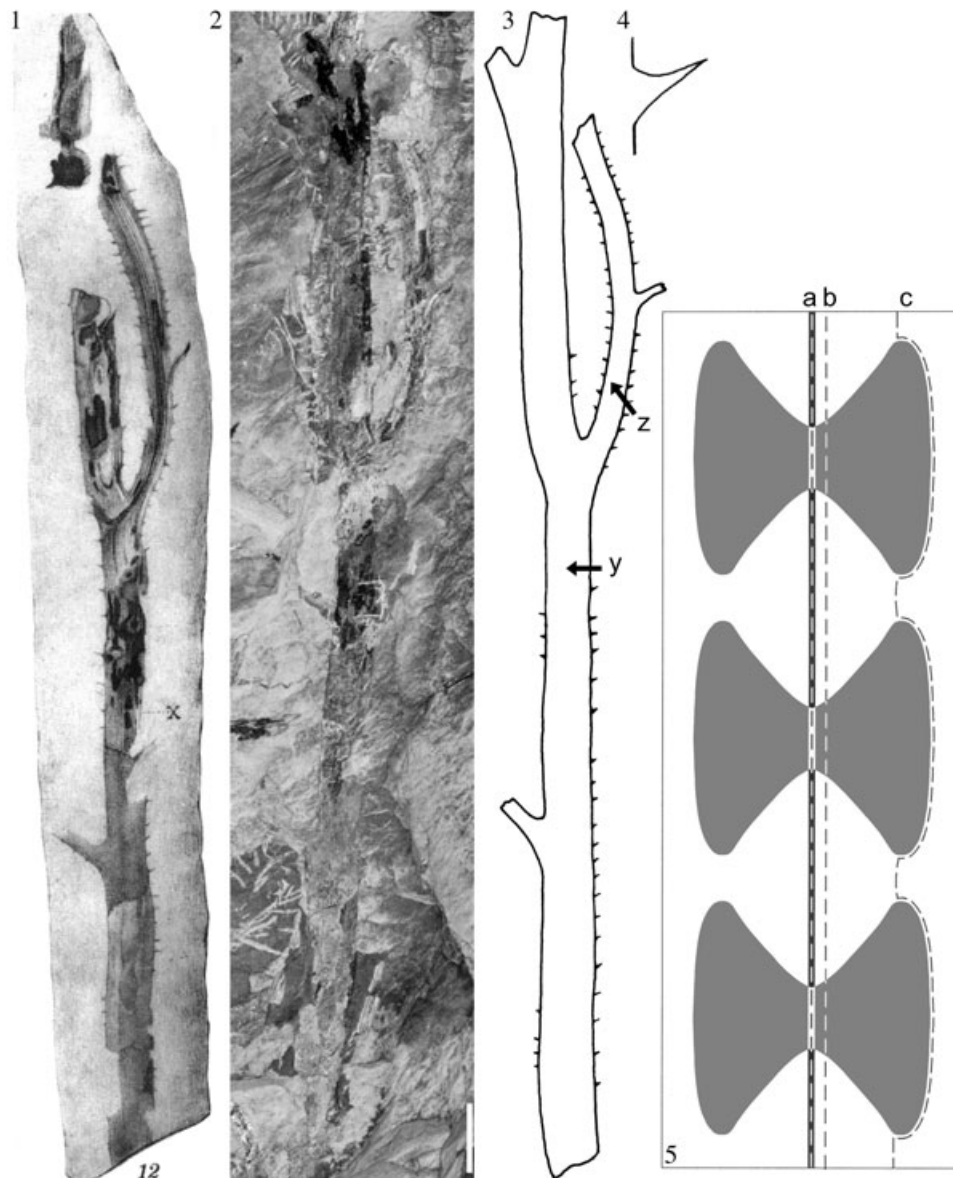
make further collections in the Røragen area. These formed the greater part of the 1916 paper. Among the numerous sterile axes with spines were some he identified as *Psilophyton princeps* Dawson, and related them particularly to axes called *P. princeps* var. *ornatum*. The specimen on which this paper is based was so called (Halle, 1916). Even then there was considerable debate on the number of taxa included by Dawson under the (now) trimerophyte *P. princeps* (Dawson, 1859, 1871), a controversy resolved a century later (Hueber & Banks, 1967; Hueber, 1967, 1971) with the erection of the zosterophyll, *Sawdonia ornata*. More recently, Schweitzer & Heumann (1993) identified fertile and sterile axes as *S. ornata* in new collections

*Corresponding author. E-mail: EdwardsD2@cardiff.ac.uk

from Røragen and illustrated G-type tracheids via scanning electron micrographs. Here we present a more detailed account of the permineralized tracheids originally illustrated by Halle from a sterile spiny axis (1916, pl. 4, figs 12–14) and described as scalariform. Our interest was prompted by the significance of xylem architecture both in taxonomy and in understanding the water relations of early land plants (Edwards, 2003; Sperry, 2003).

MATERIAL AND METHODS

The single specimen is coalified, either in sheets or as dark brown to black granular material, with the central areas of the axes, the xylem, permineralized initially by pyrite but showing some signs of oxidation (Figs 1, 2). Small fragments (positions y and z in Fig. 3) of the xylem were placed on stubs, coated in gold and examined by scanning electron microscopy



Figures 1–5. Lower Devonian spiny axis from Norway. Fig. 1. Original illustration in Halle (1916, pl. 4, fig. 12). x marks position of permineralized xylem in which he observed scalariform tracheids. Fig. 2. Recent photograph of 1. Scale bar = 1 cm. Fig. 3. Line drawing of specimen indicating positions of described xylem (y = main, z = lateral branch). Fig. 4. Spine. Fig. 5. Idealized longitudinal section through parts of wall (black area) of adjacent tracheids, black dotted lines indicating planes of fracture: a, through middle lamella; b, along inner surface of pit-closing membrane; c, through contact between interior surface of tracheids and mineral filling lumen.

(SEM) in the Institute of Palaeontology, Bonn University, Germany, in 1989.

Because of the paucity of permineralized axes, and more importantly the figured status of the specimen, it was not possible to cut thick sections.

LIMITATIONS ON ACQUISITION OF DATA

INTERPRETATION OF PRESERVATION MODE

Xylem from the main axis (Figs 6–13) was relatively uncompressed (i.e. lumina \pm isodiametric in TS) and remarkable in that although most of the original wall material (1° and 2° walls) has been replaced by mineral, the latter was not present in the lumen (Figs 9, 12). It is of course possible that any lumen casts could have been dislodged during preparation, or dissolved over time, but both explanations seem unlikely. There is some variation in the appearance of the presumed annular secondary thickenings. Some appear solid, whereas others have a hollow centre reminiscent of the condition noted in *Gosslingia breconensis* (Kenrick & Edwards, 1988) where this area was postulated as mainly cellulosic, i.e. devoid of lignification. Preservation of the original primary wall is sporadic. Some specimens show mineral overgrowth of original wall structures (e.g. Fig. 11), perhaps facilitating preservation of the three-dimensional structure, but presenting problems for measurement. Very well-developed overgrowths were illustrated by Schweitzer & Heumann (1993: Taf. 3, figs 5, 6). By contrast, lumen casts are present in the lateral branch xylem (Figs 14–34), and extend into at least the canals of the bordered pitting present. Secondary and primary walls were again replaced by mineral. No well-preserved transversely fractured tracheids have been observed; however, they do give the impression of some compression, and most longitudinally fractured examples show only one facet. The variety of appearances following longitudinal fracture depend on its plane of action. The commonest are indicated in Figure 5 with those showing the internal faces of the pit-closing membrane predominating (fracture line b, e.g. Figs 19, 25, 26). These may be very smooth, and thus interpreted as the inner surface of the membrane, or bear small amounts of further mineral (partial casts of bases of pit cavities). The double line that sometimes limits the pit-closing membrane is thought to represent the thickness of the base of the overarching 2° wall (Fig. 16). Other examples show the consequences of fracture between the interior surface of the tracheid, namely pit apertures and intervening 2° wall (fracture line c in Fig. 5: Figs 27, 31, 33) and the lumen cast (fracture line c in Fig. 5, e.g. Figs 24, 29, 30). The protuberances of the latter, which are of varying height, are casts of the apertures. Rare examples show the continuous outer surface of the

tracheid in the vicinity of the original middle lamella (fracture line a in Fig. 5, e.g. Figs 9, 17, 18).

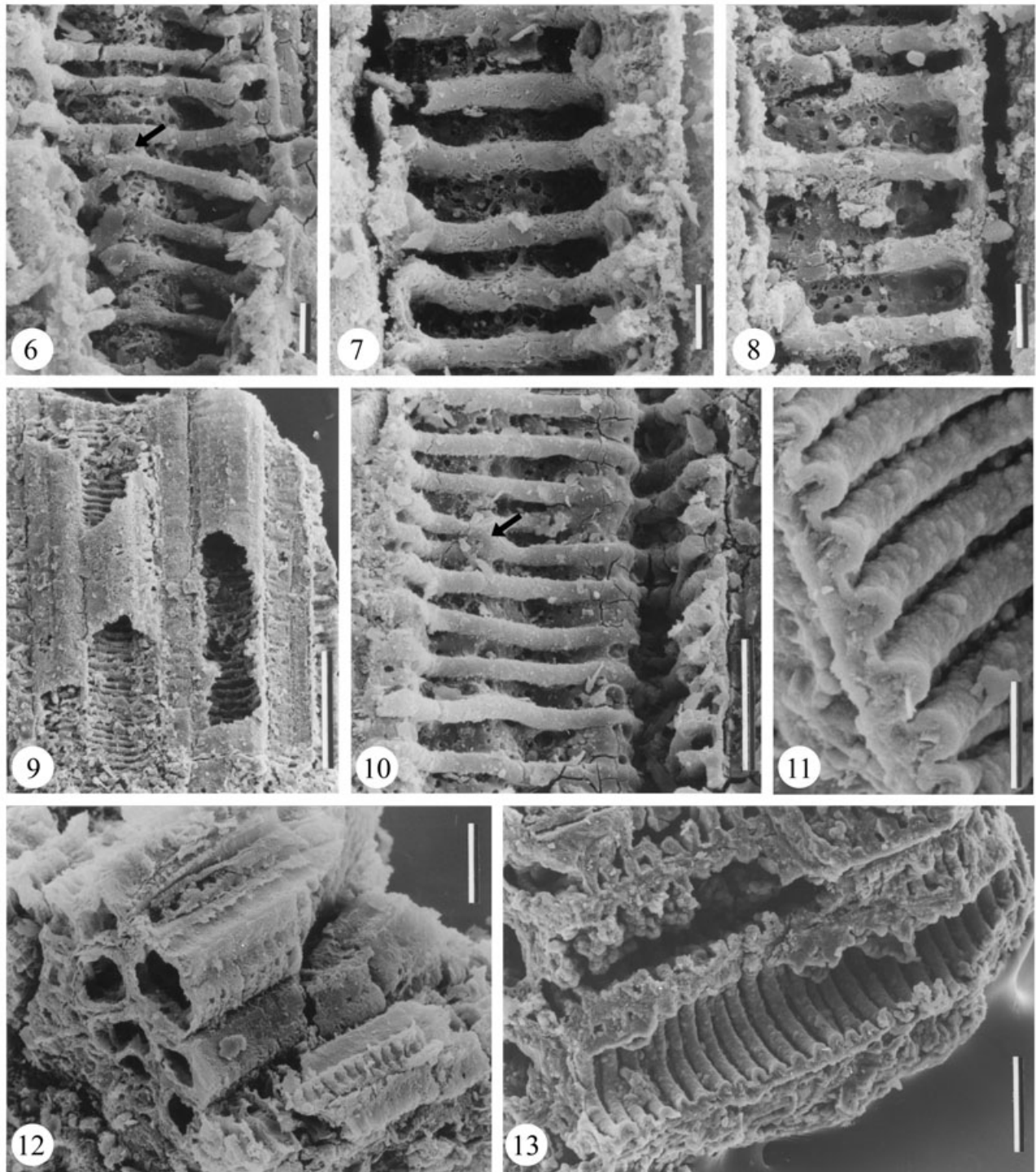
MEASUREMENTS

Anatomical measurements obtained via SEM are rarely accurate because of tilting of the stage. Here there were further problems in obtaining data for palaeophysiological processes (mainly hydraulic conductance), because it was not possible to obtain transverse sections, so that diameters of tracheids and number of facets are estimates. It was also impossible to measure all parameters (e.g. areas of pit-closing membranes, apertures) of a single individual pit. A further complication, in the absence of ground sections, is estimation of the extent of mineral overgrowth and hence, for example, the dimensions of secondary thickenings and the distance between them. In addition, we have no information on the areas of xylem in the two axes, nor numbers of tracheids therein. Finally, we have only minimum values for tracheid length and no examples of ends of tracheids. We thus have no information on tracheid overlap. However, this fact, together with the parallel-sided nature of tracheids, suggests that they were considerably longer than the values measured.

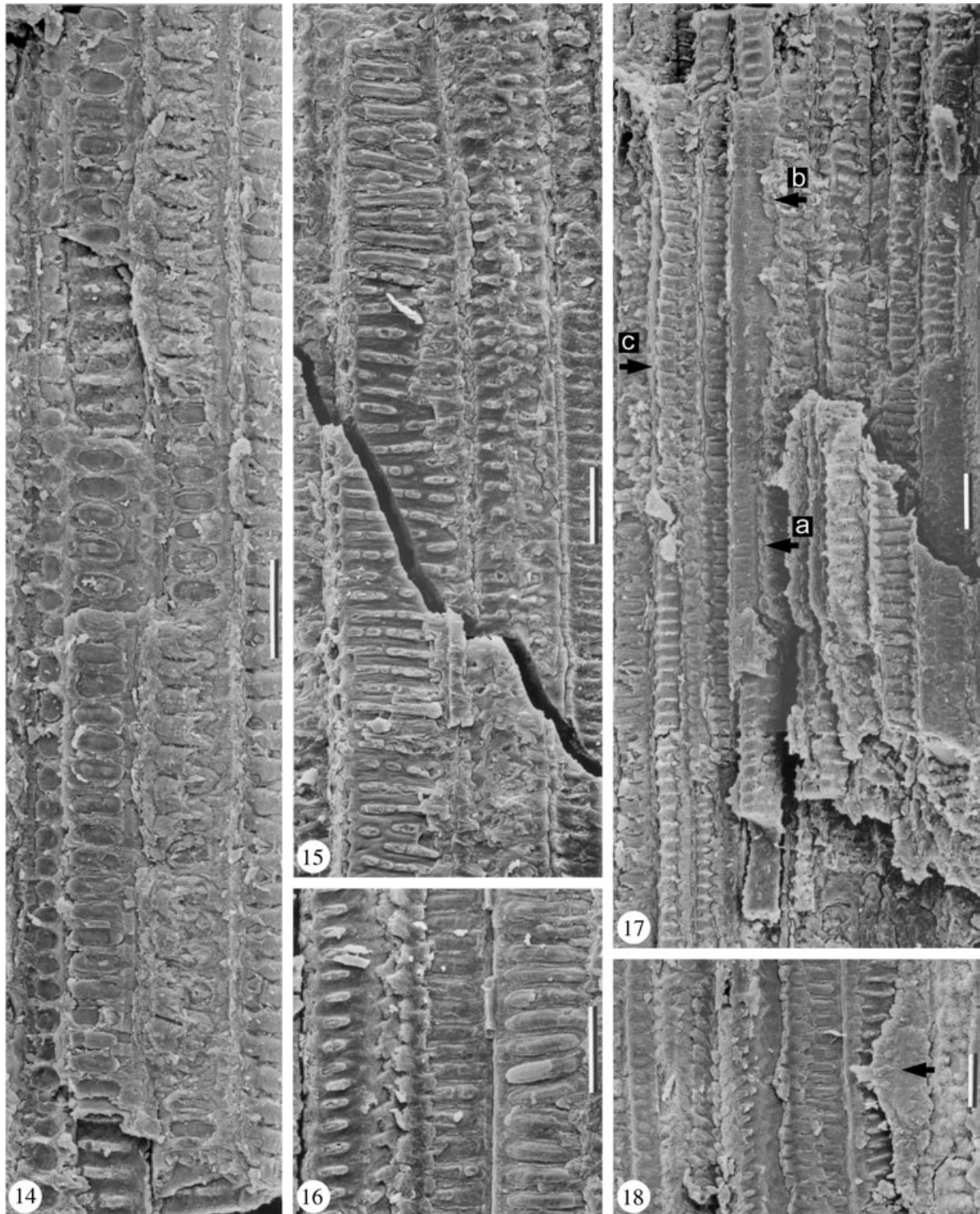
DESCRIPTION

The specimen is 17 cm long (Figs 1–3). The main axis ranges between 5.6 and *c.* 7.1 mm in width towards the base. Branching is pseudomonopodial, the narrower laterals alternately inserted. The most complete is *c.* 4 mm wide towards its base. Very slender spines are usually preserved only at the base. Rare completely preserved examples have attenuated tips and slightly decurrent bases (Fig. 4). The central permineralized strand in the main axis is 2.5 mm wide, occupying about a third of its diameter. Measurements taken along a transect show no marked changes in diameter either at the edges or at the centre of the xylem. All tracheids described here comprise metaxylem. The maximum length of the parallel-sided tracheids is 650 μ m and gives a minimum value of maximum tracheidal length. Figure 12 illustrates an isolated group of tracheids which are three dimensionally preserved. Dimensions are summarized in Table 1. Problems encountered with measurements have been outlined in the previous section.

Fractures through the position of the middle lamella reveal the continuous outer primary wall of the tracheid (Figs 9, 12). Secondary thickenings, very uniform in appearance, are probably annular and interconnections are rare (arrowed in Figs 6, 10). Distances between thickenings vary between tracheids; when small the thickenings appear as dense corrugations



Figures 6–13. Xylem of main axis. Figs 6–8, 10. Annular thickenings with pitted intervening wall. Note variation in size of pits. Arrows indicate connections between 2° thickenings. Scale bar in Figs 6–8 = 10 μm , in Fig. 10 = 30 μm . Fig. 9. Tracheids showing separation at the middle lamella. Scale bar = 100 μm . Fig. 11. Part of 13 enlarged showing 1° wall with annular thickenings and possible mineral overgrowths. Scale bar = 10 μm . Fig. 12. Three-dimensionally preserved tracheids with empty open lumina. Note lack of compression. Scale bar = 30 μm . Fig. 13. Longitudinally fractured uncompressed tracheids with close-set annular thickenings. Scale bar = 30 μm .



Figures 14–18. Longitudinally fractured tracheids of lateral branch. Scale bars = 30 μm . Fig. 14. Note various planes of fracture, shapes of pit-closing membranes and parallel-sided nature of individual tracheids. Fig. 15. Scalariform bordered pits with some vertical connections (fractured in plane b, Fig. 5). Note possible tapering towards top of example on left. Fig. 16. Oval to scalariform bordered pits (Fig. 5, plane b). Double line limiting pit-closing membrane probably indicates thickness of wall. Fig. 17. Various planes of fracture including along middle lamella (arrows a and b) and longitudinally through compound middle lamella and secondary wall (arrow c). Fig. 18. Arrow indicates fracture along middle lamella.

Table 1. Numerical characteristics of tracheids from spiny axes in Rörägen, Norway

	Tracheid (μm)		2° thickening (μm) aggregated data			
	Length	Diameter	Radial width (t)	Axial height (δ)	Distance	Pit diameter
Schweitzer & Heumann (1993)	< 550	34–50	3–7.8	1–5	6–12 < 15	< 1
This paper G type	> 650	39–80 ($n = 11$; $x = 54$)	<i>c.</i> 4.7	2.9–5.6 ($n = 26$; $x = 4.34$)	2.9–9.0 ($n = 21$; $x = 5.7$)	0.7–3.2 ($n = 123$; $x = 1.63$)
Pitted	> 1000	13–50 ($n = 37$; $x = 30$)	–	–	–	–

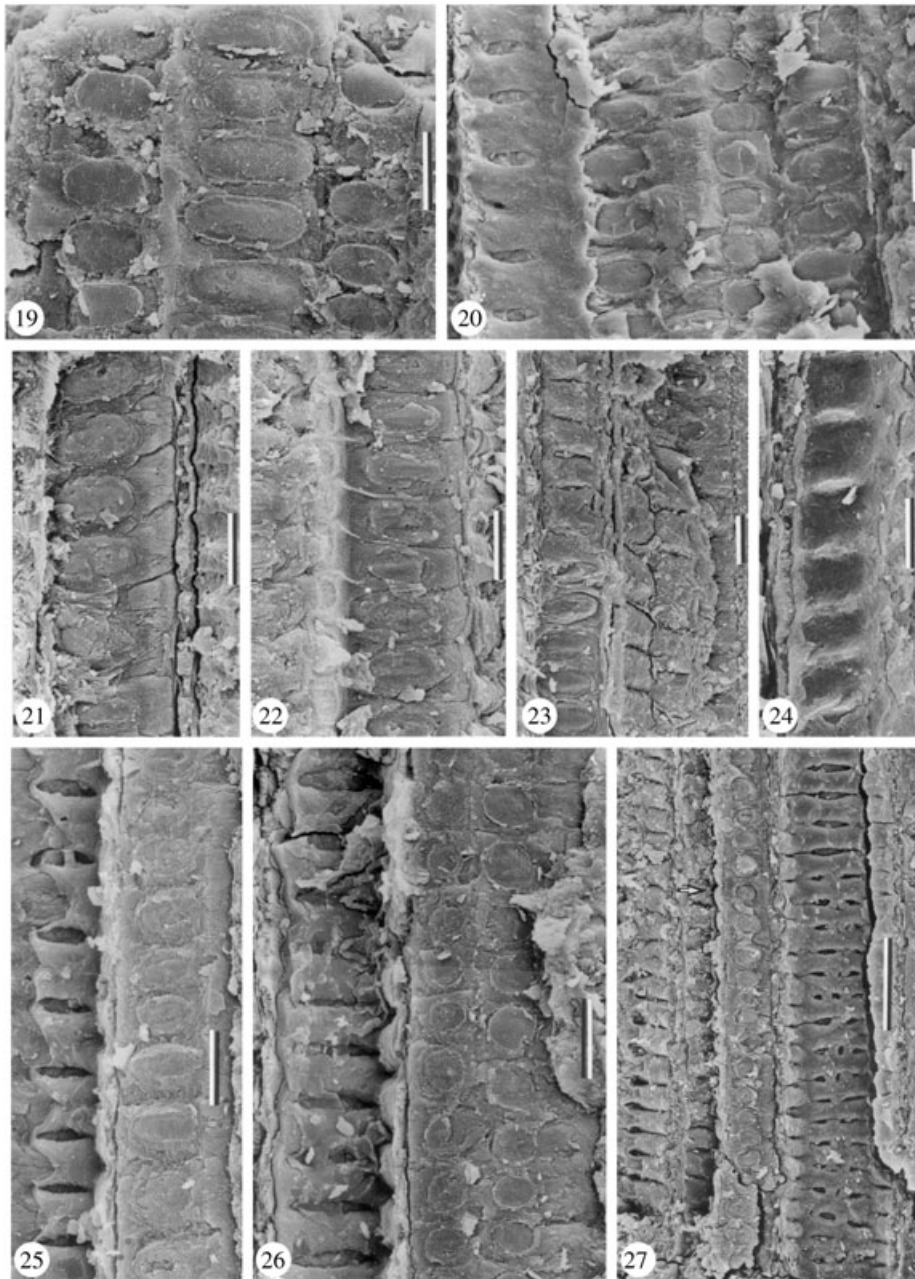
(Fig. 13) although proximity may be accentuated by crystal overgrowths (Fig. 11). The central areas of thickenings may be empty, occupied by loose aggregations of crystals, or solid (Fig. 11). More widely separated thickenings reveal irregularly distributed circular areas in the intervening wall (Figs 6–8, 10). These are interpreted as simple pits, 0.7–3.2 μm in diameter ('pitlets' *sensu* Schweitzer & Heumann, 1993) in a secondary wall, which is considered fused to the continuous primary wall. Much smaller irregular depressions present on all inner surfaces were probably produced by dislodged crystals (Figs 7, 8). This type of tracheidal thickening falls into the G-type of Kenrick & Edwards (1988).

The permineralized strand in the lateral branch (arrowed *z* in Fig. 3) is *c.* 1–2 mm wide, occupying about 30% of the branch diameter (*c.* 4 mm). Precise measurements are difficult to make. Longitudinally fractured tracheids (Figs 14–18), lacking tapering or ends and > 1000 μm long, are split along the planes explained in Figure 5. Rare examples along the position of the middle lamella (plane *a*) show an imperforate outer limiting layer, interpreted as the limit of the original primary wall (Fig. 17). Separation of the lumen cast (Fig. 5; plane *c*) reveals the very smooth innermost surface of the secondary wall of the tracheid (Figs 20, 24) with vertical rows of usually horizontal (Figs 14, 27, 31) but sometimes tilted slits (Fig. 32) or ellipses (Figs 25, 31) interpreted as pit apertures (possibly slightly occluded by overgrowths). Apertures are also preserved as horizontally elongate projections on lumen casts (Figs 16, 17, 24, 29, 30). They are almost as long as the maximum diameter of the pit-closing membrane. The ratio of the area of the latter to that of the pit aperture is *c.* 4 : 1, these measurements being based on specimens in which vertically adjacent pits on the same tracheid are fractured in planes *b* and *c* (as in Figs 14, 23, 32). Periclinal longitudinal fractures (Fig. 5; plane *b*) reveal the shapes of the pit-closing membranes. These are circular (Figs 26, 33) to oval (Figs 19, 20, 28, 29) to horizontally

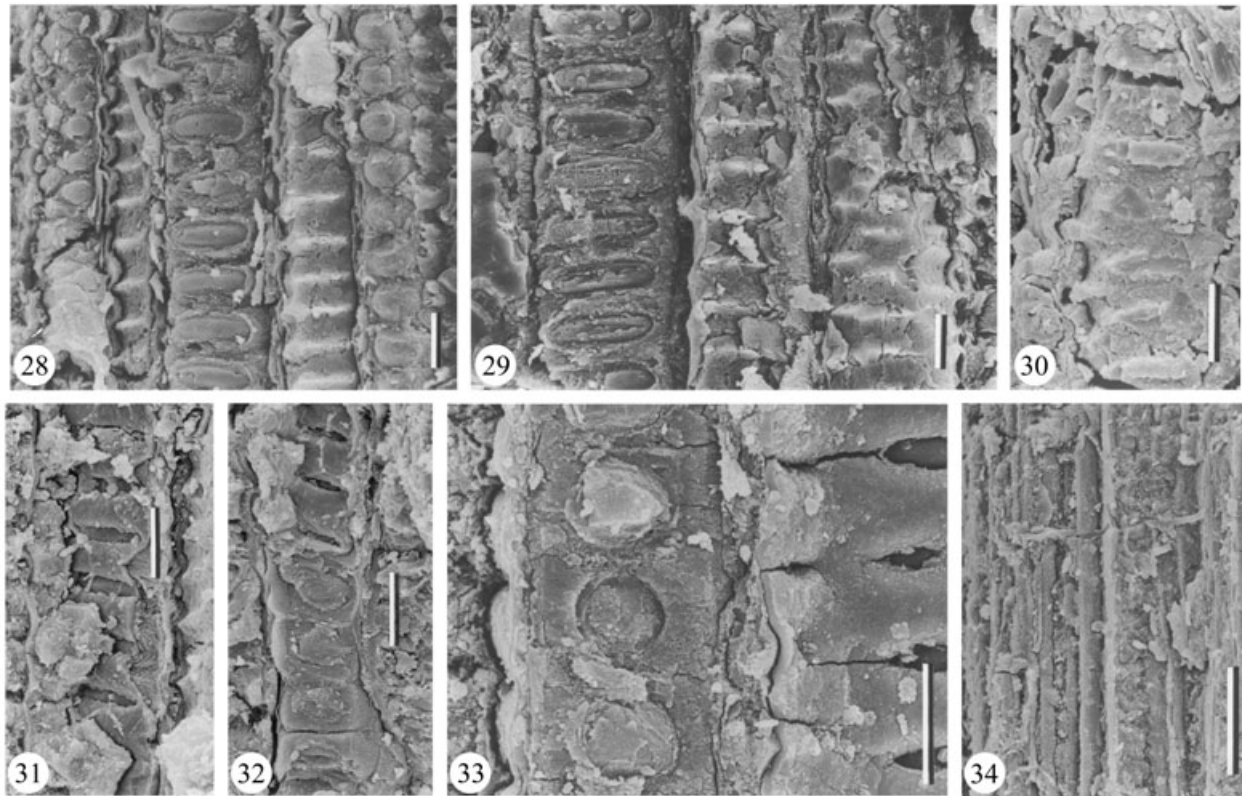
elongate, i.e. scalariform (Figs 15, 16), closely spaced in vertical rows and, being smaller in area than the apertures, the pits are interpreted as bordered. Their cavities are considered shallow, but are very rarely seen in anticlinal longitudinal section. It is quite difficult to determine limits of tracheid facets (Fig. 27). Most fractures appear to show one facet with uniseriate pitting. In very rare examples of oval biseriate pits they are opposite (see Fig. 27 for a surface view). Circular bordered pits are occasionally slightly alternate (Fig. 28). In uniseriate pitting there may be a considerable area of secondary wall between the vertical rows of more closely spaced pit-closing membranes (Figs 20, 22, 33). Pit apertures are uninterrupted, except that in extreme scalariform examples an isolated vertical? strand is sometimes observed (Fig. 15). Very rare examples of tracheids show reticulate pitting (Fig. 28). Pitting is uniform within a single tracheid.

IDENTIFICATION OF SPECIMEN AND SYSTEMATIC SIGNIFICANCE OF TRACHEID TYPES

Halle (1916) placed this specimen in *Psilophyton princeps* var. *ornatum* [now *Sawdonia ornata* (Hueber, 1971)] on the basis of spine morphology and branching, with superficial similarities in xylem structure. In a subsequent investigation, Schweitzer & Heumann (1993) reaffirmed this, and in new collections from Rörägen, added to the evidence for identity as *S. ornata* with the discovery of G-type tracheids and scattered lateral sporangia (see Rayner, 1983; Hueber, 1992). However, the assemblage contains a number of sterile spiny axis types which may not be conspecific. Unequivocal identification of the zosterophyll, *S. ornata*, requires the demonstration of the highly distinctive epidermal cell arrangement and spine construction (Edwards, 1924; Lang, 1932). This has not been found in the Norwegian material, further leaving its identity questionable. In addition, variation in



Figures 19–27. Longitudinally fractured tracheids of lateral branch. Scale bars = 10 μm . Fig. 19. Variation in pit-closing membrane shape in adjacent tracheids. Extremely smooth nature indicates that these are the exposed surfaces of the membranes. Note consistency in shape within an individual tracheid. Fig. 20. Pits with surrounding secondary wall preserved to varying extent. Tracheid on left shows pit apertures – note flattening and smooth surface of the wall lining the lumen. Fig. 21. Secondary wall and compound middle lamella longitudinally fractured; uniseriate pitting. Intervening area with ?stress cracks (note strands in a similar position in Fig. 22), in addition to depressions. Fig. 22. Note considerable areas of secondary wall between rows of pits. See also Fig. 21. Fig. 23. Tracheid on left fractured at different levels (allowing determination of ratio of pit-closing membrane to pit aperture); disordered material on right represents remains of secondary wall and compound middle lamella. Fig. 24. Single facet of lumen cast with protruding casts of pit apertures. Fig. 25. Tracheid on left with lens-shaped apertures and collapsed wall between. Tracheid on right with traces of casts of pit cavity and outlines of pit-closing membranes. Fig. 26. Tracheid on left with extended apertures. Tracheid on right with two rows of circular bordered pits. Fig. 27. Majority of tracheids showing internal surface; note at least two rows of slit-like apertures on right, with some indication of a further incomplete facet (see enlarged area in Fig. 33). Arrowed tracheid is unusual in that it shows variation in height of pit aperture. Scale bar = 30 μm .



Figures 28–34. Longitudinally fractured tracheids of lateral branch. Scale bars = 10 µm, except in Fig. 34. Fig. 28. Tracheids with range of types of pitting and planes of fracture. Note reticulate pitting on left. Fig. 29. Example of scalariform bordered pitting on left; pith casts on right. Fig. 30. Lumen cast with secondary wall disorganized. Fig. 31. Inner surface of tracheid with quite extensive pit apertures. Unfortunately, fracture of wall longitudinally is uninformative. Fig. 32. Tracheid fractured at two levels showing oval pit-closing membranes below and tilted pit apertures above, allowing calculation of relative areas of pit apertures and pit-closing membranes. Note considerable areas of secondary wall not pitted. Fig. 33. Part of Fig. 27 enlarged to show tracheid with single row of circular bordered pits with remnants of pit cavity casts and walls longitudinally fractured. Note thickness of secondary wall forming the border on right-hand tracheid and ends of apertures. Fig. 34. Section through boundary of xylem showing cells lacking secondary thickenings (?phloem). Scale bar = 30 µm.

tracheid type in different orders of branching has not been seen in the material from the type locality (Hueber, 1971) nor in the intensively studied Scottish material (Rayner, 1983). However, it should be emphasized that the xylem anatomy of *Sawdonia* has not received as much attention as that of other zosterophylls (e.g. *Gosslingia*: Kenrick & Edwards, 1988; *Deheubarthia*: Edwards, Kenrick & Carluccio, 1989). In such investigations, G-type tracheids were found in at least two levels of branching and appear to be the only type present. A possible exception is in *Koniora andrychoviensis* (Emsian of Poland) assigned to the zosterophylls on the basis of its lateral sporangia, which are attached singly to spiny axes just below a dichotomy, and on its exarch (elliptical in transection) xylem strand (Zdebska, 1982). Illustrations of polished longitudinal sections of xylem look remarkably similar to those of xylem in *Gosslingia* (see com-

ments on possible G-type status in Kenrick & Edwards, 1988), but macerations of a small spiny axis of unspecified position on the plant yielded tracheids with up to two rows of circular bordered pits (Zdebska, 1982: plate 28, figs 5, 6). Zdebska had observed pits on longitudinally fractured permineralizations but they could not be detected on polished surfaces. These Polish specimens were very fragmentary because they were recovered from bore-hole cores, but were united in their possession of spines of varying size. Their xylem requires re-investigation, but such limited evidence suggests that this is a second taxon with a similar combination of tracheid types. G-type tracheids associated with those with vertical rows of simple circular pits have been noted in *Hsüa robusta* (Li, 1992), although a second species *H. deflexa* again from the Lower Devonian of China has G-type tracheids in which minute pits also cover the secondary thicken-

ings (Wang, Hao & Wang, 2003). These plants present combinations of characters formed in a number of lineages, a character shared with *Adoketophyton verticillatum*, which exclusively possesses more conventional G-type tracheids (Li & Edwards, 1992; Hao, Wang & Beck, 2003). For a summary of the distribution of the latter see Wang *et al.* (2003).

Had the lateral axis with bordered pitted tracheids been found in isolation, it would not have been assigned to the zosterophylls, nor indeed to the two remaining well-defined clades of early vascular plants. These comprise the rhyniophytes, characterized by S-type tracheids (preserved areas of primary wall and helical secondary thickenings have a spongy texture and the lumen is completely lined by a thin layer with plasmodesmata-sized perforations: Kenrick, Remy & Crane, 1991), and the trimerophytes, where there is very limited evidence (based mainly on *Psilophyton dawsonii*) of P-type tracheids in which bordered scalariform pits have apertures traversed by a reticulum of strands (Hartman & Banks, 1980). Bordered scalariform and circular pits with simple apertures have been recorded in the early true lycophyte, *Leclercqia* (Grierson, 1976), in contrast to other coeval lycophytes such as the middle Devonian *Minarodendron* (Li, 1990), in which the pit aperture is traversed by strands reminiscent of the Williamson striations that characterize the lepidodendrids, the earliest example of which is the Upper Devonian *Leptophloeum rhombicum* (Geng, 1990).

Scalariform and, less frequently, circular bordered pits characterize the metaxylem of the Cladoxylopsida (basal Euphyllrophytina). For the Iridopteridales, one of the most detailed accounts is based on the Eifelian *Arachnoxylon minor*, in which pit-closing membranes show a range of elliptical to elongate shapes, borders are large, and both scalariform and circular bordered pits occur in the same tracheid (Stein, Wight & Beck, 1983). In (?Mid to Upper Devonian) *Compsocradus laevigatus* individual facets are occupied by a single row of pits, with much larger apertures and cavities than described here (Berry & Stein, 2000). Scalariform and circular bordered pits also occur in the Middle Devonian *Protopteridophyton* (Li & Hsü, 1987), *Metacladophyton* (Wang & Geng, 1997) and *Ibyka amphikoma* (Skog & Banks, 1973). In the Cladoxylales, the metaxylem of *Pseudosporochnus* is best known (Stein & Hueber, 1989), with reticulate or close-set elliptical bordered pits and occasional circular ones.

There is little detailed information on the metaxylem of the progymnosperms, but in the secondary xylem circular bordered pits predominate and often are so closely packed that they are hexagonal in outline. Pit apertures are slits and inclined. In *Rellimia*, an example of the Aneurophytales, pits occur on all facets (*Araucaria*-type: Dannenhoffer & Bonamo,

2003), but in *Archaeopteris* (Archaeopteridales) they are in bands on radial walls (Carluccio, Hueber & Banks, 1966). Rare examples of 1° xylem show metaxylem with reticulate to scalariform pitting (Carluccio *et al.*, 1966).

Kenrick & Crane (1997), in an analysis of character distribution in basal vascular plants, concluded that metaxylem pitting (although not specifically mentioning bordered pitting) evolved independently at least twice (Lycopsida and Euphyllrophytina). This Norwegian specimen, if indeed a member of a basal group in the Zosterophylloids, demonstrates the earliest appearance of this character in the lycophyte clade. *Hsüa robusta* (an Early Devonian plant in Hsüaceae, Li, 1982, 1992; Kenrick & Crane, 1997) possesses the metaxylem tracheids with annular thickening and one or two rows of simple pits (Li, 1992, fig. 3); the latter are not bordered.

BACKGROUND TO DISCUSSION

The anatomical information extracted from this single specimen, when related to the roles of xylem at the cellular level, offers tantalizing insights into the functioning of the tissue. But extremely frustrating is:

1. the lack of transverse sections of the strand that would provide information on the three-dimensional nature of the cells, particularly in the lateral branch, and
2. area of xylem, and hence
3. number of cells,
4. overall xylem shape,
5. nature of development (archy),
6. relationship to ground tissues and phloem (Fig. 35),
7. lack of information on overlap/ends of tracheids.

Affinity with *Sawdonia* suggests an exarch strand, elliptical in cross-section, and the presence of a stereome, a characteristic of many plants preserved in the clastic rocks of the Old Red Sandstone Continent. Coalified fossils such as these, even when permineralized in pyrite, lack evidence of parenchyma and hence assimilatory tissue and phloem. However, these are preserved in the slightly older silicified Rhynie Chert plants, and axial examples show:

1. that photosynthesis may have taken place in relatively deep-seated areas below a sometimes multi-layered hypodermis;
2. an area around the xylem of thin-walled cells lacking intercellular spaces interpreted as phloem;
3. no endodermis;
4. where exarch, the absence of a clear ring of protoxylem;
5. anatomical adaptations associated with stomata and the low frequency of stomata suggestive of high water-use efficiency (Edwards, 1993)

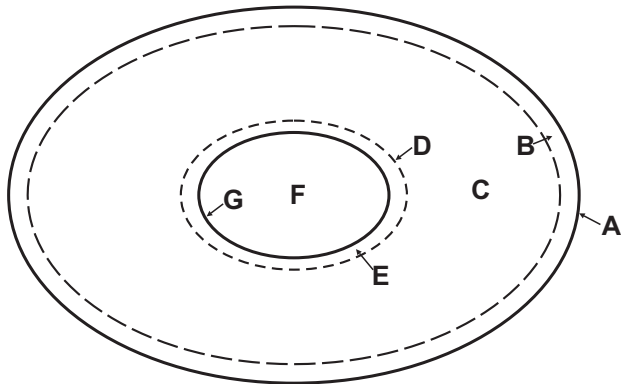


Figure 35. Putative reconstruction of a section through the specimen (main stem): A, epidermis with slightly sunken stomata; B, stereome (extent unknown, but always present in another species, *Goslingia breconensis*, which has been more extensively studied anatomically); C, cortex with intercellular spaces, outer zone with chloroplasts; D, limit of stele; E, area of phloem lacking intercellular spaces; F, elliptical strand of metaxylem; shape not the product of compression; may occupy less area in the lateral branch; G, disjunct areas of protoxylem, whose cells may have broken down during maturation, resulting in columns of water.

Possible identity with *Sawdonia ornata* would again point to adaptation to water stress (Hotton *et al.*, 2001) in that the stomata are slightly sunken, their frequencies low (McElwain & Chaloner, 1995) and the cuticle thick (Chaloner, Hill & Rogerson, 1978). However, Edwards, Abbott & Raven (1996) point out that cuticle thickness correlates poorly with resistance to water loss from extant plants, the main resistance being in the unpreserved epicuticular wax.

Synthesis of these data sources allows the hypothetical reconstruction of a cross-section through a stem (Fig. 35).

DISCUSSION

OVERALL WATER RELATIONS

According to Roth-Nebelsick & Konrad (2003) in Rhynie Chert plants, photosynthetic and, in particular, transpiration rates were very much lower than in mesophytic leaves, but water-use efficiency values were considerably higher than in extant plants, possibly facilitated by the higher (~12 times extant) atmospheric CO₂ concentrations. In attempting to interpret the functioning of xylem in Lower Devonian vascular plants such as *Sawdonia ornata* we must turn to work on the most anatomically similar extant plants. There are relevant data from extant pteridophytes on the relationship of xylem hydraulic conductance to the conductance of photosynthetic tissue to water vapour, and on the vulnerability of the xylem tissue to hydraulic failure, i.e. embolism and cavitation.

Work on extant ferns, including the leafless *Psilotum nudum*, as a morphological analogue of *Sawdonia ornata* suggests that xylem conductance varies among species with the potential for transpiratory water so as to maintain a relatively constant water potential gradient among species (Woodhouse & Nobel, 1982; Nobel, Calkin & Gibson, 1984; Calkin, Gibson & Nobel, 1985, 1986; Schulte, Gibson & Nobel, 1987; Schulte & Gibson, 1988). This could be construed as consistent with the optimality principle in evolution (Rosen, 1967), with the corollary that the xylem hydraulic conductance of Lower Devonian plants would be lower in parallel with their lower water vapour conductance to water vapour of their photosynthetic tissue in the high-CO₂ atmosphere. This tenuous line of argument would suggest similar water potential gradients in the xylem of Lower Devonian vascular plants to those in extant pteridophytes.

Brodribb & Holbrook (2004) examined four species of pteridophytes (including the lycophyte *Selaginella palescens*) and four species of co-occurring angiosperms in Costa Rica for the leaf water potential at which the xylem hydraulic conductance was halved. They found a similar interspecific range of leaf water potentials in pteridophytes (~-1.3 to ~-2.5 MPa) as in angiosperms (~-1.5 to ~-2.2 MPa). This suggests similar water potential dependence of the induction of xylem embolism/cavitation in the two structurally different kinds of xylem. However, Brodribb & Holbrook (2004) also showed that the leaf water potential for stomatal closure was lower for the angiosperms than for the pteridophytes. They concluded that the angiosperms have a smaller safety margin than do pteridophytes, i.e. the leaf water potential for stomatal closure is much closer to the value at which 50% of xylem conductance is lost in flowering plants than in pteridophytes. If this greater pre-emptive role of stomata in pteridophytes in relation to restricting xylem dysfunction also occurred in the Lower Devonian it is possible that the xylem of these early vascular plants was to some extent protected from embolism and cavitation. As far as embolism is concerned, the early vascular plants could have been more vulnerable at a given xylem water potential in the absence of an endodermis (Edwards, 1993), restricting the possibility of an air-water interface moving under pressure from gas spaces in the cortex into the xylem. Brodribb & Holbrook (2004) comment that it is typically the below-ground parts of vascular plants that are most prone to xylem dysfunction; however, the lowest xylem water potentials occur close to transpirational termini.

In addition to these more 'whole-plant' settings, we are aware that detailed quantitative comparisons of water transport through tracheids of extant plants – a combination of modelling and experimentation –

require measurements unavailable to us. To those mentioned earlier must be added detailed measurements of individual pits, including dimensions of the pit cavity, and sizes of micropores in the pit-closing membranes that will influence both their mechanical and their permeability functions. For the latter, acquisition of such detail is perhaps unwarranted as data have rarely been obtained even for extant plants. Despite all these limitations, the variation in tracheidal architecture and, less convincingly, tracheid diameter we have observed between the main and lateral branch seems to us to demand explanation in terms of functioning, even if this self-indulgence approximates to yet another example of Harper's 'facile adaptationist guesswork' (Harper, 1982).

Many authors have commented on the antagonistic demands of tracheid wall construction relating to water movement, namely the need for reduction of resistances to longitudinal and a requirement for lateral (i.e. loading and unloading) water transport. The former may be achieved by reduced secondary wall, maximum pit areas and elimination of pit-closing membranes, and the latter by increased lignified secondary walls and reduction in pitting (e.g. Bailey, 1953; Zimmermann, 1983; Carlquist, 1988; and most recently Sperry & Hacke, 2004). Indeed, the various 'designs' of pitting in secondary walls often seem to present an ideal compromise between these conflicting roles and have generated a number of papers based on modelling or experimentation on quantitative aspects (Petty, 1972; Calkin *et al.*, 1986; Lancashire & Ennos, 2002; Hacke, Sperry & Pittermann, 2004; Sperry & Hacke, 2004). Sperry & Hacke (2004) emphasized a third function, that of containment of embolisms, this associated with reduction in size and porosity of pit-closing membranes.

XYLEM IN MAIN BRANCH

G-type tracheids, found throughout the strand, have annular thickenings interpreted as composed of a cellulose framework and with lignification only towards the outside or extending throughout. In contrast to a typical protoxylem element, where an imperforate cellulose primary wall connects the rings, here a further interrupted wall containing a recalcitrant polymer (probably lignin) is present between thickenings (Kenrick & Edwards, 1988). The interconnecting wall is thus interpreted as simply pitted, although, until the present study, pit-closing membranes had never been demonstrated (Edwards, 2000). Pits are of variable size (\pm consistent in a tracheid) with random distribution such that they are only occasionally coincident between adjacent cells. Many are thus blind-ending (and indeed even useless in lateral water and solute movement if the intervening 2° wall is lignified), but

increased density and area of pits would increase lateral water movement. In addition, polished longitudinal sections of other taxa (e.g. *Gosslingia*) indicate that adjacent annular thickenings may coincide but only occasionally, further restricting lateral movement. Thus, although total area of pitting exposed to the lumen of a G-type tracheid would be greater than that of pit apertures in bordered pitting, the area for lateral movement within the tracheid may have been more limited. Very little evidence from Rhynie Chert plants indicates that similar pitting occurred throughout the tracheid and length of overlap was not extensive.

The annular secondary thickenings are more close set here than in many other taxa, giving a corrugated appearance to the inside of the cell with little intervening wall area. Annular thickenings as in protoxylem are usually considered least 'structurally sound' but capable of elasticity in intervening wall (i.e. stretching at expense of rigidity), but here their frequency, together with the vertical thickenings, would seem to impose mechanical strength plus resistance to implosion. The relatively small, often non-coincident, pits would prohibit the spread of embolism, but would be extremely inefficient in lateral transport of water. Vertical movement within an individual tracheid would be enhanced, compared with lateral branches, because of larger tracheid diameters, even when cross-sectional area between thickenings is used in calculations (Jeje & Zimmermann, 1979). The values of the fossil tracheid diameter in Table 2 are inclusive of secondary thickenings. The close setting of the thickenings, resulting in reduced eddies, may also minimize resistance to flow in tracheids of this type. Jeje & Zimmermann (1979) showed that the relevant parameter for calculations on flow through a vessel with helical and annular thickenings is the radial distance between thickenings. Their experimental work on isolated metaxylem and protoxylem vessels of *Plantago* indicated that resistance to flow is lowest for elements where the distance between the uniform

Table 2. Data relevant to resistance to flow in a single element; parameters based on Jeje & Zimmermann (1979)

	<i>Plantago</i>	Fossil	
		Single tracheid	Aggregated data
$\delta/(\delta + \epsilon)$	0.45	0.48	0.34
t/D	0.19	0.11	0.105
δ (μm)	2.3	4.8	4.34

δ , secondary wall longitudinal dimension; t , secondary wall radial dimension; ϵ , distance between thickenings; D , radial distance between thickenings, i.e. effective lumen diameter.

thickenings is of a similar magnitude to that of their (small) longitudinal width, and despite the thickenings (t/D in Table 2) protruding significantly (almost 20% of the lumen diameter) into the lumen. Such features create a cylindrical conduit with minimum interference from eddies. Jeje & Zimmermann (1979) found that longitudinal flow encountered the least frictional resistance in a single protoxylem vessel of *Plantago* when values for certain parameters were as in Table 2.

Jeje and Zimmermann's data for a number of categories of vessels show that, when t/D and $\delta/(\delta + \epsilon)$ (see definitions in Table 2) decrease and ring space increases, resistance to longitudinal water flow increases. Our data on metaxylem tracheids would seem to indicate a greater resistance to flow resulting from the secondary thickenings than in the extant plant's protoxylem vessels. However, even the lowest frictional resistance measured by Jeje & Zimmermann (1979) for *Plantago* vessels was significantly higher than that for an ideal non-porous, smooth-walled capillary (their fig. 4).

Resistances to longitudinal movement cannot be evaluated in the absence of information on tracheid length and overlap, although our failure to observe ends points to long tracheids and maximization of increase in tracheid diameter demands an increase in length in overcoming resistances of end walls (e.g. Comstock & Sperry, 2000; Hacke *et al.*, 2004). Indeed, should the overlapping ends of the tracheids have similar G-type pitting as seen in some Rhynie Chert examples, there would be major resistance to longitudinal/axial flow in these areas. Conductance itself would be enhanced by the increased number of tracheids in the larger strand (see McCulloh, Sperry & Adler, 2003).

Lateral delivery of water from peripheral tracheids to presumed assimilating regions and proximal transpiring surfaces would encounter major resistance, bearing in mind the small pits in the lateral walls of the tracheids. Previous analyses of this pathway of water movement have considered only the part of the pathway distal to the walls of the xylem conducting elements (Raven, 1994a, b). By the same token, risks of embolism may have been reduced, although we know nothing of the physical properties of the pit-closing membranes. Lateral transport from longitudinal water columns would be facilitated if water was moving in the cavities left by disintegration of protoxylem, e.g. the carinal canals of *Equisetum* spp. However, Raven (1977) points out that although conduction of water in such canals has been demonstrated, water under tension in such conduits would be poorly protected from implosion. Furthermore, such conduits would not be well protected from embolism, although the presence of endodermis both centripetal and centrifugal to the ring of vascular bundles in the stems of

Equisetum spp. would help to restrict gas seeding from intercellular gas spaces in the centripetal and centrifugal parenchyma. The centrifugal endodermis would also constrain and regulate radial water flows from the vascular bundle to the transpiratory surfaces.

XYLEM IN LATERAL BRANCHES

Pitting in the lateral walls ranges from simple (i.e. non-bordered) reticulate (rare) to scalariform (oval to elongate) and circular bordered. In this case the area of pit-closing membrane per unit area of tracheid wall is greatly enhanced compared with the main axis, thus creating less resistance to vertical and lateral flow. Again tracheid length and overlap are unknown. However, the estimated tracheid diameter is less than in the main axis, so that the rate of flow of water in a conduit in the branch is less than that in the main axis. This follows from the Hagen–Poiseuille equation based on ideal capillaries and circular cross-sections, which shows that the volume flow rate ($\text{m}^3 \text{s}^{-1}$) through a cylindrical conduit under a given pressure gradient is directly proportional to the fourth power of the diameter of the conduit, all other things being equal.

The smaller diameter of tracheids in the branch agrees with the changes in tracheid diameter noted by Gibson, Calkin & Nobel (1984) in the rachis of *Cyrtomium falcatum*, with smaller-diameter tracheids occurring most distally and related by the authors to reduced conductance at the 'drop of pressure'. More generally, McCulloh *et al.* (2003) showed that the xylem of a number of species of angiosperm obeyed Murray's law, provided that the xylem functioned much more in conduction than in mechanical support. Murray's law (Murray, 1926) predicts the optimal taper in blood vessels in vertebrates in terms of an optimality model relating the spatial distribution of a fixed volume of conducting tissue to maximal hydraulic conductance. Here the diminishing diameter of individual conduits in increasingly distal branch ranks is more than offset, in terms of total conduit area in each branch rank, by the increasing total number of conduits in successive branch ranks. Although the observed smaller tracheid diameter in the branch relative to the main axis agrees with Murray's law, we do not have information on the sum of conduit numbers in all of the branches of a given rank to test further the fit with Murray's law. This specimen shows early (geologically speaking) development of sophisticated pitting in plants of relatively short stature, pitting which is ubiquitous today. Considering simple pits, a parallel-sided channel through the secondary wall is limited by a pit-closing membrane of the same size as the channel, such that the wider the pit, and hence the greater the flow of water, the weaker the

conduit as secondary wall is replaced. In bordered pits the secondary wall is reinforced by extensions of the secondary wall (imposing greater mechanical strength) and the pit-closing membrane can thus be much larger. The optimum structure would be a wide pit-closing membrane through which the rate of flow of water would be the same as that through the much narrower aperture to the pit chamber, and where maximum membrane area is exposed without weakening the wall. Circular bordered pits are considered to be most effective in this, particularly when alternately and compactly arranged (Mauseth, 1988). Most authors comment on the rare occurrence of circular bordered pits in extant pteridophytes (but see Bierhorst, 1960). However, surveys of Devonian tracheids (including this specimen) indicate widespread occurrence of circular borders in all basal lineages of free-sporing plants. All borders, although increasing mechanical strength clearly decrease resistance to conductance. Modelling and experimentation have indicated that their removal shows similar values in increased conductance (e.g. by 66% in scalariform pitting: Calkin *et al.*, 1986; 72% in circular bordered pits: Lancashire & Ennos, 2002). Calkin *et al.* had calculated that for certain diameters of tracheids hydraulic conductances per unit length derived from the Hagen–Poiseuille equation were overestimates of actual conductance, and that in the fairly uniform scalariform pits of *Pteris*, removal of membranes with cellulase increased actual conductance by 62%. In larger diameter tracheids numbers of pits remained the same, but their size has been related to ‘containment’ of embolism under the water stress experienced by the laterals. This was based on comparisons with extant plants showing similar anatomy (Niklas & Banks, 1985). However, pit membranes contributed more to increased resistivity as lumen diameter increased (see also Schulte *et al.*, 1987) for scalariform pitting in *Psilotum nudum*. In scalariform bordered tracheids of certain seed plants, a linear relationship between conductance and lumen diameter was demonstrated.

Where tracheids had large circular bordered pits, conductance decreased with increasing diameter. This suggests that there was an optimum size for tracheid lumina which actually falls into the top of the range reported in zosterophylls where the largest diameters are seen in the G-type tracheids. Niklas (1984) had noted that this had been achieved by the Middle Devonian in zosterophylls and some lycopods and there was no further increase with decreasing geological age.

Considering embolism in tracheids, the likelihood of its occurrence would seem greatest in the tips of the lateral branches, with the lowest water potentials closest to actively transpiring surfaces, and this is where pit-closing membranes are extensive in the fossil. Given the seasonal climate of the Old Red Sand-

stone continent, it is envisaged that there would have been extended periods of water stress, a phenomenon compounded by the possibly ephemerally wet nature of the habitat (Hotton *et al.*, 2001). We know nothing of properties of fossil pit-closing membranes but from their extent it would seem that these tracheids would have been vulnerable to embolism. As we have indicated above, the absence of an endodermis in pre-Carboniferous plants could make the xylem more vulnerable to air-seeding at a given xylem water potential than is the case for plants with an endodermis. Tori have not been recorded. However, the pits would have facilitated rapid lateral delivery of water to transpiring, photosynthesizing regions, which might have relied more on turgor for support and metabolism than the main axis, thus ‘prioritizing’ the conduction role against structural and safety roles. With regard to the latter, we have not seen the xylem constrictions present in *Psilophyton dawsonii* at the bases of lateral branches. These have been postulated as an adaptation to restrict embolisms to lateral branches and hence to protect the main conducting channels (Niklas & Banks, 1985). Earlier, Tomlinson (1983) in considering the supply of water to various branches of a tree had postulated that extremities (branches and leaves) wilted first under water stress as a consequence of hydraulic constrictions in vessels at the bases of branches. He further suggested that the evolution of overtopping from an isotomously branching system was the ‘first morphological manifestation of this simple physiological requirement’ (i.e. favouring the main axis against laterals as regards water supply – Tomlinson, 1983: 147). However, we note that comparison of the tendency for embolism in above-ground relative to below-ground xylem elements in extant plants shows that root xylem elements embolize more readily, and operate at water tensions closer to their cavitation threshold, than do stem elements (e.g. Sperry & Tyree, 1988; Sperry & Saliendra, 1994; McElrone *et al.*, 2004), despite the lower water potentials in stems than in roots. Of course, these data do not directly address the question of susceptibility to embolism of conduits near the transpiring surface in laterals relative to conduits in the main above-ground axis (Tomlinson, 1983).

To sum up, tracheids in the lateral branch are adapted for rapid lateral water transfer at the expense of their structural role when compared with the main axis. However, although partial compensation on the mechanical side derives from bordered pitting and the areas of secondary wall between vertical rows of pits, the latter increasing resistance to conductance. The relative area of the lateral branch occupied by xylem was more or less the same as in the proximal parts of the main axis (half the actual width), but the total number of tracheids would probably be lower even

when their smaller axial diameter is taken into account. Thus, smaller numbers and diameters of tracheids will also reduce volume and rate of water movement.

CONCLUSIONS

This specimen has shown that early in the evolution of vascular plants, tracheids had acquired some structural sophistication, e.g. via bordered pits, and were close to achieving maximum diameter for efficiency of conduction (Niklas, 1984). Furthermore, differing optimization of the three major roles of tracheids (conductivity, mechanical strength, safety) can be related to different pressures in different parts of the plant, and Bailey's contention in 1953 (p. 5) that tracheary modifications do not occur at an equal evolutionary rate throughout the xylem of the entire plant holds for early vascular plants, although his comment related to secondary xylem. And finally, from a developmental view point, if we suppose that growth was similar to that of axial plants in the Rhynie Chert, a large multicellular apical member would have divided asymmetrically producing a main and a lateral branch. Differentiation of the resulting two procambial strands would then have proceeded in two entirely different ways, the main axis continuing as before, but the lateral showing synchronized development between adjacent tracheids such that the large pits with arching borders were perfectly coincident. Although detailed descriptions of the xylem here are based on anatomy below the branching off of the lateral, above the latter, G-type tracheids have also been observed in the main axis.

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