Anatomically preserved conifer-like stems from the Upper Carboniferous of England

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SUMMARY

Gymnosperm stems preserved in volcaniclastic deposits, from the Upper Carboniferous (Westphalian C) of the West Midlands, England, U.K., provide anatomical characters of the wood, pith and primary xylem which allow us to interpret them as conifers. They would represent the earliest report of an anatomically preserved member of this group, complementing the previous assignment to conifers of fusainized leafy twigs from the Westphalian B of Yorkshire, U.K., mainly based on detail of leaf structure.

1. INTRODUCTION

Conifers, which are a prominent component of the extant flora, have a very long fossil record from the Palaeozoic era. Their radiation in Permian and Mesozoic times has been well documented (Florin 1951; Miller 1977; Clement-Westerhof 1988). In contrast, the question of their origin remains unsolved and is the matter of considerable discussion and contradictory theories. One hypothesis, based on vegetative shoot structure, suggests that the Devonian progymnospermous Archaeopteridales are conifer progenitors (Beck 1981), although it has been speculated that conifer origin involved a developmental change in shoot structure among either Pteridospermales or Cordaitales (Rothwell 1982). Our most complete examples come from the Upper Pennsylvanian-basal Permian limestone of Hamilton, Kansas (Mapes & Rothwell 1988). They comprise leafy branches, assigned to *Walchia*, showing anatomical preservation. Older limonitized twigs have been recorded from sediments of possibly late Westphalian D age from Oklahoma, U.S.A. (Rothwell 1982). However, the oldest presently known conifer comprises small fusainized leafy twigs from the lower Westphalian B of Yorkshire yielding information on the leaves and stomata (Scott 1974; Scott & Chaloner 1983). We report here the earliest occurrence of woody stems providing anatomical characters of conifers.

2. STRATIGRAPHY AND SEDIMENTOLOGICAL SETTING

The fossil conifer-like stems were collected from the lowermost part of a volcaniclastic unit within the Etruria Formation (Westphalian C, Upper Carboniferous), recently exposed by quarrying for brick clay near Kingswinford in the West Midlands, U.K. (figure 1) (Glover *et al.* 1992).

During late Carboniferous (Westphalian B and C) times the area lay close to the southern margin of the Pennine Basin, bounded to the south by the emergent Wales–Brabant Massif, and sedimentation was greatly influenced by early Hercynian orogenic movements (Besly & Turner 1983; Besly 1988). The sequence, exposed in the quarry and deduced from borehole records in the area (figure 2), exhibits an upward change from mottled, grey–yellow (waterlogged) to red–purple (well drained, oxidized) paleosol horizons over this stratigraphic interval, which predominantly consists of mudstone and siltstone with thin channellized sandstones (Besly 1988). The conifer-bearing lapilli tuff forms the basal bed of the volcaniclastic unit (figure 2). This consists, in upward sequence, of a basal, scoriaceous lapilli tuff (0.6 m thick) with well-preserved conifer stems, passing up to thinly laminated tuffaceous mudstone and siltstone (0.4 m thick), which in turn is overlain by a coarse volcaniclastic breccia (up to 30 m thick in boreholes). The conifers are preserved *in situ* mostly as single stems, ranging from 5 to 15 mm in diameter, and up to 250 mm in length, and with a vertical or near-vertical orientation, but we have no proof that they were preserved in position of growth. The stems are partly fusainized (Scott 1989) and are also preserved as calcareous permineralization, best known from analogous environments from the Lower Carboniferous (Scott 1990). The surrounding tuff exhibits faint, parallel lamination, and, in thin section, scoriacious lapilli together with fresh and altered plagioclase laths are apparent. The gymnosperm stems do not extend to the upper, thinly laminated, tuffaceous mudstone and siltstone which

Proc. R. Soc. Lond. B (1992), **247**, 211–214
Printed in Great Britain

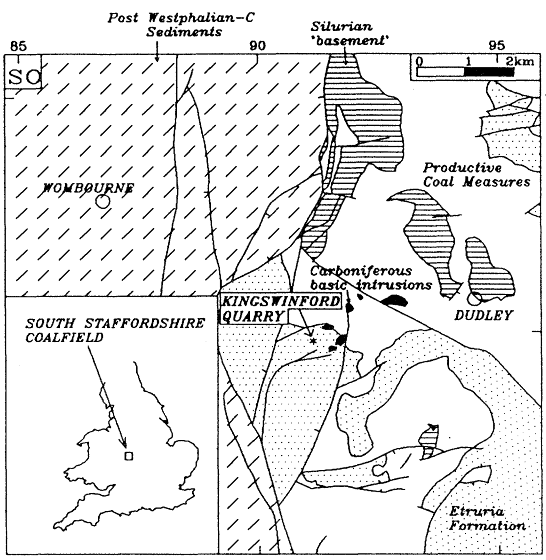

Figure 1. Generalized geological map of the Kingswinford area; inset map shows the location of the South Staffordshire Coalfield.

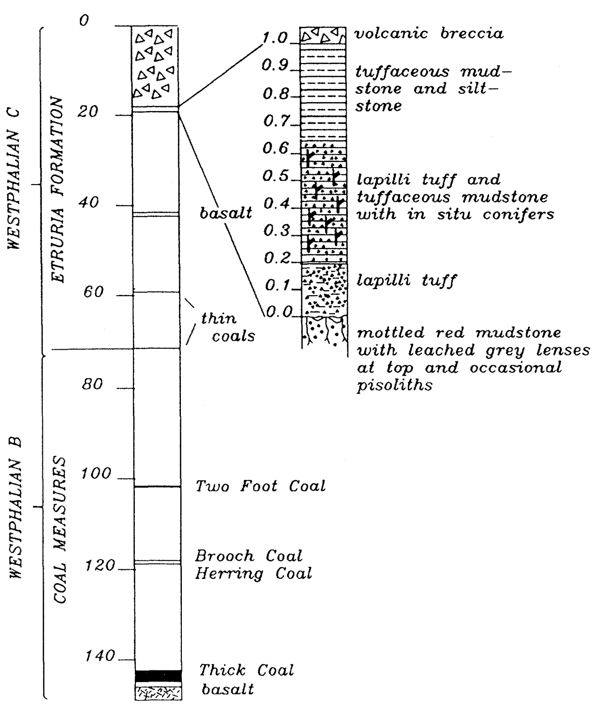

Figure 2. Generalized vertical section through part of the Upper Carboniferous strata in the Kingswinford area; inset shows details of the conifer-bearing volcaniclastic horizon. Scale in metres.

exhibit possible surge-flow structures. The overlying volcanic breccia clasts include large blocks of country-rock and basalt; some of the latter show quench texture typical of volcanic bombs.

The tuff and volcanic breccia are interpreted as the pyroclastic, and possibly epiclastic, deposits of a tuff-cone, built up by phreatomagmatic eruptions (Glover *et al.* 1992; Wohletz & Sheridan 1983; Cas & Wright 1987). The faint lamination of the lowermost tuff, vertical or near-vertical orientation of the delicate conifer stems, and their near-perfect preservation suggest gentle but rapid deposition of the surrounding volcaniclastic sediment. Planar lamination in the overlying tuffaceous mudstone and siltstone implies subaqueous deposition, probably in a shallow lake or mire, although a subaerial or subaqueous depositional environment for the underlying conifer-bearing horizon is equivocal. Absence of the outermost bark layer of most stems suggests that they were charred by the heat of an air-fall deposit. The remarkable internal preservation may also be in part due to early diagenetic mineralization of the conifers by fluids rich in calcium carbonate derived from the entombing tuff.

3. ANATOMY OF THE STEMS AND PALAEOBOTANICAL INTERPRETATION

All the stems studied, except one, are decorticated (figure 3*a*). Where preserved, the cortex is about 1 mm thick and shows evidence of poorly preserved leaf bases and leaves in attachment, but histological detail is not visible because of incomplete coalification. In contrast, excellent preservation of the pith, primary xylem and secondary xylem provides us with decisive characters consistent with the interpretation of these stems as conifers.

The pith (2–3 mm in diameter) consists of a continuous parenchyma (figure 3*b*) with cells commonly arranged in vertical series (figure 3*c*). These cells generally have distinctive black opaque contents, and range from 42 to 96 μm in diameter and 48 to 144 μm in height. At the periphery of the pith, and in contact with the xylem, smaller cells without dark content occur (figure 3*c*). Scattered within the pith are also clusters of larger cells, up to 130 μm in diameter, which are broader than high (figure 3*b*, SN). These cells have dark contents and apparently thicker walls; their function (secretory, storage, strengthening) is problematical. The eustele consists of a number of discrete primary xylem strands with endarch maturation. Metaxylem tracheids have annular to scalariform thickenings on all walls (figure 3*c*). Secondary xylem tracheids are small, averaging 24 μm in diameter both in radial and tangential dimensions; they have uni- to biseriate pitting on radial walls only (figure 3*e*). Bordered pits (9–12 μm in diameter) have oblique, elliptical, crossed apertures (figure 3*g*). Where the arrangement is biseriate, the pits are polygonal; where it is uniseriate, the pits are round but more or less contiguous, rarely spaced (figure 3*g*). Rays are small, uniseriate (rarely two cells wide near the pith) and 1–7 (commonly 2–3) cells high (figure 3*d*). They are composed of parenchyma cells without any evidence of ray tracheids. Individual ray cells are 24–35 μm high, 7–24 (commonly 10–14) μm wide and 40–90 μm long radially (figure 3*e*). Cross-field areas show 2–6 simple to bordered pits with an oval, oblique aperture (figure 3*f*). Secondary xylem thickness ranges from 2.5 mm to 5.5 mm in the larger specimen. There is no evidence of growth rings in the small twigs (figure 3*a*) but there is some irregular zonation in the large stems. Leaf traces are small and helically arranged (figure 3*a*, LT). One branch trace has been observed in a large specimen.

An alternative interpretation of these stems is to attribute them to cordaites or to putative arborescent

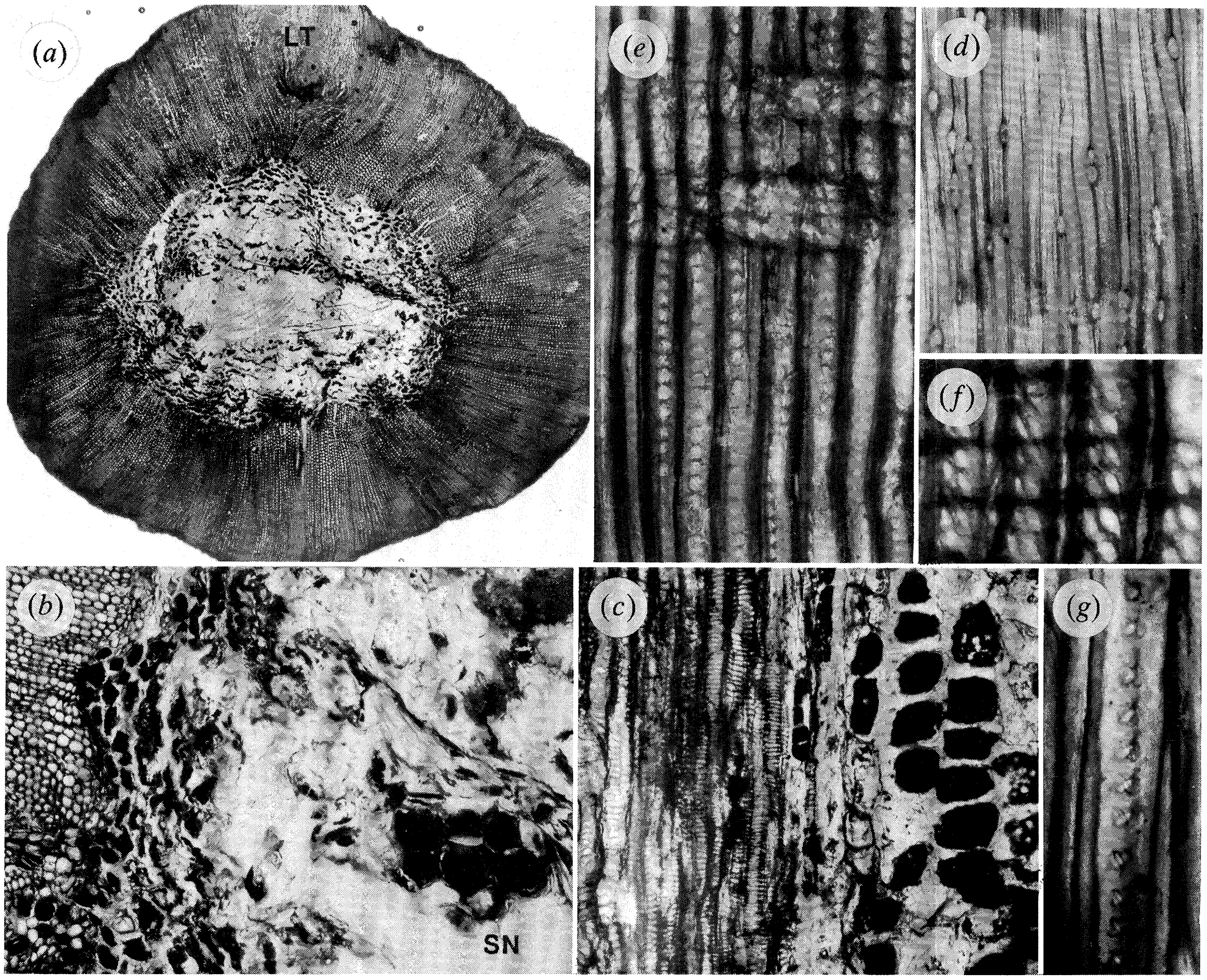

Figure 3. Anatomical characters of the conifer-like stems. (*a*) Transverse section of decorticated twig showing the parenchymatous pith and cylinder of wood with one leaf trace (LT) (magnification × 15). (*b*) Transverse section of the secondary xylem (on left) and the pith with one 'secretory' or 'sclerotic' nest (SN) (× 62). (*c*) Longitudinal radial section through the inner secondary xylem (on left), primary xylem with scalariform tracheids and parenchymatous pith (× 124). (*d*) Longitudinal tangential section of the secondary xylem showing small rays (× 100). (*e*) Longitudinal radial section through the secondary xylem showing tracheid pitting and rays (× 200). (*f*) As (*e*), detail of ray cross field pitting (× 400). (*g*) As (*e*), detail of one tracheid with uniseriate pitting (× 400).

pteridosperms like the Lower Carboniferous *Pitus* or *Eristophyton* (Long 1979; Lacey 1953; Galtier & Scott 1990), which have been sometimes considered as possible progenitors of cordaites and conifers because of their dense wood. However, these differ from the present stems in their broader leaves, very wide pith and larger tracheids in both secondary and primary xylem (Galtier 1992). Distinguishing cordaites and conifers on the basis of wood is difficult; however, most cordaites exhibit secondary xylem tracheids of larger diameter, with bi- to multiseriate crowded polygonal pits and no uniseriate circular pitting (Doubinger & Marguerier 1975; Rothwell 1988). In addition, cordaite stems are often characterized by diaphragms in the pith, a feature also shown by a few conifers but absent in our specimens. However, pith 'secretory' or 'sclerotic' nests have never been reported in cordaites although they are of common occurrence in fossil and some extant conifers (Mapes & Rothwell 1988; Doubinger & Marguerier 1975). In contrast to the contemporaneous Westphalian cordaites, for which stem anatomy has long been known (Rothwell 1988), there was no information available on the vascular organization of conifers before the Westphalian D. Conifer twigs from the Pennsylvanian of the U.S.A. (Rothwell 1982; Mapes & Rothwell 1988) have not been described in great detail; however, the published data suggest a close similarity with our specimens regarding features of pith, stele, wood and, more precisely, characters of tracheid size and pitting, rays and pith nests. The only significant difference concerns the occurrence, in the oldest American twigs, of supposed resin canals in the pith. Similar structures are apparently absent in our gymnosperms.

4. CONCLUSION

We propose that the combination of characters allowing the interpretation of these twigs as conifers are those of the continuous parenchymatous pith with 'secretory' or 'sclerotic' nests, narrow secondary xylem tracheids with uni- to biseriate pitting, small rays and evidence of narrow leaves in connection. Several of these characters are present in some cordaites

(Rothwell 1988), but this conforms to the close affinities of the two groups; future studies must try to define the polarity of such characters to be used in cladistic analysis. Our finding extends the range and documents the oldest data on vascular structure for a conifer, complementing the previous assignment to this group of fusainized leafy twigs from the Westphalian B of Yorkshire mainly based on detail of leaf structure. This supports the idea that conifers originated at least during mid-Carboniferous times. Palaeoecological interpretations also fit well with the observation that early conifers appear to be from drier sites, often near presumed upland areas (Scott & Chaloner 1983; Rothwell & Mapes 1988; Lyons & Darrah 1989).

We thank Redland Bricks for access to the quarry, and particularly Dr N. Griffiths of that company for bringing the site to our attention and for access to borehole records. We thank Mr J. Guiraud for help in the preparation of the material. This paper is published with the approval of the Director, British Geological Survey (NERC).

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Submitted by W. G. Chaloner; received 10 December 1991; accepted 8 January 1992