

Xylem in early tracheophytes

D. EDWARDS

Department of Earth Sciences, Cardiff University, PO Box 914, Cardiff CF10 3YE, UK

ABSTRACT

The architecture of the presumed water-conducting cells of the major lineages of early tracheophytes recorded in Silurian and Devonian rocks is reviewed, together with descriptions of further diverse types whose derivation remains uncertain. Evidence has been obtained from a wide gamut of fossils including coalified compressions, silicified, pyritized and calcium carbonate permineralizations. Most of the cells, only a few having been unequivocally demonstrated to be tracheidal, have walls with two layers, the inner sometimes broadly similar to annular, spiral and scalariform secondary thickenings of extant xylem. There are, however, very few cases of identical construction and the fossil representatives show greater complexity and variety. Their walls are presumed to have been lignified, but the polymer has not yet been directly identified in the fossils. The implications of these wall architectures on the functioning of the cells in water conduction are briefly considered, as is their relevance to hypotheses on inter-relationships of early tracheophytes and on tracheid ontogeny.

Key-words: Devonian; Euphyllophytina; lignin; Lycophytina; permineralizations; pitting; plasmodesmata; protosteles; Rhynie Chert; Silurian; tracheids.

INTRODUCTION

‘... so prodigiously curious are the contrivances, pipes, or sluces by which the *succus nutritius*, or Juice of a Vegetable is convey’d from place to place’. Thus wrote Robert Hooke (1665; *Observ.* XVI, p. 101), when using his newly invented microscope he compared the secondary xylem of plants such as ‘*Cocus*’, ‘ebony’ and ‘*lignum vitae*’ with that in Recent charcoal (‘a Vegetable burnt black’). Later in his *Micrographia* (1665; *Observ.* XVII, p. 107) he extended his observations to ‘Petrify’d wood’ and noted that ‘though they [his pores – our vessels] were a little bigger, yet they did keep the exact figure and order of the pores of Coals [his charcoal] and rotten Wood, which last also were much of the same size.’ And so began comparative wood anatomy, a subject which remains of major palaeobotanical significance today not only in biodiversity and phylogenetic studies, but also to the evolution of plant physiology and via dendrology, to palaeoecology, dating and even climate change.

Correspondence: D. Edwards. Fax: +44(0)2920 8742326; e-mail: EdwardsD2@cardiff.ac.uk

For researchers on early land plants in the Silurian and basal Devonian, a major preoccupation has been the necessity to demonstrate the presence of tracheary elements in fossils of morphologically simple plants with no extant representatives as unequivocal evidence of their tracheophyte status (Lang 1937; Gray & Boucot 1977; Edwards, Bassett & Rogerson 1979; Niklas & Smocovitis 1983; Edwards, Davies & Axe 1992). In classical research this verification was more or less confined to the demonstration of elongate cells with regular transverse banding which were then described as spiral or annular tracheids (Dawson 1859; Kidston & Lang 1917; Lang 1927) and consequently appeared to highlight the extremely conservative nature of tracheary architecture in their apparent similarities to extant examples. More recent anatomical studies, particularly those using scanning electron microscopy (SEM) have provided far more detailed three-dimensional information that, in its complexity and diversity, has demonstrated the utility of tracheid construction in differentiating major lineages of early tracheophytes (e.g. Kenrick & Crane 1991, 1997). Xylem has also figured strongly as part of the suite of characters associated with homoiohydry in palaeophysiological studies centring on the ‘conquest of the land’ (e.g. Raven 1977, 1993, 1994a).

In this review I bring together data on xylem architecture in Silurian and Lower Devonian plants as a database for systematic, evolutionary and functional anatomical studies. More general information relating to pertinent fossils is given in Fig. 1, which also includes ranges of other homoiohydric features and the early history of land plants based on spores.

SOURCES AND ACQUISITION OF ANATOMICAL DATA: WHY DOES TYPE OF PRESERVATION MATTER?

Coalified compressions, small, three-dimensionally preserved, coalified fossils (mesofossils) and permineralizations, in which the most important minerals are calcium carbonate, silica and iron compounds (particularly pyrite), are the major sources of information on the xylem of early land plants.

Coalified fossils

Compressions (Figs 2a & 3l)

In the vast majority, all the original tissues have been converted during diagenesis, involving high temperatures and

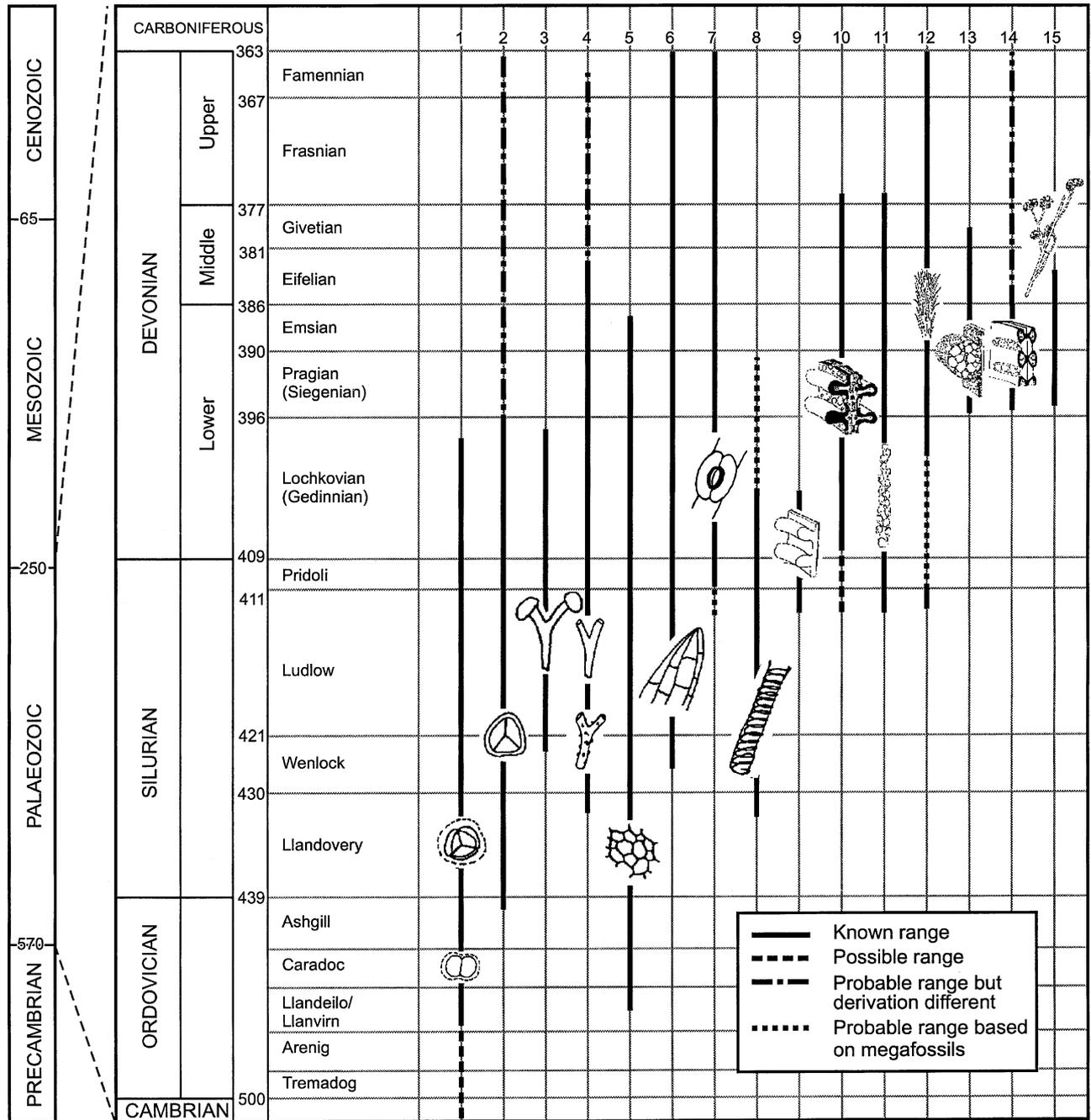


Figure 1. Stratigraphic ranges of microfossils, megafossils and anatomical features mentioned in the text. (1) Dyads and tetrads (cryptospores) believed to derive from bryophytes. (2) Single spores with trilete marks. *Ambitisporites* = spore from *Cooksonia pertoni*. (3) *Cooksonia* megafossils. (4) Bifurcating axes, possibly from tracheophytes. (5) Nematophyte⁺ cuticles. (6) Higher plant cuticles. (7) Stomata on axial fossils and lycophytes. (8) Banded tubes. (9) C-type tracheids. (10) G-type. (11) *Zosterophyllopsida**. (12) *Baragwanathia*, *Drepanophycus*, Lycopsida. (13) S-type. (14) P-type. (15) Trimerophytes**.

*Nematophytes: taxon erected by Lang (1937) to include terrestrial plants he considered neither algal nor higher plant. Includes microfossils (e.g. cuticles, meshes of small tubes, banded tubes) and *Prototaxites* recently reinterpreted as a fungus (Hueber 2001).

**Zosterophyllopsida*: an extinct group of leafless homosporous plants with isotomous, anisotomous and pseudomonopodial branching. Sporangia lateral either aggregated into strobili or distributed over axes. Sporangia split into two valves. Xylem mainly exarch. Tracheids: G-type. Closely allied (sister group) to the Lycopsida.

**Trimerophytes: small group of extinct leafless homosporous plants with similar branching to zosterophylls, but pseudomonopodial type more pronounced such that numerous elongate sporangia terminate much branched, distinct lateral systems. Xylem centrarch. Tracheid P-type. Most information from *Psilophyton*. Trimerophytes are early members of the sphenopsid/fern, seed-plant clade, termed the Euphyllophytina (see Kenrick & Crane 1997; Fig. 6).

pressures to a film of coal in which no cellular detail remains. A few examples show a central longitudinally running strip and even fewer, within the strand, longitudinally orientated elements with transverse banding indicative of tracheary thickenings. These may be removed on film pulls or isolated by oxidizing the amorphous coal with nitric acid, and examined by light microscopy. Pyrolysis of such coalified residues followed by gas chromatography–mass spectrometry (GC–MS) reveals some of the original chemistry of cell wall macromolecules. In the case of presumed lignin, the presence of alkyl phenols and benzenes confirms the aromatic nature of the original molecules, but because these compounds represent the building blocks of a multitude of plant polyphenols, they cannot be considered unequivocal evidence that lignin was originally present (Ewbank, Edwards & Abbott 1997).

Mesofossils (Figs 2b, c, g, k–m; q; 3g, j, k & 4a–c)

Mesofossils reveal the three-dimensional architecture of the central strand cells (Edwards 1996, 2000) and are ideally suited to SEM examination. They can also be embedded for transmission electron microscopy (TEM) (Edwards *et al.* 1992). In rare examples, cells are preserved throughout the axial fossils suggesting that even cellulose cell walls must have been preserved. In such examples, the simple dogma, that cells with lignified wall are preserved in fossils, others, except where cutinized, are not, is not tenable. Ongoing studies suggest that this type of preservation was a consequence of wild-fire.

Permineralizations

Silica (Fig. 2d, h, p, r; 3e, f & 4d–n)

The Lower Devonian Rhynie Chert silicifications, formed when siliceous water from hot springs permeated whole ecosystems with precipitation of silica within plant cells and voids, remain the best source of data involving all tissues. Cell walls persist as coalified residues, but lose their integrity when the silica is removed using hydrofluoric acid (HF). Chemical signatures from pyrolysis are very weak. Silicifications are best studied using light microscopy from ground sections or from successive film pulls of HF-etched surfaces. Interpretation of fractured surfaces via SEM is hampered by the microcrystalline structure of the silica combined with the paucity of organic residues.

Calcium carbonate (Figs 2f & 3h, i)

In contrast to those in the abundant concretions (coal balls) found in later Palaeozoic coals, plants preserved in calcium carbonate have been recorded at only one locality in the Lower Devonian (Gaspé: Emsian). The microenvironmental conditions that facilitated the development of the enclosing limey/clay concretions within a medium-grained sandstone are unknown. The plants preserved are sporangia and axes of the trimerophyte *Psilophyton dawsonii* (Banks, Leclercq & Hueber 1975), and have been studied from serial cellulose acetate peels, produced after etching

with hydrochloric acid. Tissues recovered on bulk maceration of the matrix show cellular integrity and xylem strands have been further embedded and sectioned for light microscopy or examined by SEM (Hartman & Banks 1980). These coalified residues show similar pyrograms to those from compressions (Edwards *et al.* 1997).

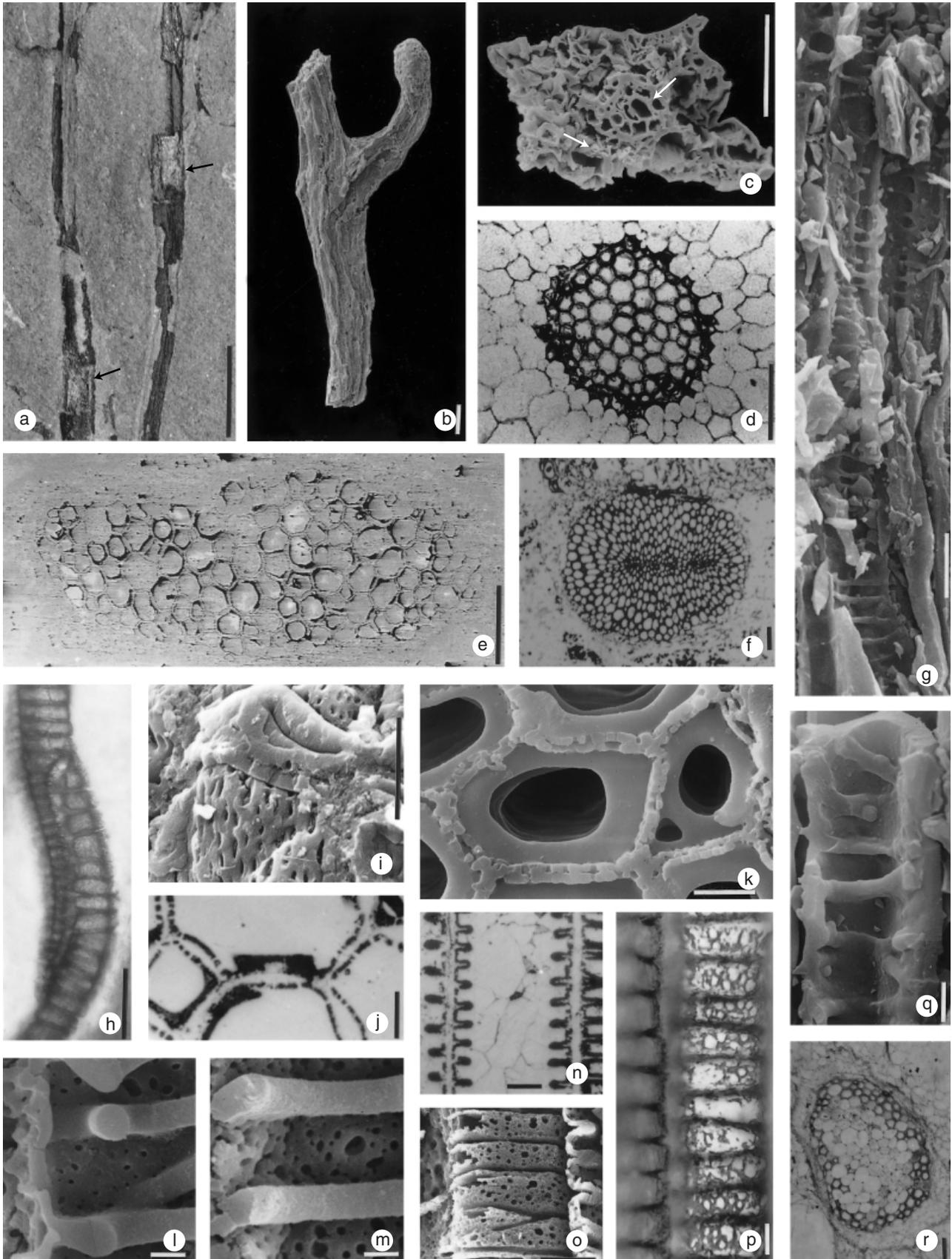
Pyrite (Figs 2a, e, i, .j, n, o & 3a–d)

Pyritizations and their oxidized derivatives (e.g. limonite) are the most ubiquitous permineralizations available for anatomical studies in the Lower Devonian, but have the disadvantage that the mineral is opaque and hence is usually studied from highly polished thick sections using incident light. In the case of pyrite, black coalified lines marking cell walls contrast strongly with the highly reflective pyrite, but in oxidized examples the distinction between wall and matrix has to be enhanced by bleaching (e.g. with oxalic acid). In pyritized examples, cell walls, when originally lignified, show some integrity on dissolving the mineral with nitric acid, but parenchymatous tissues are rarely preserved in this mode, and hence are not recovered intact. Anatomical interpretation is complicated by the fact that, unlike the two previously described types, bacteria are directly involved in the process. In anaerobic environments sulphate reducing bacteria decay organic material and produce hydrogen sulphide which subsequently reacts with dissolved iron (II) monosulphide (Rickard 1997; Grimes *et al.* 2001). Thus in attempting to explain the presence of pyrite in the positions of the compound middle lamella and centres of secondary thickenings in Lower Devonian *Gosslingia breconensis*, Kenrick & Edwards (1988) postulated that precipitation had occurred in those areas originally occupied by more readily metabolized cellulose, but lignified regions of walls had not been degraded, and hence persisted to become the coalified layers in the fossils. More recent experimental studies have shown that pyrite can nucleate within the primary cellulose wall and middle lamella (Grimes *et al.* 2001) and may grow thus displacing the original organic material.

DESCRIPTIONS

General introduction

- 1 Most of the data illustrated here derive from the *lateral* walls of elongate centally placed cells. Their geological antiquity points to tracheids as opposed to vessels, but there is little evidence of end walls in the record, and, at best, tracheidal status can be inferred from overlapping ends of cells in Rhynie Chert plants (e.g. *Ventarura*; Powell, Edwards & Trewin 2000) where there are no indications of perforations (Fig. 2h), with supporting evidence from minor variations in cell diameter consistent with tapering ends.
- 2 In the absence of developmental information, the use of the terms primary (1°) and secondary (2°) wall must be treated with caution. This particularly applies to forms (e.g. S-type tracheids) which have little or no resemblance to extant examples (Fig. 3a–d).



- 3 The absence of developmental information also demands caution relating to identification of protoxylem, and is usually based on concentrations of the elements of smallest diameter, which are usually poorly preserved. The size distribution criterion works well in strands which are centrarch and large (e.g. *Psilophyton*; Fig. 2f), but exarchy, particularly in pyrite permineralizations, is more difficult to demonstrate convincingly (Fig. 2e, but see the silicified zosterophyll axis in Fig. 2d). The vast majority of cells show no examples of distortion relating to extension growth and from their usually very regular thickenings are considered metaxylem. Isolated 'spirals of secondary thickening' have been illustrated in *Leclercqia complexa* (Grierson 1976) whereas in another lycophyte, *Drepanophycus qujingensis*, the vertical stretching of pits in the wall between secondary thickenings (Fig. 2i) is also suggestive of elongation experienced by protoxylem (Li & Edwards 1995). Secondary xylem has not yet been demonstrated in pre-Middle Devonian plants.
- 4 Although it is assumed from comparative biochemistry and phylogenetic relationships that the 'secondary' walls are lignified, this polymer has not yet been demonstrated in fossils of early land plants (see Ewbank *et al.* 1997 and above). This point is worthy of emphasis because the walls of bryophyte hydroids are reinforced by other polyphenols, and some of the cells described here have novel architecture which is difficult to match with conducting cells of embryophytes. However, the resistance to decay exhibited by these cells suggests that their walls were impregnated by lignin or a precursor.
- 5 The detailed descriptions and extensive illustrations presented here are necessary because reference cannot be made directly to tracheids of extant plants. In the case of the earliest xylem, the present is certainly not the key to the past, although some general similarities assist in its interpretation. The oldest examples of pitting which have been investigated in depth and which do not require such extensive exposition in view of their similarities to mod-

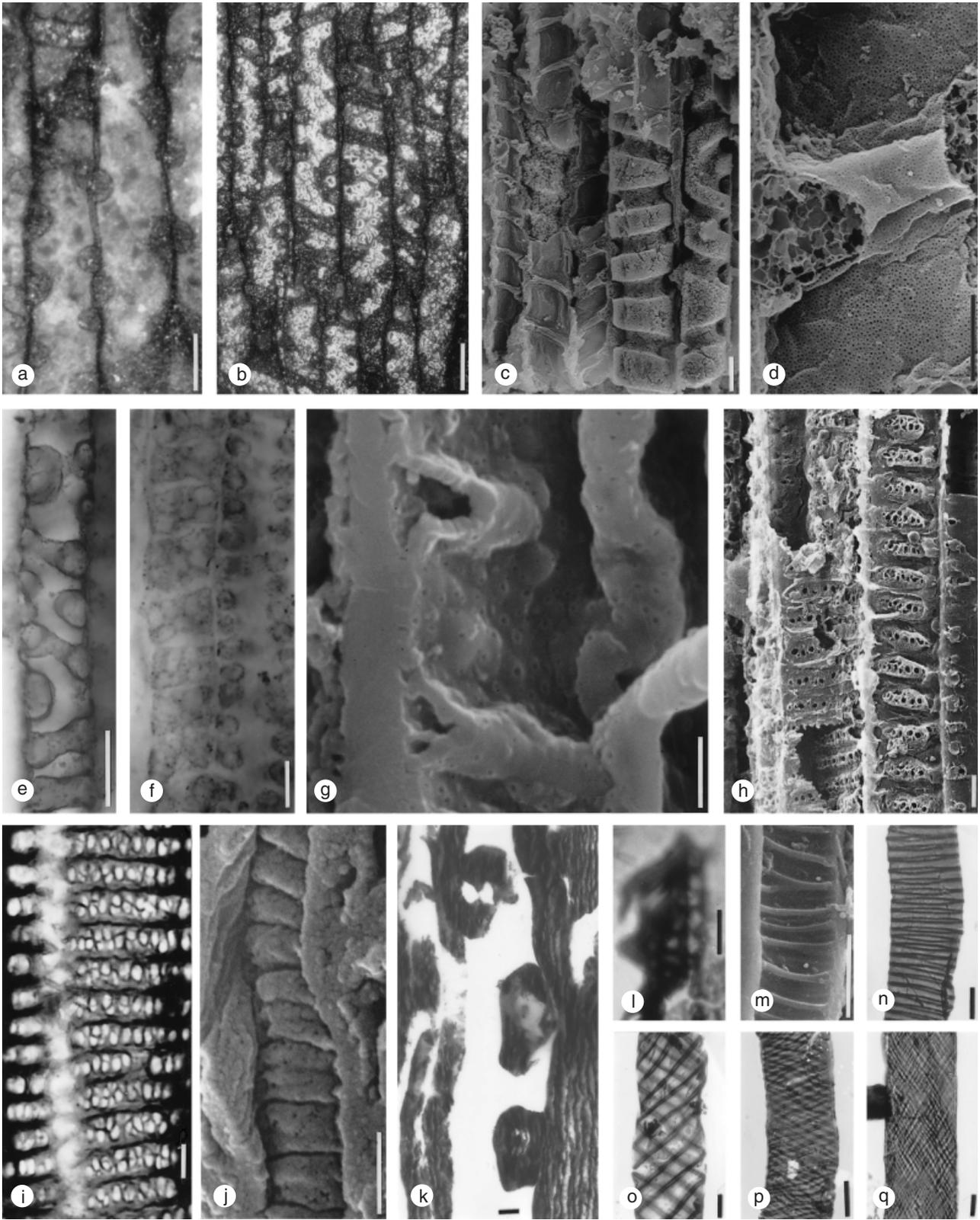
ern forms include the circular and scalariform bordered pits in the metaxylem of the Middle Devonian herbaceous lycophyte *Leclercqia*. 'Conventional' protoxylem, represented by annular and helical secondary thickenings and remnants of primary wall, was also illustrated (Grierson 1976).

- 6 The letter prefixing tracheid types usually refers to the genus in which cells were first described (Kenrick & Edwards 1988; Kenrick, Edwards & Dales 1991a; Kenrick & Crane 1991).

G-type [Fig. 5, based on *Gosslingia breconensis*, a Lower Devonian zosterophyll (Kenrick & Edwards 1988)]

Secondary thickenings are annular, helical to occasionally approaching reticulate and are connected by a sheet of resilient material which is fused to the presumed primary wall. The sheet is perforated by holes of varying size and usually rounded shape (Fig. 2l, m, o & p). Some are laterally fused. Sizes may vary in a single sheet, and between tracheids in a strand, although appear generally consistent within a single tracheid. The surface of the thickenings are smooth and they sometimes have a presumed cellulose core (Fig. 2n). Inferences on the chemistry of the wall layers are based on the distribution of coalified material and mineral in pyrite permineralizations (Kenrick & Edwards 1988), and the assumption that spaces filled with pyrite within wall systems (e.g. Fig. 2j) were areas where more readily metabolizable insoluble material (i.e. cellulose) had been removed by bacteria whereas coalified layers in the fossil were less easily biodegraded (i.e. lignified). The overall distribution of these perforations does not exactly match in adjacent tracheids (cf. conventional pits in tracheids, sclereids), although occasionally they coincide such that the cells appear directly connected (Fig. 2k). Whether or not the equivalent of a pit-closing membrane was origi-

Figure 2. (a) *Gosslingia breconensis* Heard. Smooth sterile predominantly coalified axes, with some areas flaked off revealing impressions below. Arrows indicate pyritized regions. NMW2001.41G.1. Pragian, Brecon Beacons, S. Wales. Scale bar = 5 mm. (b) Unnamed coalified mesofossil comprising branching axis with intact right hand apex (SEM). NMW99-20G.8. Lochkovian, Welsh Borderland. Scale bar = 100 μ m. (c) Fractured proximal end of axis in (b) (SEM). Arrows indicate central strand. Scale bar = 50 μ m. (d) *Trichopherophyton teuchansii* Lyon & Edwards. TS central part of aerial axis preserved in silica, with exarch xylem (LM). Pb4884/2. Pragian, Rhynie Chert, Aberdeenshire. Scale bar = 100 μ m. (e) *Gosslingia breconensis*. TS elliptical xylem strand preserved in pyrite, with coalified residues (black areas). (LM – incident light). NMW2001-41G.2. Scale bar = 100 μ m. (f) *Psilophyton dawsonii* Banks, Leclercq & Hueber. TS centrarch xylem strand preserved in calcium carbonate (LM). Protoxylem is elongate below a branch point. CUPC 190, slide 13-4.1-15. Emsian, Gaspé, Canada. Scale bar = 100 μ m. (g) Longitudinally fractured strand from (b/c) (SEM). Scale bar = 10 μ m. (h) Rhizome associated with *Venturura lyonii* Powell, Edwards & Trewin showing ends of two overlapping G-type tracheids (LM). GLAHM 114030. Pragian, Windyfield Chert, Aberdeenshire. Scale bar = 50 μ m. (i) *Drepanophycus qujingensis*. Part of presumed protoxylem G-type tracheid showing vertical extensions of the pitting of the secondary wall. Annular thickening to top (SEM). CBYn 9001031a (Stub 6). Emsian, Yunnan Province, China. Scale bar = 5 μ m. (j). *G. breconensis*. TS pyritized tracheids (LM). Black areas are coalified. NMW87-19G.1. Scale bar = 10 μ m. (k). G-type tracheids from unidentified plant (SEM). NMW99-20G.1. Lochkovian, Welsh Borderland. Scale bar = 5 μ m. (l, m) Longitudinally fractured cells from xylem in (k), showing range in size of pits in secondary wall between spiral thickening. Scale bars = 2 μ m. (n). *G. breconensis*. LS tracheids (LM). Note pyrite within cores of secondary thickenings. NMW87-19G.2. Pragian, Brecon Beacons, S. Wales. Scale bar = 10 μ m. (o) *G. breconensis*. Coalified 'skeleton' remaining on removal of pyrite. NMW2001-41G.03. Pragian, Brecon Beacons, S. Wales. Scale bar = 10 μ m. (p) *Asteroxylon mackiei* Kidston & Lang. LS silicified G-type tracheids (LM). Münster 3471. Pragian, Rhynie Chert, Aberdeenshire. Scale bar = 10 μ m. (q) Longitudinally fractured tracheid with annular secondary thickening from b. Scale bar = 2 μ m (r) TS xylem of rhizome associated with *Venturura*. Note unthickened cells to centre. GLAHM 114033. Pragian, Windyfield Chert, Aberdeenshire. Scale bar = 100 μ m.



nally present in these regions remains uncertain, particularly as in degradation of extant tracheary elements, pit closing membranes are the first wall structures to be metabolized and disappear (Boutelje & Bravery 1968). However, such a layer persists in the P-type tracheids (below). Such uncertainty is frustrating in considering implications of the pit-closing membrane for the functioning of the elements.

Recent experimental studies on pyritization of plants indicate that pyrite can be precipitated and subsequently grow within cellulose cell walls and middle lamellae, thus possibly accentuating the thickness of the compound middle lamella in the fossils. Extant pteridophyte tracheids frequently show a core of cellulose and Cook & Friedman (1998) have recently demonstrated a partially lignified 'degradation prone' region within the secondary thickenings of the lycopsid *Huperzia selago* and of *Equisetum* (Friedman & Cook 2000). Thus layering of walls occurs in extant forms. However, the frequently perforated connecting sheet has not been seen in extant metaxylem. The closest is in the protoxylem of the Psilotaceae (Bierhorst 1960), where, following the development of typical annular and helical thickenings, an additional wall is deposited over the primary wall and covers all or part of the area between the thickenings. Such cells are frequently distorted and show no regular perforations of the sheet extended between the thickenings. This is developed to a varying extent and thus 'outlined [one or two] simple pit-like areas.' Bierhorst called the interconnecting layer the 'secondary secondary wall' with lignification complete or tapering away on either side of the secondary thickening.

Distribution

G-type tracheids characterize certain early members of the Lycophytina (*sensu* Kenrick & Crane 1997) including the Zosterophyllopsida, and a few early Lycopsida (e.g. *Asteroxylon*, *Drepanophycus*). They are normally recorded in silicified and pyritized xylem, and rarely in conventional coalified compressions (but see Hueber 1983; *Baragwanathia*). Thus, for example, *Zosterophyllum myretonianum* is described as possessing annular tracheids (Lang 1927). These taxa, where three-dimensionally preserved,

have exarch (Fig. 2d & e) or weakly mesarch strands. However, G-type tracheids also occur in the centrarch xylem of the Barinophytales (e.g. *Barinophyton citrulliforme*) (Brauer 1980) and Hsuaceae (Li 1992), whose gross morphology (strobili with or without bracts borne on naked axes and lateral trusses of terminal sporangia on naked axes, respectively) does not fit comfortably with either zosterophylls or lycopsids, and in *Eophyllophyton*, considered a basal euphyllophyte by Kenrick & Crane (1997).

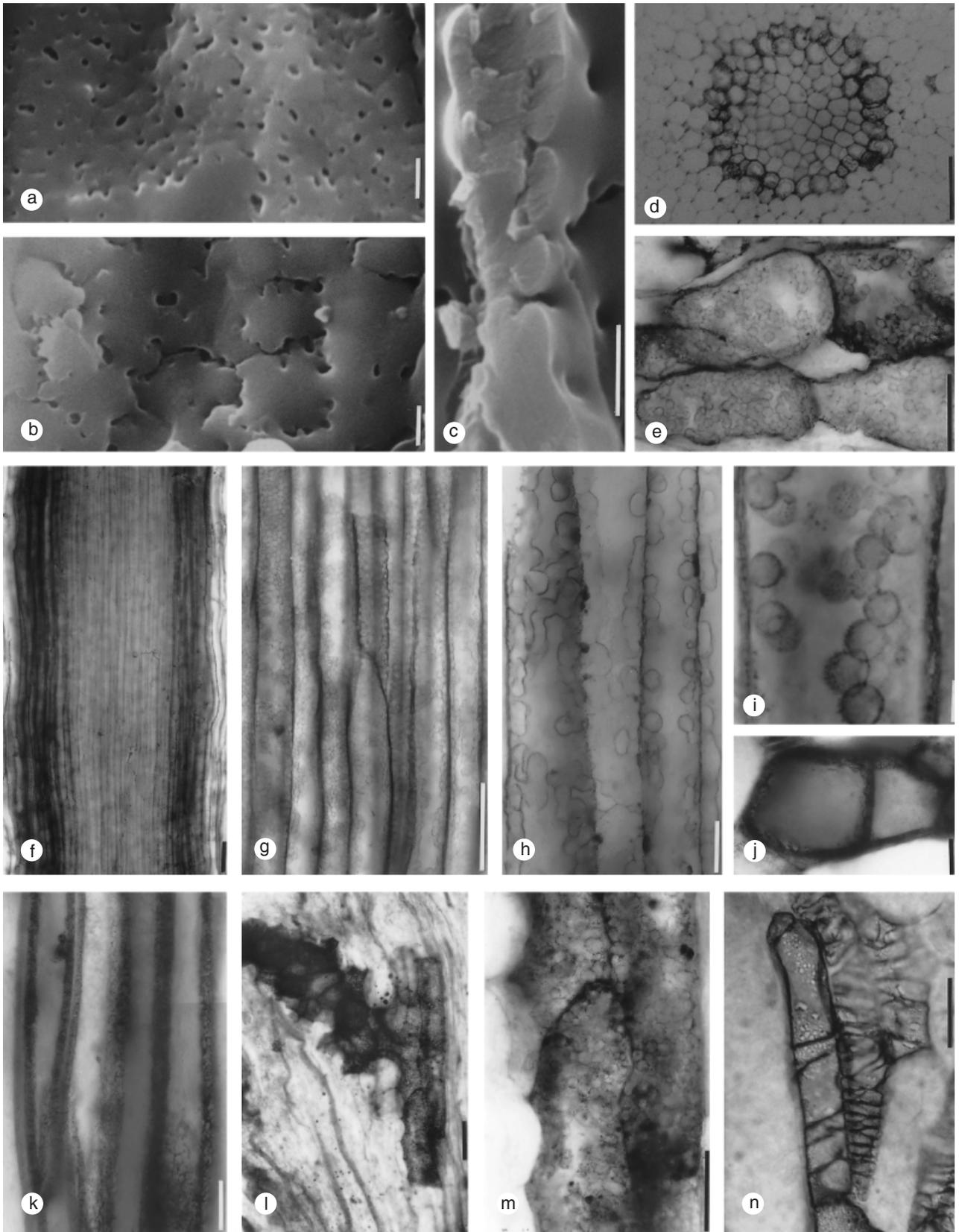
P-type [Fig. 5, based mainly on *Psilophyton dawsonii* a Lower Devonian trimerophyte (Hartman & Banks 1980)]

Metaxylem tracheids are long (< 3.0 mm) and markedly faceted (5–7 sides) compared with G-type. Pitting is essentially scalariform and, in specimens superbly preserved in calcium carbonate-rich nodules, pit-closing membranes are present. SEMs of the thickenings (Fig. 3h), when the latter and compound middle lamella have been stripped away show the attachments of the thickenings as ridges (crassulae) emphasizing the narrowness of the attachment sites. Thus in section the vertically adjoining and adjacent thickenings produce a butterfly-like appearance, and the pitting may be described as scalariform bordered. Rare examples show almost circular bordered pits. However in addition, the transversely elongate pit aperture is transversed by a sheet of material which is perforated by rough circular holes arranged in one or two transverse rows or which comprises less regular strands or a reticulum (Fig. 3i). As in G-type tracheids the cores of the coalified thickenings are hollow, again suggestive that this area was originally occupied by cellulose, but in contrast to the G-type, the perforated sheet between thickenings is attached at the pit aperture rather than in the position of the pit-closing membrane. Protoxylem is described as having narrow spiral and scalariform elements (Banks, Leclercq & Hueber 1975), but was not examined ultrastructurally.

Distribution

Gensel (1979) recorded similar pitting in *Psilophyton forbesii* and *P. charientos* [and possibly in the trimerophyte

Figure 3. (a–d) *Sennicaulis hippocrepiformis* Edwards. Lower Devonian. S. Wales. a. LS pyritized S-type tracheids. (LM incident). Brecon Beacons. NMW90-42G.2. Scale bar = 20 μm . (b) LS polished pyritized tracheids before etching. Pembrokeshire. PK Stub 168. Scale bar = 20 μm . (c). SEM of tracheids. Pembs. NMW90-42G.3. Scale bar = 20 μm . (d) Close up of (c) illustrating spongy texture of thickenings below the perforated lining layer. Scale bar = 5 μm . (e, f) *Rhynia gwynne-vaughanii*. LS silicified tracheids showing 'vesicles' in secondary thickenings. Pragian, Rhynie Chert, Aberdeenshire. Münster 1588, 2222. Scale bars = 10 μm . (g) Part of conducting element from unnamed smooth axis. Note homogenized layer between cells and perforated layer lining lumen and forming thickenings (SEM). NMW99-20G.7 Lochkovian, Welsh Borderland. Scale bar = 1 μm . (h, i) *Psilophyton dawsonii*. Banks, Leclercq & Hueber. Emsian, Gaspé, Canada. (h) SEM of two adjacent tracheids with facet viewed from outside (left) and inside (right). NMW2001-41G.4. Scale bar = 10 μm . (i) LM part of tracheid. CUPC 192. Slide 4-3.L.4. Scale bar = 10 μm . (j, k) *Cooksonia pertoni* Lang. Lochkovian, Welsh Borderland. (j) SEM of lumen cast of part of tracheid. NMW94-60G.17. Scale bar = 1 μm . (k) TEM part of coalified tracheid. Thickenings have incomplete cores. Scale bar = 1 μm . (l). Part of coalified tracheid, isolated on a film pull from a sterile axis (*Hostinella*). Ludlow Series, S. Wales. Scale bar = 10 μm . (m) SEM of internal surface of longitudinally fractured banded tube (*Porcatitubulus annulatus*). NMW2001-41G.5. Lochkovian, Welsh Borderland. Scale bar = 10 μm . (n) Examples of thickenings in *Porcatitubulus spiralis* (LM). (MPK 6028, 6046, 6049, 6051, respectively). Wenlock, S. Wales. Scale bars = 10 μm .



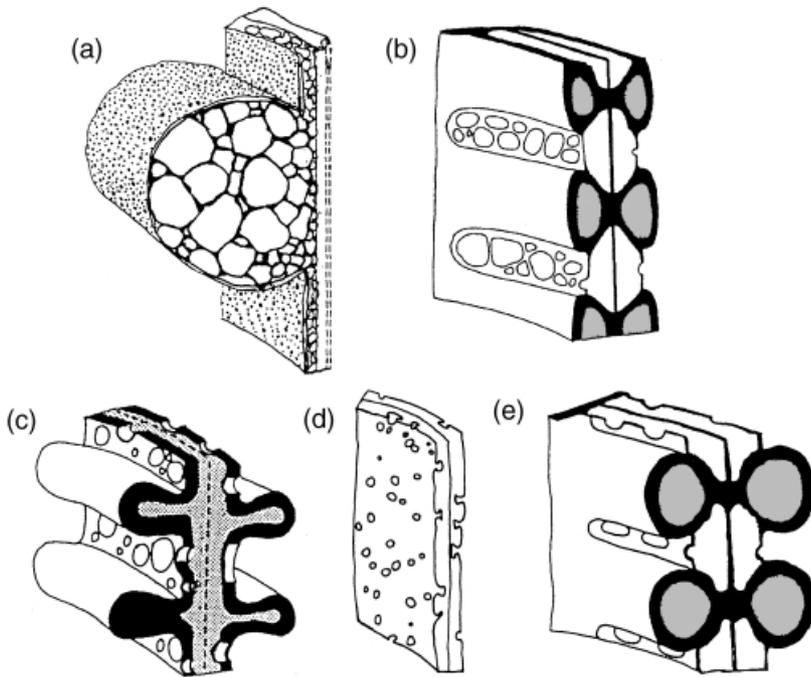


Figure 5. Schematic diagrams of areas of tracheid wall. Stippling indicates predominantly cellulose. (a) S-type. (b) P-type. (c) G-type. (d) I-type. (e) *Minarodendron*.

Gothanophyton] and is currently researching this type in *Pertica*-like fossils (Gensel pers. comm. 2001). P-type thickenings might well therefore characterize tracheid architecture in early members of Euphyllophyta (*sensu* Kenrick & Crane 1997). However, broadly similar tracheids with perforated sheets, strands or a reticulum traversing pit apertures also occur in later Palaeozoic lycophytes. The best described is *Minarodendron*, a late Mid Devonian herbaceous lycophyte (Fig. 5; Li 1990), which differs in that the free surfaces of the scalariform thickenings extend prominently into the lumen, forming ridges and the resulting slightly depressed connecting sheets bear one or two transversely orientated rows of circular perforations (pittles). A single row characterizes the axial xylem of *Barsostrobus*, an Upper Devonian lycophyte cone (Fairon-Demaret 1977). Perforations also occur in Carboniferous herbaceous forms *Selaginellites* and *Eskdalia*. Vertical strands or a reticulum replace the perforated sheet in certain Carboniferous lepidodendrids and, in some taxa, are described as 'Williamson's striations'. See Li (1990) for more detailed consideration.

S-type tracheids [Fig. 5, first identified in *Sennicaulis hippocrepiformis*, a taxon of sterile axes from the Lower Devonian (Kenrick *et al.* 1991a)]

Prominent helical (possibly annular) thickenings (Fig. 3a & b) show a spongy texture which is also present in the underlying and intervening lateral walls of the elements (Fig. 3c & d). Both thickenings and intervening lateral walls are covered by a very thin layer with numerous closely spaced holes. This construction (Fig. 5a) was originally elucidated from pyritized axes of *Sennicaulis* (Kenrick *et al.* 1991a) and to a lesser extent from limonite/goethite permineralizations of plants assigned to the Rhyniaceae (Kenrick & Crane 1991; Kenrick, Remy & Crane 1991b). The skimpy lining layer and spongy skeleton were thought to be composed of a lignin-like polymer because of their persistence in the fossils. The voids in the 'sponge' may have been filled with fluid or easily biodegraded polysaccharides (e.g. cellulose). Kenrick & Crane (1991) concluded that a similar construction occurred in silicified *Rhynia gwynne-vaughanii* and illustrated helical secondary thickenings which comprised large

Figure 4. (a–c) Unidentified coalified mesofossil axis with I-type tracheids (SEMs). NMW99-20G.11. Lochkovian, Welsh Borderland. Scale bars = 1 μm . (a, b) forma α & β pitting in surface view. (c) Longitudinally fractured wall between adjacent elements. (d–i) *Aglaophyton major* Edwards. Silicified presumed water-conducting cells. Pragian, Rhynie Chert, Aberdeenshire. (d) TS central part of axis. Note central strand with core of thicker walled cells. UCTC1. Scale bar = 100 μm . (e) 'Transition' cells with vesicles in rhizome. Münster 1876. Scale bar = 50 μm . (f) LS central strand of aerial axis. Münster 1652. Scale bar = 100 μm . (g) LS cells of outer zone of central strand. Münster 1675. Scale bar = 100 μm . (h). LS outer cells of central strand showing some coalescence of vesicles. Münster 346. Scale bar = 20 μm . (i) Vesicles in central strand showing unusual preservation. Münster 1981. Scale bar = 10 μm . (j, k) *Nothia aphylla* Lyon. Pragian, Rhynie Chert, Aberdeenshire. (j) LS 'transition' tracheids. Münster 2926. Scale bar = 20 μm . (k) LS tracheids of aerial axis with uniformly thick, ?bilayered walls. Münster 3032. Scale bar = 20 μm . (l, m) *Rhynia gwynne-vaughanii* 'transition' tracheids. Münster 2278. (l) Strand associated with central axis strand (right). Scale bar = 100 μm . (m) 'Transition' tracheids from (l) filled with vesicles. Scale bar = 50 μm . (n) 'Transition' tracheids showing G-type thickenings in rhizomes associated with *Ventarura*. GLAHM 114041. Pragian, Windyfield Chert, Aberdeenshire. Scale bar = 50 μm .

globular structures (approximately 4.5 μm diameter) intermingled with smaller examples (Fig. 3e & f). Because of the limitations of the chert for ultrastructural studies they could not provide details of the walls between elements, nor unequivocal evidence for a perforated lumen-lining layer. However, they did illustrate an extremely thin opaque layer (100–300 nm thick) in this region. Comparisons of the density of staining within cellulose walls in other tissues preserved in the chert with that in the interiors of the globule structures do not support a cellulosic composition.

Considering the perforations, although they are similar in size to plasmodesmata, their presence on the presumably last deposited layer of the wall covering the presumed sponge-filled secondary thickenings, make it unlikely that they had a similar developmental origin.

Distribution

This xylem architecture has been unequivocally demonstrated in *Sennicaulis*, *Stockmansella*, *Huvenia*, the probable gametophyte, *Sciadophyton*, and may occur in *Rhynia gwynne-vaughanii* (Kenrick & Crane 1997). In all cases the xylem was probably centrarch, although distribution of cell size is difficult to distinguish in strands as small as in *Rhynia* and there appears to be a central zone of ?smaller cells in the strand of *Sennicaulis*. These plants are further united because their sporangia, where known, may have been abscised or isolated from the parent axes at maturity, and they were placed in the Rhyniopsida by Kenrick & Crane (1997). Perhaps relevant to this account are the centrarch strands of tubular cells of *Taeniocrada dubia* described by Hueber (1982) in abstract, but not illustrated, as possessing 'sponge-textured helical thickenings within the walls of the tubes and not the final innermost layer in the lumen as characteristic in the formation of walls in the tracheids'. A microporate layer lined the lumen and the limiting layer was described as thin and fibrillar. The latter has not been seen nor described in detail in the S-type tracheid. S-types are not illustrated in plants younger than the Middle Devonian. Figure 3g shows a possible coalified example from the Lochkovian (basal Devonian) in which central cells are two-layered, the inner perforated with pores, the smallest of plasmodesmata size (approximately 60 nm), the outer homogeneous and fused with that of adjacent cells. The lateral walls may be internally smooth (i.e. no helical/annular thickenings) or the perforated wall may form irregular \pm horizontal folds or extend as hollow strands across the lumen. The latter may branch and partially occlude the lumen. These fragments of cells have the perforated layer in common with S-type tracheids, although it is much thicker than in the latter. (Cell diameter is much smaller, < 20 μm). A very small number show a spongy or granular texture in the outer wall, but this never extends into the folds.

Uniformly thick-walled cells

Examples are confined to plants with branching sporophytes and stomata. They have not been assigned a letter, because it seems likely that the plants in which they occur

are not closely related, and the chemistry of the walls cannot be assumed to be similar

Nothia aphylla (Lower Devonian Rhynie Chert; El-Saadawy & Lacey 1979)

Kerp, Hass & Mossbruger (2001) recently described the water-conducting cells in this Rhynie Chert plant as elongate (< 700 μm long) fusiform cells with strongly thickened walls (2–3 μm thick) and tapering ends (Fig. 4k). They thus lack additional secondary thickenings or pitting. The walls appear dark and thus suggestive of lignification and were thought more similar to fibres or hydroids than tracheids by the authors. The existence of possible bilayering is evidenced by examples where the walls are split but remain attached at the corners. In the rhizome these cells occur in a central core with three other types including possible sieve cells. Xylem in erect axes is similar with smaller elements (approximately 10 μm diameter) in the centre and larger (< 30 μm) to the outside.

Aglaophyton major (Lower Devonian Rhynie Chert; Edwards D.S. 1986)

The central strand (Fig. 4d) of *Aglaophyton* has a core of thin-walled cells, which are angular in cross section and, although of variable shape and diameter (18–44 μm), show no regular gradation of size. It is surrounded by a few layers of cells with uniformly thick walls (1.5–2.0 μm), which are 22–50 μm in diameter. A further encircling zone is interpreted as phloem (Edwards, D.S. 1986). The two inner types have dark-coloured walls, which Edwards attributed to the presence of lignin-like polyphenols. He found no evidence of conventional secondary thickenings, but variations in the appearance of the walls may hold clues to a more elaborate construction. In some examples he found evidence of bi-layering, a narrow outer layer and an inner thicker one, parts of which had separated or broken away, with fragments preserved in the matrix of the lumen. In others the walls exhibited a reticulate or more regular hexagonal appearance which Edwards attributed to partial degradation of the coalified wall (see also Lemoigne & Zdebska 1980). He considered the regularity in patterns indicative of crystallization and suggested that this had occurred in association with bacterial attack. Vesicles and their fusion were also observed in the elongate cells of the main central strand (Fig. 4h). A similar patterning was observed in the less robust central cells, and in both types he noted small spheres of remarkably regular size, termed vesicles (Figs 4g & i). These have been superbly illustrated in small 'transition' cells (Fig. 4e) in sporophyte and gametophyte (Remy & Hass 1996). Ongoing research at Münster (Kerp and Hass, pers. comm.) suggests that vesicles lining the thinner wall form a continuous layer by lateral fusion which is of similar dimensions to Edwards' thicker inner wall layer.

Distribution

Neither *Nothia* nor *Aglaophyton* have been found outside the Rhynie Chert. Kerp & Hass (pers. comm.) point to sim-

ilarities in the construction of the secondary thickenings of *Rhynia gwynne-vaughanii*, where the spongy structure appears composed of vesicles of varying size (see also p. 65 and 66; (cf. Figs 3e & 4h) Kenrick & Crane 1991). The larger ones are of similar dimensions to those in *Aglaophyton*. Vesicles have not been observed in *Nothia*. Smooth cells have recently been demonstrated in the central strand of a small naked, stomatous fragment from the basal Devonian, which is impossible to name (Edwards & Axe 2000).

The lack of conventional tracheidal thickenings in the central cells of the terete strand of *Aglaophyton* was pivotal to the removal of this genus from *Rhynia* and its isolation from the Tracheophyta (Edwards, D.S 1986; Edwards & Edwards 1986). Kenrick & Crane (1997) placed it in the protracheophytes, a group of nonvascular polysporangiates. Other authors have commented on the similarities with a bryophytic conducting strand, particularly polytrichaceous examples (Edwards, D. S. 1986). On the basis of all other anatomical attributes, *Aglaophyton* sporophytes and gametophytes (called *Lyonophyton*) would seem to have functioned as homoiohydric plants. The smooth walls of *Nothia* were considered to have been secondarily derived from G-type pitting by Kenrick & Crane (1997), who placed it in the zosterophylls, despite major differences in sporangial organization and dehiscence.

C-type tracheids (as seen in *Cooksonia pertoni*; Edwards *et al.* 1992)

These resemble conventional annular and spiral tracheids except that the imperforate lateral walls are thick (Fig. 3j & k) when compared with the primary wall in protoxylem. TEM observations show voids in the centre of the tracheids (Fig. 3k). Similar cells in a smooth unidentifiable branching axis (Fig. 3b) show homogeneous thickenings which range from annular to sparsely reticulate (Fig. 3g & q). The composition of the lateral walls is unknown: all the data come from mesofossils.

Distribution

To date such organization has been described from only three *Cooksonia pertoni* specimens (Fig. 3j & k; Edwards *et al.* 1992) and in one sterile branching axis with intact naked tip (Edwards, Axe & Duckett in press). It may also be the type present in the earliest illustrated tracheids (Upper Silurian: Edwards & Davies 1976) which were recovered on a film pull, and show similarities in diameter between transverse thickenings and vertical walls (Fig. 3l).

I-type [Fig. 5, known from indeterminate smooth stomatous axes; Edwards & Axe 2000; Edwards *et al.* in press]

Information derives from mesofossils. Central cells (approximately 12 μm diameter) have bilayered walls (Fig. 4a–c). The outer is imperforate and fused with that of adjacent cells (on homogenization 2 μm thick). The inner, sometimes detached layer, has rounded perforations,

approximately 100–300 nm in diameter, with bevelled edges. In section, these holes widen slightly to the base of a cavity, thus superficially resembling bordered pits, but with much smaller dimensions. They do not appear to coincide on adjacent cells, but suitably fractioned cell wall complexes are rare (Fig. 4c). The distribution of pits led Edwards and Axe to divide the elements into two types α (Fig. 4a) and β (Fig. 4b). In retrospect this terminology was unfortunate and should be replaced by forma α and β . In forma α , the pits are scattered ($< 4 \mu\text{m}^{-2}$); in forma β some are aligned, others fused. Fracture between aligned examples and separations of the inner layer, results in the production of partially detached squarish flakes. Some cells are characterized by solid fringes or rod-like projections with smooth surfaces.

Distribution

Three specimens are known, one of which shows branching (Edwards *et al.* in press). Occasional stomata are present. The absence of any sporangia precludes identification. A further impediment is the lack of information on the chemistry of the walls. This type of wall structure is superficially similar to simply pitted tracheary elements, although the shapes and distribution of the pits lack their regularity. Edwards & Axe (2000) noted similarities in sizes of pits with the perforations in hydroids of gametophytes of liverworts (Calobryales and Pallaviciniinae: Ligrone, Duckett & Renzaglia 2000), but stomata are absent in these lower plants.

Tubular structures with internal thickenings 'Banded tubes' (*Infraturma Endomurali*; Burgess & Edwards 1991)

Tubular aseptate structures with internal regular annular or helical thickenings (Fig. 3n–q) that are continuous (homogenized) with lateral walls (Fig. 3m) occur in organic residues produced when Upper Llandovery (basal Silurian) through Lower Devonian rocks are dissolved in hydrofluoric acid (Edwards & Wellman 1996). Helical thickenings may be single or arranged in up to four spiralling bands in parallel that produce a diamond lattice type appearance in transmitted light (*Porcatitubulus spiralis* Burgess & Edwards 1991). More complex examples show close-set transverse ridging (*P. microspiralis*, *P. microannulatus*) and these can reach 750 μm long (Wellman 1995). The vast majority are parallel-sided, quite wide (approximately 30 μm) and incomplete at both ends. One example is reported with an imperforate papillate tip (Pratt, Phillips & Dennison 1978); another shows abrupt narrowing, but here the tube is broken (Burgess & Edwards 1991). Although most are recovered as isolated tubes, they also occur in clusters with parallel alignment or less regular organization. Some are associated with meshes of smooth-walled tubes.

Distribution and affinity

When recovered on maceration of rocks, banded tubes are associated with phytodebris (cuticle and spores) indicative

of a terrestrial origin. They occur in limited numbers in the Upper Llandovery, but increase in abundance and diversity throughout the Silurian. Burgess & Edwards (1991) named them using an artificial classification system devised for dispersed spores to facilitate their use in biostratigraphy. Their derivation remains controversial. Their similarities with tracheary elements are clear, and relatively thick lateral walls allow favourable comparison with the C-type, although the latter do not show such regularity, frequency and complexity in the thickenings. Niklas & Smocovitis (1983) isolated a strand of uniformly thick-walled and banded tubes from an irregularly shaped compression which they concluded was an indeterminate non-vascular land plant. In dispersed assemblages banded tubes are consistently associated with smooth tubes and cuticles of the Nematophytales, erected for land plants neither algal nor vascular (Lang 1937), and have been recovered from nematophytalean *Prototaxites*-type plants (*Nematosketum* Burgess & Edwards 1988). *Prototaxites* itself has recently been assigned to the fungi (Hueber 2001), and the presence of isolated tubes on and within a variety of organs has also led to the suggestion that they belonged to a saprotroph (e.g. Edwards & Richardson 2000). Further possible sources are the walls of bryophyte sporangia (Kroken, Graham & Cook 1996). From these reports it is obvious that the presence of banded tubes in Llandovery rocks cannot be accepted as evidence for vascular plants and indeed even their functioning as water-conducting cells remains conjectural.

FUNCTIONING

Elaboration of the palaeophysiological implications of the architectures described here is beyond the remit of this review, except to emphasize that, in conducting elements of small diameter, the influence of the type of secondary thickening should not be overlooked and that the extensive development of pitting in lateral walls was essential to supply water to peripheral regions of axes which were photosynthesizing throughout their aerial extent. The latter was taken into account in Raven's calculations on specific conductance in an early land plant (Raven 1977, 1984, 1993) although exactly what was measured as tracheid diameter (the basis for estimations of cross-sectional area of water movement) was not clear. His estimates for specific conductance ($10^{-9} \text{ m}^2 \text{ s}^{-1} \text{ Pa}^{-1}$) fell into the lower end of those obtained from direct measurements of fern tracheids (Woodhouse & Nobel 1982) and the latter were in turn less than those predicted from models based on tracheid dimensions and the Hagen-Poiseuille equation (Raven 1994). Niklas (1985) had earlier commented on the importance of effective diameter (i.e. lumen width) in such calculations on conductance, whereas Jeje & Zimmermann (1979) had shown experimentally that in metaxylem vessels of *Plantago*, resistance varied with the nature of the secondary thickenings and that, for example, for helical thickenings, effective diameter was defined as that between their inner extremities. In the types described here, in tracheids of

approximately equal diameter (e.g. $34 \mu\text{m}$), the G-type secondary thickenings of *Gosslingia breconensis* are about half as thick and less widely spaced as the S-type in *Sennicaulis*. (Data taken from Kenrick *et al.* 1991b). Thus in *Gosslingia*, the effective minimum diameter is $26\text{--}30 \mu\text{m}$ compared with a minimum of $24 \mu\text{m}$ in *Sennicaulis* (one thickening only per diameter taken into account). The situation is even more complex in some basal Devonian plants in which the thickenings almost occlude the lumen (Edwards 2000).

Compared with the G-type tracheids in *Gosslingia*, the P-types in *Psilophyton* are wider ($60\text{--}80 \mu\text{m}$ middle lamella to middle lamella) and the membranes across the mouths of the scalariform pits produce an almost flat internal surface thus reducing the resistance to flow caused by turbulence between secondary thickenings. The perforations would allow lateral movement of water in association with the fully permeable pit-closing membranes. However, in *Minarodendron* ($< 90 \mu\text{m}$ maximum diameter) with similarly spaced pitting, the thickenings again stand proud of the lumen lining! Such are the pitfalls of indulgence in 'facile adaptationist guesswork' (Harper 1982).

Although the above account serves to highlight ultrastructural variation in water-conducting cells in early land plants, their organization into simple usually terete protosteles seems to mirror the relatively simple bauplans of the organisms. However, Rhynie Chert examples show that xylem is not merely represented by a column of cells linking the water source to aerial sinks, and that rhizomatous axes in particular, show quite complex internal differentiation. Powell *et al.* (2000) illustrated small strands of short tracheidal cells in anomalously branching rhizomes associated with *Venturura lyonii* (Fig. 4n). They occur among parenchyma, their outlines tracing those of their parenchymatous neighbours. Thickenings are predominantly transverse, irregularly spaced, but connected with a perforated secondary wall, very similar to those of G-type tracheids. 'Transition' cells (Fig. 4e) with wall thickenings similar to those in xylem of aerial axes of *Aglaophyton* occur in bulges bearing rhizoids on the lower surface of its rhizomes (Remy & Hass 1996). These cells differentiate in one or more strands in tissues between the rhizoids and the axial strand and connect with the latter. Similar cells are produced in the vicinity of areas infected with fungi in aerial axes of *Aglaophyton* and *Rhynia gwynne-vaughanii* and may reconnect damaged conducting tissues (Fig. 4l & m). In *Nothia*, thick- and thin-walled parenchyma similar to that in the central strands of rhizomes connect the latter with its laterals via a 'connector' (Fig. 4j).

A further example of morphological simplicity masking sophistication at the cellular level (See Edwards, Kerp & Hass 1998 for tissues associated with stomata) is seen in the tracheids of *Psilophyton dawsonii*. Niklas & Banks (1985) showed that although mean tracheid diameter is the same between daughter branches in the vicinity of an equal dichotomy, in unequal branching the diameters are statistically significantly smaller in the narrower branch in the branching region. The authors concluded that these narrower tracheids ('xylem constrictions') would have pos-

sessed 'lower pressures' and consequently would have been preferential sites for embolism development during water stress or injury. Thus in those early vascular plants, as in extant seed plants, lateral branches, both fertile and sterile, could have been sacrificed to maintain water flow to the main growing regions (Tomlinson 1983; Zimmermann 1983).

Xylem configurations

With the exception of those (G-type) in lycophytes s.s. and one trimerophyte (P-type), the tracheids described above are aggregated into central columns which are terete or elliptical in cross section. The majority are composed entirely of tracheids; rare examples are medullated (Fig. 2r) or have scattered parenchyma in rhizomes (*Nothia*). Some changes in outline are associated with branching (e.g. *Psilophyton dawsonii*; *Goslingia breconensis*) and with sporangial traces (e.g. *Nothia*). Lower Devonian lycophytes possess deeply lobed protosteles (actinosteles, e.g. *Drepanophycus* and *Baragwanathia*) and one unnamed complex but regular trimerophyte branching system has a deeply three-lobed xylem with several groups of protoxylem which break down (Gensel 1984). In protostelic forms in the Rhynie Chert, a zone of differentiated parenchymatous tissue, completely surrounding the xylem, is usually identified as phloem on its location and to a lesser extent cell shape. Unequivocal sieve areas have not been found (Satterthwait & Schopf 1972; Edwards 1993). Xylem and phloem lack airspaces. An endodermis appears absent. The physiological significance of these aspects has been discussed by Raven (1984, 1994a). Niklas (1985) surveyed variations in relative volumes of xylem and axes throughout the Devonian and revisited Bower's hypothesis that increasing volume of xylem demanded by increasing size necessitated increased surface area of xylem in contact with surrounding living tissues. Morphologically this is translated by changes from a terete protostele to actinostele and various kinds of dissected xylem. Such issues were also addressed by Roth, Mossbrugger & Neugebauer (1994), and Raven (1994b) with some consideration of the disadvantages of the protostele in minimizing distances over which water and metabolite travel to and from sites of photosynthesis. In contrast, Wight (1987) and Stein (1993) concluded that shape of xylem is related to number and type of lateral appendages.

Phylogeny and ontogeny

Finally, in that Tracheophyta, now generally concluded as monophyletic on the basis of molecular (e.g. Qiu *et al.* 1998), and morphological (Kenrick 2000) data, are actually defined by the presence of water-conducting cells with secondary walls reinforced by lignin (Kenrick & Crane 1997), it seems appropriate to mention, albeit briefly, phylogenetic inferences from the tracheids themselves. Figure 6 shows an overview of the phylogenetic relationships of land plants based on Friedman & Cook (2000) and Kenrick & Crane

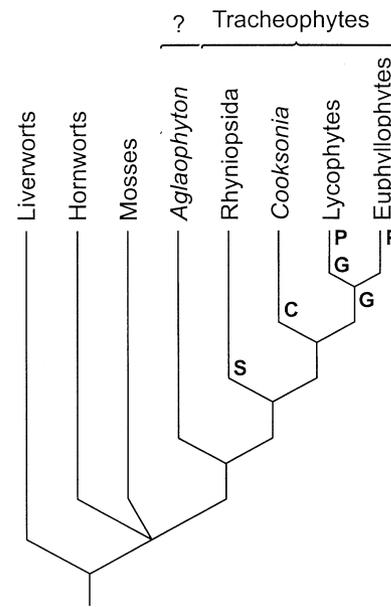


Figure 6. Overview of phylogenetic relationships of embryophytes based on Friedman & Cook (2000) (P, G, C, etc. refer to tracheid types).

(1997) with additions including incorporation of tracheid types. The position of *Aglaophyton* relies on the apparent absence of tracheidal secondary thickenings (Friedman & Cook 2000). *Cooksonia pertoni* has been included as part of a plexus of plants considered as sister groups to the Lycopytina.

As a consequence of a study on the development and composition in the components of the secondary wall in metaxylem of *Huperzia selago* and *Equisetum*, Cook & Friedman (1998) and Friedman & Cook (2000) suggested that the developmental sequence in these extant basal vascular plants may recapitulate that in the oldest representatives. Such a conclusion provides support for a single origin of tracheids. The studies of Friedman & Cook (2000) did not cover the development of a further wall (the secondary secondary wall) between the helical and annular thickenings of the tracheids. These latter characters, as exemplified by extant protoxylem examples, were considered by Kenrick & Crane (1997) as plesiomorphic in vascular plants, with subsequent evolution of pitted examples in metaxylem taking two routes in the Lycopytina and Euphyllophytina. They further hypothesized that the perforated sheet in the G-type tracheid was homologous to that covering the pit-aperture in the P-type. The varying position of the sheet (towards the P-type) in members of the Lycopytina would then be an example of homoplasy. As yet we have information only from *Psilophyton*, *Gothanophyton* and probably *Pertica* within the trimerophytes (Hartman & Banks 1980; Gensel pers. comm.) and so have no data on the xylem of basal members of that group, nor indeed how those members might be defined. Such issues were discussed by Kenrick & Crane (1997), whose cladistic analyses placed a Chinese plant, *Euphyllophyton bellum* with G-type tracheids (Hao

& Beck 1993) as a basal member of the Euphyllophytina, and also favoured the rejection of the Trimerophytina. Instead they recognized the *Psilophyton* complex as a well-defined group within the basal euphyllophytes.

The evolution of S-type tracheids has little support from comparative developmental studies or from the fossil record. Our researches on the basal Devonian mesofossils provide little evidence for regular helical and spiral and annular thickenings and well-defined spongy layer (Edwards 2000; Edwards *et al.* in press) but demonstrate the existence of cells with a similar lumen lining. They also reveal a further group of plants with a central strand of cells with somewhat larger perforations in an inner wall (I-type). This in turn leads to speculation on the homologies between the tracheids of vascular plants and the hydroids of mosses, and to the possibility that micropitting preceded the evolution of other types. However in the mosses, comparative developmental studies do not support homology between the water-conducting cells of the two groups (e.g. Ligrone *et al.* 2000). Unfortunately our mesofossil observations are based entirely on sterile smooth and very small axial fossils, all the more frustrating because the same locality has yielded the only information on the gross morphology of the producers of the dyads and tetrads – spores that are considered evidence for the existence of higher plants on land earlier in the Palaeozoic (e.g. Wellman & Gray 2000). Despite such deficiencies, these fossils and others included in this account demonstrate that the fossil record still has much to offer, not least in revealing anatomical diversity and novelty in early tracheids compared with the highly conservative nature of that other essential homoiohydric invention, the stoma.

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