Transactions of the Royal Society of Edinburgh: Earth Sciences, **84**, 261–266, 1994 (for 1993)

Arborescent gymnosperms from the Viséan of East Kirkton, West Lothian, Scotland

Jean Galtier and Andrew C. Scott

ABSTRACT: Plants of gymnospermous affinities are the most important component of the flora at East Kirkton. Four genera of anatomically preserved gymnosperm stems with well developed secondary xylem are interpreted as arborescent. The largest specimens (trunks up to 50 cm in diameter) are attributed to the genus *Pitus*. Features of the wood, including ray size, are characteristic of the species *Pitus withamii* Lindley & Hutton which has long been described from the Strathclyde (former Oil-Shale) Group of Scotland. Decorticated axes of *Eristophyton fasciculare* are more common; their study has enlarged our concept of the species with regard to maximum diameter, internode length and phloem organisation. Similarly, the decorticated specimens of *Bilignea solida* Kidston found at East Kirkton exceed in diameter the original material described from Ayrshire. The fourth taxon is *Stanwoodia* recently described by Galtier and Scott (1991). In all these plants, features of leaf traces suggest that leaves were relatively large and densely borne on ultimate branches. These leaves were shed ultimately, prior to a later phase of wood development; they certainly correspond to (? most of) the compression foliage commonly found in association: *Sphenopteridium*, *Adiantites* and *Spathulopteris*.

KEY WORDS: Plants, stems, trees, Lower Carboniferous, Brigantian, gymnosperm, wood, xylem, phloem, leaf traces, Scotland, East Kirkton.

This study is part of a series (Galtier & Scott 1991; Scott *et al.*, this volume) dealing with the plants preserved in the Lower Carboniferous sequence at East Kirkton, near Bathgate, West Lothian. This sequence has been the subject of a major international research investigation following the discovery of an important terrestrial fauna (Wood *et al.* 1985). The excavation of the site under the direction of W. D. I. Rolfe has yielded an important flora in addition to the abundant fauna. The plants are preserved as compressions, permineralisations and as fusain (Brown *et al.*, this volume). Fossil plants have long been known from the East Kirkton sequence, either as compressions such as *Sphenopteridium crassum* (Kidston 1923) or as permineralised wood (Cunningham 1838), but the first published detailed palaeobotanical study was the description of the gymnosperm stem *Stanwoodia* (Galtier & Scott 1991). A number of permineralised specimens attributed to the primitive gymnosperms *Bilignea*, *Eristophyton* and *Pitus* have been collected during the present investigation; they represent fragments of woody axes ranging in diameter from one to tens of centimeters; their description is the subject of the present paper.

1. Geological setting

At East Kirkton the plant assemblages change throughout the sequence (Scott *et al.*, this volume). The East Kirkton Limestone is one of a series of limestones within the Strathclyde Group, (formerly the Oil-Shale Group) and occurs near the top of the sequence. This limestone is considered to be of Brigantian (Upper Viséan) age (Rolfe *et al.* 1990; Scott in preparation); details of stratigraphy and location are given by Rolfe *et al.* (this volume). Associated with this sequence is a series of volcanic rocks interdigitated within the oil shales and limestones. The associated volcanic sequences have yielded anatomically preserved plants. Many permineralised gymnosperm stems described in this paper have been found as loose blocks in the quarry spoil, but most specimens of *Eristophyton* have been collected in the bed by bed excavation between Units 72 and 88 (Rolfe *et al.*, this volume). Specimens are held in The National Museums of Scotland (NMS). The British Museum (Natural History), London (BMNH) and the Hunterian Museum, University of Glasgow (HM).

2. *Eristophyton fasciculare* D. H. Scott stems

Decorticated branches of *Eristophyton* ranging from 12 mm to 60 mm in diameter are the most common gymnosperm stems (Units 72, 82, 88 and loose). Comparison with the original material of *Eristophyton fasciculare* (slides in the Kidston collection, HM, and in the Scott collection, BMNH) supports the assignation of the East Kirkton stems to this species as described by D. H. Scott (1902). Material originally described by D. H. Scott came from two localities: one specimen was collected at Loch Humphrey Burn, in the upper horizon which is considered as Viséan in age (Scott *et al.* 1984), and another specimen was derived from the Carboniferous Limestone near Haltwhistle. Thus all specimens are of Lower Carboniferous age. The study of the East Kirkton specimens provides new data on the ontogenetic variability, the stelar and leaf trace organization and on the phloem which is described for the first time.

2.1. Ontogenetic variability

In the eight specimens studied the primary xylem diameter remains small (2–3 mm), whereas wood thickness varies from 6 mm to 35 mm. These stems are interpreted as branches.

—Transverse and tangential sections made at different distances from the pith show variation in secondary xylem tracheid diameter, ray size and ray density.
—With the exception of the eight to ten innermost secondary xylem tracheids which are characteristically broader (Fig. 1a), the tracheid diameter regularly increases from inside to outside; the average radial diameter of a tracheid is 28 μm at 1 mm from pith, more than 40 μm at 6 mm and 50 μm at 20–30 mm (compare Fig. 1a and b at the same magnification).
—The ray height varies from 1 to 31 cells and 32 μm to 735 μm (Fig. 1c). In fact, the ontogenetic variability is not very pronounced: the average ray height varies from 6 cells at 6 mm from the pith to 7 cells at 30 mm in the largest specimen (Fig. 2i) whilst the taller rays range from 17 to 31 cells in the same sections.
—The most significant change certainly concerns the density of rays which is higher near the pith; we measured 40–60 rays by mm square at 6 mm from pith and 20 rays or less at 20 mm (compare Figs 1c and 2i).

2.2. Stele and leaf traces

Reinvestigation of the original slides of *E. fasciculare* confirms the accuracy of D. H. Scott's (1902) interpretation of the stelar organisation, leaf trace formation and phyllotaxis. However, some of the new specimens show up to 14 primary xylem strands, a number largely exceeding the value (8–9) given by Scott. This may indicate that some stems had more than five sympodial strands or that repeated division of axial bundles produced accessory strands.

At the level where they are occluded in the wood the leaf traces have up to three protoxylem strands (Fig. 1d) and not two as indicated by Scott. In one specimen (NMS G 1993.14.41, Unit 72) we have been able to map 25 successive leaf traces and thus to evaluate the internode length to about 2·5 mm.

2.3. Phloem zone

Two specimens show the tissue external to the secondary xylem preserved to a maximum thickness of 5 mm. Beyond the cambium zone the secondary phloem consists of thin-walled cells, fibres and rays. Cells with thick walls, interpreted as fibres, are absent or rare near the cambium (Fig. 1e), but their number increases further out where they are arranged in tangential bands of 3–4 cells alternating regularly with thin-walled cells (Fig. 1f). Fibres are square to rectangular in transverse section, 24–60 μm in diameter and more than 1 mm long (Fig. 1g). Most of the thin-walled cells are devoid of contents and may correspond to sieve cells (C, Fig. 1f) and parenchyma elements; other cells (P, Fig. 1f) have dark contents and resemble tanniniferous cells (Fig. 1f, g). Rays are one to (rarely) two cells and 36–120 μm wide, showing tangential expansion towards the periphery. This tissue resembles the secondary phloem described in *Stanwoodia* axes from the same locality (Galtier & Scott 1991). However, this gymnosperm stem also showed secondary cortex with a sequent periderm; evidence of such a tissue is lacking in *Eristophyton*.

3. Trunks assignable to *Pitus* Witham

Permineralised trunks occur as loose blocks, probably from the basal limestone sequence. The largest pieces of wood collected represent portions of trunks which originally exceeded 50 cm in diameter.

3.1. Description

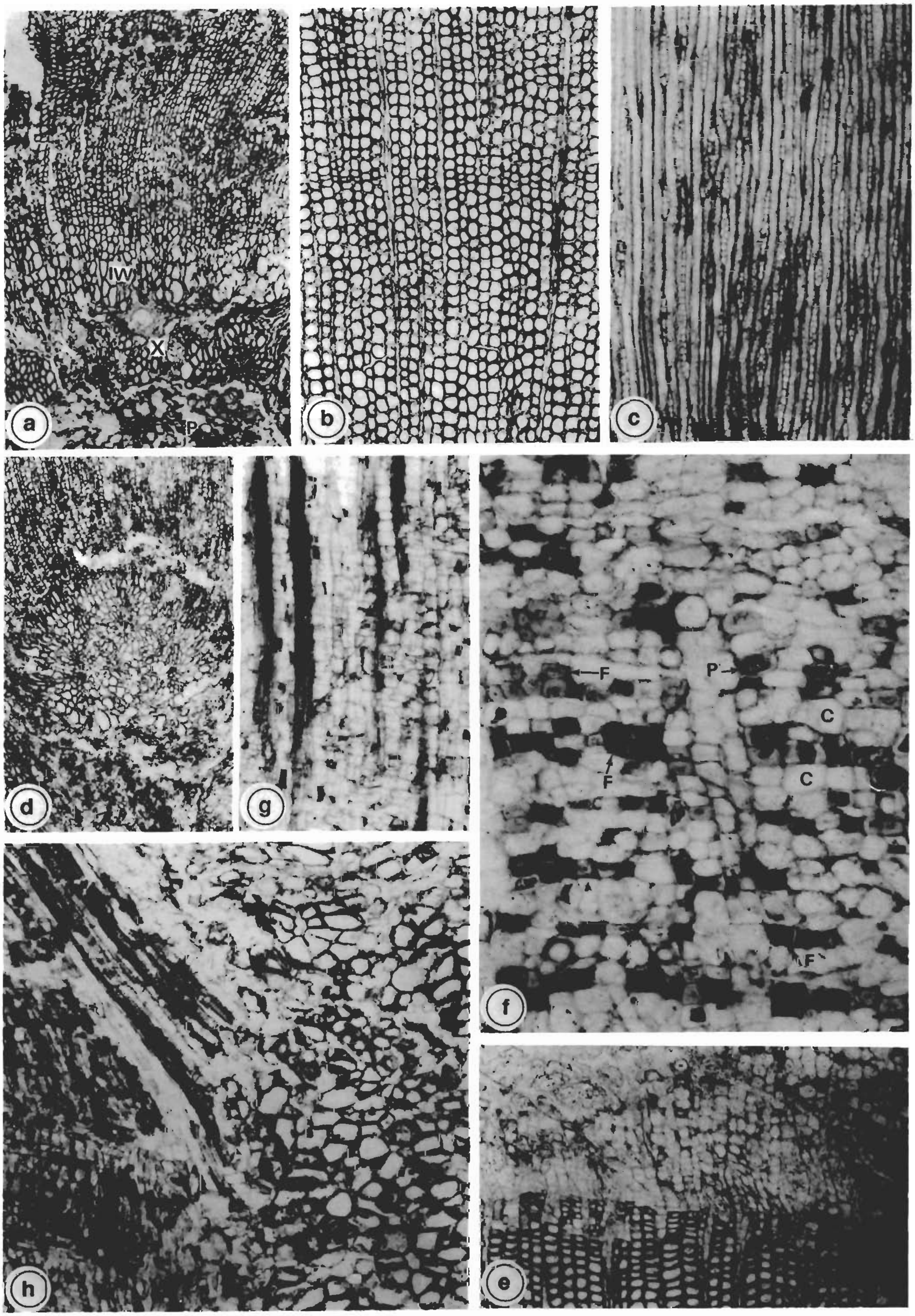
In all the specimens the secondary xylem tracheids average 50–60 μm in radial diameter (Fig. 2b, c). They exhibit 1–4 (more commonly 3–4) alternate rows of circular to hexagonal bordered pits on their radial walls. The rays are 1–3 (commonly 2) cells wide and 2–90 (average 14) cells high or 50–2000 (average 380) μm in height (Fig. 2d, e). Features of this wood conform to the original material of *Pitus withamii* Lindley & Hutton (Fig. 2g, h) in the Kidston collection (HM) and the D. H. Scott collection (BMNH). *P. withamii* L. & H., which is one of the most important Lower Carboniferous trees, was first described by Witham (1830) from the Craigleith quarry near Edinburgh (see also Long 1979) which is of late Viséan (? Asbian) age. According to the measurements made by one of us (JG), in *Pitus withamii* the rays are 1–4 cells wide and 2–78 (average 12–14) cells high or 60–2200 (average 380) μm in height.

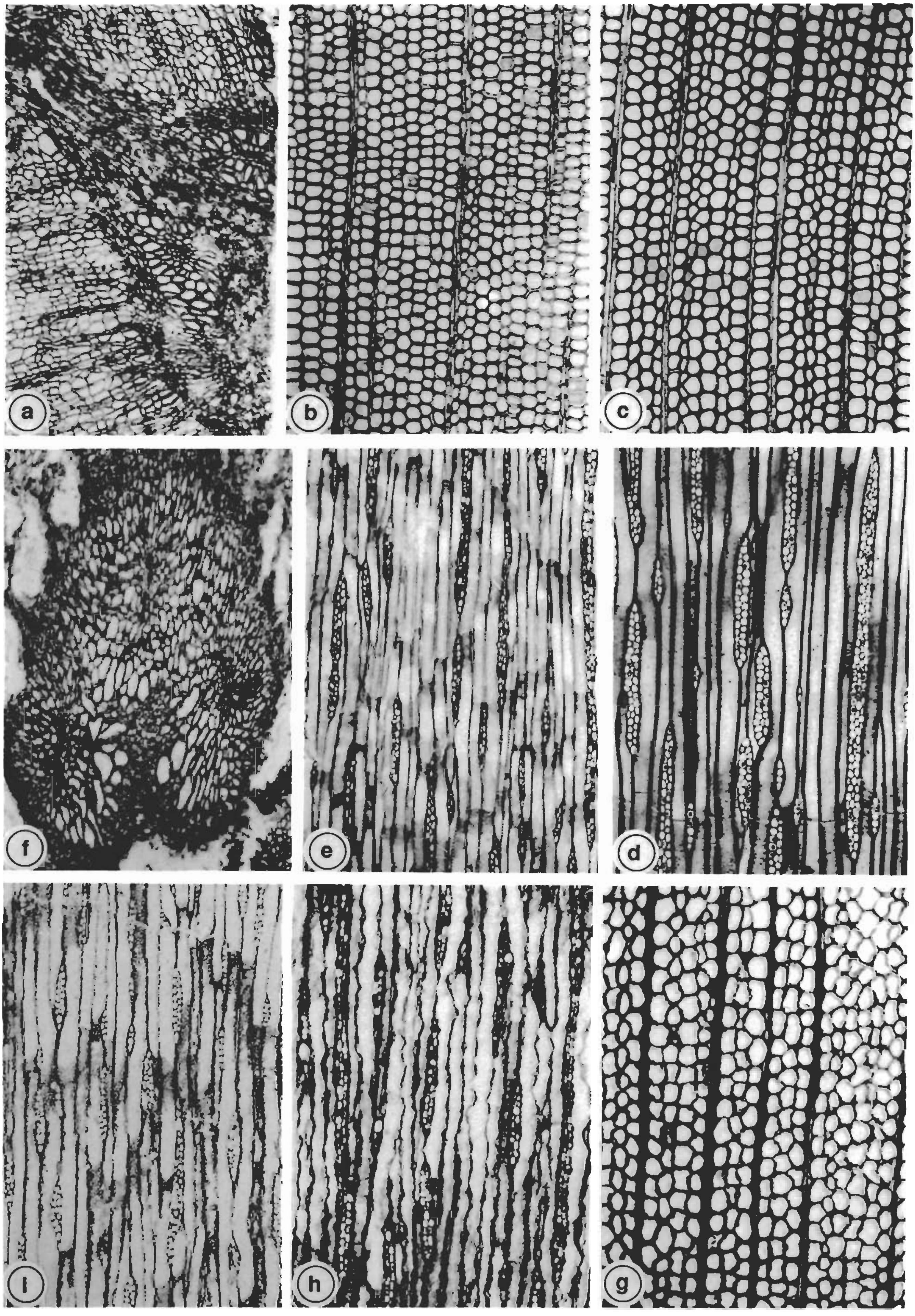
The size of the tracheids in the specimen HM Kidston 194 (average radial diameter 60 μm) fits with that observed in the East Kirkton wood but, in contrast, the tracheid diameter (*c.* 78 μm) in the specimen HM Kidston 483 (Fig. 2g) largely exceeds this value. We consider, however, that this difference may be explained by variation in tracheid size related to different positions in the trunk as discussed below.

3.2. Ontogenetic variability

In one specimen (NMS G 1993.14.43) showing a small portion of the pith preserved (Fig. 2a), we have been able to quantify the variability of tracheid and ray size along a radius more than 20 cm long. We observed that the radial diameter of the innermost tracheids averages 40 μm and increases up to 60 μm at 200 mm from the pith (compare Fig. 2a, b and c). This suggests that one might expect that at the periphery of bigger trunks the radial diameter of wood tracheids would exceed 70 μm, as observed in Kidston's slides of *Pitus withamii*. In contrast, the ray size shows no significant change (Fig. 2d, e), the average height being 356 μm at 18 mm from pith and 384 μm at 200 mm from pith; this is confirmed by the average height in number of

Figure 1 (a–g) *Eristophyton fasciculare* Kidston; (a) detail of transverse section of the pith (P), primary (X) and secondary xylem, note the broader innermost (IW) secondary xylem tracheids, NMS G 1993.14.39a BTO4, Unit 72, ×50; (b) secondary xylem of the same axis at 10 mm from the pith, note the faint 'growth ring', NMS G 1993.14.39b FT 02, ×50; (c) Tangential section of the secondary xylem showing uni-to biseriate rays of various height, NMS G 1993.14.39c FLT 02, ×50; (d) leaf trace in the secondary xylem with three protoxylem strands, NMS G 1993.14.41 E2T01, Unit 72, ×40; (e) transverse section of the secondary xylem, cambium and inner secondary phloem, NMS G 1993.14.7a CT01, loose, ×50; (f) detail of the secondary phloem, transverse section showing tangential tiers of fibres (F), probable sieve cells (C) and parenchyma cells with dark contents (P), NMS G 1993.14.7b CT01, ×100; (g) detail of phloem, longitudinal section showing long, thick-walled fibres and parenchyma, NMS G 1993.14.7c C1 ALR01, ×50. (h)*Bilignea cf. solida.* Longitudinal section of the central column and secondary xylem (on the left) with the proximal termination of an oblique leaf trace, note the connection of the elongated tracheids of the leaf trace with the short tracheids of the central column, NMS G 1993.14.22 ELO7, loose, ×50.


IW
X
P
a
b
c
d
g
←F
P→
C
F
C
F
f
h
e


a
b
c
f
e
d
i
h
g

cells, which is constantly 14 cells. However, the maximum height of rays increases from 48 to 90 cells.

3.3. Leaf traces and stelar organisation

Large pieces of wood generally show no leaf traces because the traces are occluded by parenchyma after a course of about 15 mm in the wood. This has been demonstrated on specimen NMS G 1993.14.43 where the leaf trace is at first circular (600–700 μm in diameter) with 1–2 protoxylem strands. This trace enlarges as it passes obliquely through the wood, exceeding 1 mm in diameter, then it becomes U-shaped to trilobed, with 3 protoxylem strands (Fig. 2f) before being occluded by parenchyma. A comparable pattern has been described in the stem of *Eristophyton waltonii* (Galtier & Scott 1990). This suggests that these arborescent plants bore leaves on stems and branches no more than 20–30 mm in diameter and that these leaves were shed ultimately when axis diameter increased due to secondary xylem and secondary cortex development.

A very small portion of the pith is preserved (Fig. 2a), and it shows only three mesarch primary xylem strands which are separated from the wood by several rows of parenchyma cells. Owing to the very incomplete preservation, it is difficult to interpret the stelar organization of this plant.

3.4. Comparison with *Eristophyton*

Several features of *Eristophyton*, such as the massiveness and lateral coalescence of primary xylem strands or the organization of the innermost secondary xylem with narrow rays and tracheids of homogeneous size (Fig. 2a), differ from what is generally observed in *Pitus* where the rays broaden near and towards the pith. The organization and size of the primary xylem strands, leaf traces and tracheids of the innermost secondary xylem are more reminiscent of the situation in *Eristophyton fasciculare* (compare Figs 1a and 2a). On the other hand, the ray size and density differ in the two types at the same ontogenetic stage (compare Fig. 2e and i). Additional investigations are necessary to decide whether such trunks of *Pitus* type and *Eristophyton fasciculare* branches could belong to the same plant.

4. *Bilignea* Kidston stems

Decorticated axes ranging from 20 mm to 35 mm in diameter (from Unit 88 and loose) are attributed to the genus *Bilignea* Kidston and resemble those of the species *B. solida*, considering characters such as the dense secondary xylem and the occurrence of a 'central column' composed exclusively of short tracheids (Fig. 1h). In the type material of *B. solida* the wood cylinder is 13 mm in diameter and includes a central column, almost 5 mm, and a zone of secondary xylem 4 mm in thickness; our specimens largely exceed these values with a cylinder of wood up to 35 mm in diameter, secondary xylem more than 15 mm thick and a primary xylem column about 7 mm in diameter. The central tracheids are 60–240 μm in transverse diameter and 24–140 μm in length (Fig. 1h); this corresponds to the values given by D. H. Scott (1924) for *B. solida*. Surrounding the short central tracheids is a ring of 12–14 discrete primary xylem strands; they constitute the axial and leaf trace system of the stem. These strands vary greatly in size, the largest (about 1 mm in diameter) are leaf traces just leaving the stele. They consist of elongated tracheids and are quite distinct from the tracheids of the central mass. Internodes are short (1–2 mm). The leaf traces have a steep-oblique course in the innermost secondary xylem, then a horizontal course before their occlusion.

Several features, not described by D. H. Scott (1924), must be mentioned. Longitudinal sections show the abrupt proximal termination of the leaf traces at the level where they connect to the tracheids of the central column (Fig. 1h); at this level the leaf trace tracheids become shorter and broader. This feature has not been recognised on the original slides of *B. solida* which we have re-examined and where the leaf traces preserved their individuality, passing down for several internodes at the edge of the central column before undergoing lateral fusion with the next strand on the anodic side as described by D. H. Scott (1924). Lateral fusion of sympodial strand and leaf trace along a tangential plane has not been observed in the East Kirkton specimens. These differences in the pattern of leaf trace divergence must be considered in more detail in a subsequent study because they may justify the taxonomic separation of the East Kirkton specimens from *B. solida*. According to D. H. Scott (1924), the original material of *B. solida* came from the Carboniferous of Ayrshire, but the series to which it belongs is not known.

5. Conclusions

The objective of this paper was to summarise data on the woody gymnosperms present at East Kirkton in addition to *Stanwoodia* Galtier & Scott (1991) recently described. This study raises a number of questions concerning relationships of *Pitus*-type trunks with *Eristophyton* branches, and the range of variation within the species *Eristophyton fasciculare* and *Bilignea solida*, which will be discussed in detail elsewhere. We illustrate (Fig. 1b; see also Galtier & Scott 1991 their fig. 2a, c) but do not discuss the occurrence of 'growth rings' in the wood of these axes. Their development is irregular and we attribute them to a reaction of the plant to the stressful environment, rather than to regular seasonal variations. This study suggests that all the trees of the East Kirkton plant assemblages were gymnosperms, of which we have found transported fragments of trunks and branches

Figure 2 (a–f) *Pitus cf. withamii*; (a) detail of the pith, primary xylem and innermost secondary xylem, transverse section, NMS G 1993.14.43a A7T01, loose, ×50; (b) secondary xylem of the same stem at 20 mm from the pith, NMS G 1993.14.43b A7T01, ×50; (c) secondary xylem of the same at 200 mm from the pith, NMS G 1993.14.43c A3T01, ×50; (d) tangential section of the secondary xylem at 200 mm from the pith, corresponding to Fig. 2c, NMS G 1993.14.43d A3LT02, ×50; (e) tangential section of the same at 20 mm, corresponding to Fig. 2b, NMS G 1993.14.43e A9LT01, ×50; (f) U-shaped leaf trace in oblique transverse section before its occlusion, note the three protoxylem strands, NMS G 1993.14.43f A8 T04, ×40. (g–h) *Pitus withamii* Lindley & Hutton. Slides 484–485 Kidston collection, HM. (g) transverse section of secondary xylem, ×50; (h) corresponding tangential section, ×50. (i) *Eristophyton fasciculare*. Tangential section of the secondary xylem at 35 mm from the pith, compare to Figs 1c and 2d, e, h, NMS G 1993.14.19 A2L02, Unit 72, ×50.

belonging to three or four different taxa. These plants are interpreted as arborescent pteridosperms (see Galtier 1992) differing from smaller forms like *Lyginopteris*, *Calamopitys*, etc., in the characters of their denser wood and relatively smaller leaves (as suggested by the size of leaf traces). The leaves were densely borne (short internodes) on the distalmost branches and were shed prior to a later phase of wood development. Considering the abundance of compression foliage of *Sphenopteridium*, *Adiantites* and *Spathulopteris* (Scott *et al.*, this volume), which are putative leaves of these plants, we may suggest that the vegetation surrounding the East Kirkton lake was dominated by these gymnosperms. However we have no way of knowing if they constituted dense forests or a more open vegetation.

6. Acknowledgments

We thank W. D. I. Rolfe and the team from the National Museums of Scotland for their assistance in the field and for providing most of the material studied, N. D. L. Clark, Hunterian Museum for the loan of slides from the Kidston collection, Brigitte Meyer-Berthaud for reading and commenting upon the manuscript and J. Guiraud, Montpellier for technical assistance with thin-section preparation. This work was supported by a grant Alliance (British-French Joint Research Programme 1992). Publication N° 93056 de l'Institut des Sciences de l'Evolution (URA 327 CNRS).

7. References

Brown, R., Scott, A. C. & Jones, T. P. 1994. Taphonomy of plant assemblages from the Viséan of East Kirkton, West Lothian, Scotland. TRANS R SOC EDINBURGH: EARTH SCI **84**, 267–274.

Cunningham, R. J. H. 1838. On the geology of the Lothians. MEM WERNER NAT HIST SOC EDINBURGH **7**, 103–60.

Galtier, J. 1992. On the earliest arborescent gymnosperms. COUR FORSCH INST SENCKENBERG **147**, 119–23.

Galtier, J. & Scott, A. C. 1990. On *Eristophyton* and other gymnosperms from the Lower Carboniferous of Castelton Bay, East Lothian, Scotland. GEOBIOS **23**, 5–19.

Galtier, J. & Scott, A. C. 1991. *Stanwoodia*, a new genus of probable early gymnosperms from the Dinantian of East Kirkton, Scotland. TRANS R SOC EDINBURGH: EARTH SCI **82**, 113–23.

Kidston, R. 1923. Fossil plants of the Carboniferous rocks of Great Britain. MEM GEOL SURV GT BRIT **2**, 1–681.

Long, A. G. 1979. Observations on the Lower Carboniferous genus *Pitus* Witham. TRANS R SOC EDINBURGH **70**, 111–27.

Rolfe, W. D. I., Durant, G., Fallick, A. E., Hall, A. J., Large, D. J., Scott, A. C., Smithson, T. R. & Walkden, G. 1990. An early terrestrial biota preserved by Viséan vulcanicity in Scotland. *In* Lockley, M. G. & Rice, A. (Eds) *Volcanism and fossil biotas: implications for preservation, evolution and extinction*, 13–24. GEOL SOC AM SPEC PAP, **244**.

Rolfe, W. D. I., Durant, G. P., Baird, W. J., Chaplin, C., Paton, R. L. & Reekie, R. J. 1993. The East Kirkton Limestone, Viséan, West Lothian, Scotland: introduction and stratigraphy. TRANS R SOC EDINBURGH: EARTH SCI **84**, 177–188.

Scott, A. C., Brown, R., Galtier, J. & Meyer-Berthaud, B. 1994. The distribution of fossil plants from the Viséan of East Kirkton, West Lothian, Scotland. TRANS R SOC EDINBURGH: EARTH SCI **84**, 249–260.

Scott, A. C., Galtier, J. & Clayton, G. 1984. Distribution of anatomically-preserved floras in the Lower Carboniferous in Western Europe. TRANS R SOC EDINBURGH **75**, 311–40.

Scott, D. H. 1902. On the primary structure of certain Paleozoic stems with the *Dadoxylon* type of wood. TRANS R SOC EDINBURGH **40**, 331–65.

Scott, D. H. 1924. Fossil plants of the *Calamopitys* type from the Carboniferous rocks of Scotland. TRANS R SOC EDINBURGH **53**, 569–96.

Witham, H. T. M. 1830. Vegetation of the first period of an ancient world. PHIL MAG **7**, 23–31.

Wood, S. P., Panchen, A. L. & Smithson, T. R. 1985. A terrestrial fauna from the Scottish Lower Carboniferous. NATURE **314**, 355–56.

JEAN GALTIER, Laboratoire de Paléobotanique, Institut des Sciences de l'Evolution, URA 327 CNRS, Université de Montpellier II, Sciences et Techniques du Languedoc, 34095 Montpellier, France.
ANDREW C. SCOTT, Geology Department, Royal Holloway and Bedford New College, Egham Hill, Egham, Surrey TW20 0EX, UK.

(*Published* 9 *February* 1994)