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Notes
Tree trunks of *Pitus primaeva* in Mississippian (Courceyan) rocks at Montford, near Rothesay, Isle of Bute, Scotland

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**Synopsis**

Silicified tree trunks are described for the first time from Montford, near Rothesay, Isle of Bute, Scotland. The fossils occur in a fault-bounded succession, which is probably part of the Mississippian (Courceyan) Kinnesswood Formation. Quantitative anatomical analysis indicates that the tree trunks belong to the arborescent pteridosperm, *Pitus primaeva* Witham. Growth interruptions preserved in branches imply that these trees experienced aperiodic water stress, perhaps reflecting monsoonal seasonality in this part of palaeoequatorial Laurasia.

**Introduction**

Anatomically preserved fossil plants are extremely common in Mississippian rocks in Scotland’s Midland Valley and surrounding areas (Scott *et al.* 1984a). Most spectacular of all are the large fossilized tree trunks belonging to the genus *Pitus*, first discovered, in 1826, at Craigleith Quarry, Edinburgh (Witham 1831, 1833), and subsequently recognized at many other sites across the region (Gordon 1935; Long 1979; Galtier & Meyer-Berthaud 2006). For many years, the systematic position of *Pitus* was enigmatic (Scott 1900). However, anatomical studies have since provided support for the hypothesis that it was a large arborescent pteridosperm (Long 1963).

Where found in growth position at Kingwater, Cumbria, tree stumps of *Pitus primaeva* are up to 2.5 m in diameter (Long 1979). Based on these dimensions, biomechanical inferences suggest these trees were more than 40 m high (Mossbrugger 1990), making them the largest trees on Earth at that time. Evidently, *Pitus*, together with other gymnosperms and ferns, formed a prominent component of the seasonally dry tropical forests that covered southeast Laurasia in Mississippian times (Falcon-Lang 1999a, 2000). Here we report a new site containing tree trunks of *Pitus primaeva* Witham 1833 from the Isle of Bute, Scotland.

**Geological setting**

The fossil tree trunks, which form the focus of this paper, were found at Montford, 1.5 km SE of Rothesay, on the east coast of the Isle of Bute. The fossils occur in very poorly exposed, barnacle-encrusted, intertidal outcrops that begin immediately adjacent to the entrance of Ardencraig Road, Montford (Grid Reference NS 1068 6448) and extend 170 m south along the coast towards Ascog within the confines of a small unnamed bay (Grid Reference NS 1067 6431). According to the 1: 6300 British Geological Survey map (Scotland Sheet 29, Rothesay, 1971) this area lies within a small NE–SW-trending fault-bounded basin containing Mississippian rocks, close to the NW basin margin (Fig. 1).

The precise age of the fossil-bearing strata is uncertain. A British Geological Survey borehole (NS 06 SE/8) drilled at Ascog (Grid Reference NS 0986 6302), 1.1 km SW of the site, proves the existence of a 296 m thick Mississippian succession within the basin (Amstrong 1978). From base to top, the stratigraphic succession comprises the Tournaisian Kinnesswood, Ballagan, and Clyde Sandstone formations (Paterson & Hall 1986), and the early Visean Clyde Plateau Volcanic Formation (Waters *et al.* 2007). Cementstones of the Ballagan Formation occur downdip of our fossil site, 200 m to the south, at Mill Hole (Grid Reference NS 1067 6411) on the downthrow of a fault (Hill 1979). This structural relationship implies that beds at our site are older than the Ballagan Formation. Following Hill (1979), we therefore assign these rocks, with uncertainty, to the Kinnesswood Formation, which is of early Courceyan age (c. 350–359 Ma; Waters *et al.* 2007).

Between April 2007 and June 2008, one of us (EH) collected about 350 fossil wood fragments from the inter-tidal zone at the Montford site (Fig. 2). Almost all of these specimens occurred as water-worn pebbles and cobbles, 0.04–0.21 m in diameter, having earlier eroded out of the underlying rocks. However, a few specimens were observed in situ demonstrating that the rest of the material had originated in the immediate vicinity.
vicinity. The largest of these in situ specimens was a trunk, 0.72 m in diameter and <1.84 m long, its full extent being obscured by overlying rocks and beach gravel. Many of the water-worn specimens of fossil wood share very close petrographic similarities and probably represent fragments of a relatively small number of large tree trunks, which have disintegrated in the intertidal zone over the past few decades. This process can be seen in action, as small fragments have broken off the large in situ trunk in the course of our own observations.

Fossil wood occurs in one of two modes at Montford. The first type, dark calcified wood, is confined to the north of our collection area. Where rarely seen in situ it occurs in successions of carbonate-cemented basalt tuffs and vesicular agglomerates showing undulatory lamination. The second type, pale- to dark-coloured silicified wood, is found in a few barnacle-encrusted outcrops in the southern part of our collection area. Specimens occur in medium- to coarse-grained, poorly sorted sandstone and siltstone beds showing undulatory lamination, ripple cross-lamination, symmetrical ripples, and draped mounds.

These very limited observations imply that the fossil-bearing succession was deposited in a shallow, standing body of water (probably a small lake) near a basaltic volcanic centre. The fossil assemblages probably represent tree trunks that were either stripped from the adjacent shoreline following a volcanic eruption (waterlain basaltic tuffs and agglomerate facies) or carried to the lake by drainage channels (sandstone and siltstone facies). The concentration of abundant fossils adjacent to the basin margin may suggest that the tree-trunks were growing on Devonian rocks to the NW. Poor exposure limits further interpretation.

**Fossil tree trunks**

Most of the c. 350 fossil wood specimens were transversely sectioned, polished, and examined with a hand lens to assess the quality of preservation of plant anatomy and to undertake preliminary identification. On the basis of these observations all specimens comprise a gymnospermous structure with prominent multicellular rays, and probably represent a single morphotype. Specimens range from compressed or recrystallized material with poor anatomical preservation to those showing excellent cellular detail. Generally, silicified material shows far better anatomical preservation than calcified material.

Seven of the best-preserved silicified specimens were selected for thin sectioning. For each, three standard...
petrographic sections were prepared along Radial Longitudinal (RLS), Tangential Longitudinal (TLS) and Transverse (TS) sections. This material, and associated thin sections, is stored in the Bristol University Geology Museum (accession numbers: BRSUG 28880–28886). Although well preserved, in four of these specimens (BRSUG28880–28883), organic material was entirely lacking, such that there was no colour contrast between the silicified cell walls and the crystals filling the lumen. This made detailed anatomical observation very difficult.

The following anatomical description is based on the remaining three mature trunk specimens (BRSUG28884–

Fig. 3. Anatomical features seen in trunk wood of *Pitus primaeva* at Montford, Isle of Bute. All images from BRSUG28884. (A) Tracheids showing 2–3-seriate, alternate bordered pitting, scale: 75 µm, RLS; (B) tracheids showing 1–2-seriate, alternate bordered pitting, scale: 75 µm, RLS; (C) tapered ends of tracheids showing terminal curvature, probably around a ray, scale: 100 µm, RLS; (D) ray showing elongate parenchyma with oblique end-walls, scale: 100 µm, RLS; (E) cross-field pitting, scale: 25 µm, RLS; (F) 2–4-seriate rays, scale: 300 µm, TLS; (G) rays, up to 12-seriate, scale: 150 µm, TLS; (H) files of tracheids, separated by rays, scale: 350 µm, TS; (I) profusely pitted ray parenchyma, scale: 25 µm, TS.
28886), which to varying degrees retain organic material in their cell walls. A lateral branch, 14 mm in diameter, is embedded in one of these trunks (BRSUG28886) and this juvenile material is described separately from the mature wood seen elsewhere. Following the standard quantitative approach to wood anatomy (Falcon-Lang & Cantrill 2000; Falcon-Lang 2005; Oakley & Falcon-Lang 2009), 100 measurements were taken for each character, and the mean and range are given.

Trunk wood

Mature secondary xylem is best preserved in BRSUG28884, a 0.11 m diameter specimen, representing a fragment of a much larger trunk. It shows the following characters: In RLS, tracheid bordered pitting is 1-seriate (19%), 2-seriate (63%), 3-seriate (16%) or 4-seriate (2%), with pits always being alternately arranged and contiguous (Fig. 3A, B). Tracheid pits are circular to hexagonal (10.4 µm diameter) with circular or oval, obliquely orientated apertures (4.8 µm diameter). Tracheids are commonly short (1.2–1.8 mm high), show a terminal taper and curvature near their tip (Fig. 3C). Clusters of 3 or 4 adjacent curved tracheids may locally terminate at the same height in the trunk (probably around rays). Ray parenchyma cells are elongate (245–307 µm long) with oblique end-walls (Fig. 3D) and show 3–7 (mean 5.62, n=100) circular to oval pits (4 µm diameter) in each cross-field (Fig. 3E). Cross-field pits are of taxodioid or araucarioid type.

In TLS, rays are typically 1–6-seriate or rarely up to 12-seriate (mean 4.41, n=100) and 1–29 cells high, or very rarely up to 55 cells high (mean 11.71 cells, n=100; Fig. 3F, G). Measured with a graticule, rays comprise 30–42% of the tangential area of the wood (mean: 34%, n=15), the remainder made up of tracheids; this equates to 7.3 complete rays per tangential mm² (n=10). Ray parenchyma cells are 20–32 µm high (median 26 µm) and 18–30 µm wide (median 24 µm), and locally filled with opaque material; cells are commonly circular in TLS and leave small intercellular spaces between adjacent cells. Rare bordered pits occur on tangential tracheid walls as uniseriate, contiguous rows, comprising up to 3–4 pits.

In TS, tracheids are rectangular to square with a radial diameter of 37–74 µm (mean 61 µm, n=100) and a tangential diameter of 35–68 µm (mean 59 µm,
TABLE 1
Quantitative comparison of our specimens with the four known morphospecies of *Pitus*, based on description of type material

<table>
<thead>
<tr>
<th>Morphospecies</th>
<th>Ontogeny</th>
<th>Tracheid diameter (µm)</th>
<th>Rays (no. of cells)</th>
<th>Ray cells (µm)</th>
<th>Ray density (rays/mm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Radial</td>
<td>Tangential</td>
<td>High</td>
<td>Wide</td>
</tr>
<tr>
<td>P. antiqua</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>KID 674 HM</td>
<td>Mature</td>
<td>64–85 (72)</td>
<td>79</td>
<td>3–146 (29)</td>
<td>1–8 (4.4)</td>
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<tr>
<td>KID 598 HM</td>
<td>Juvenile</td>
<td>47–73 (58)</td>
<td>43</td>
<td>2–80 (18)</td>
<td>1–4 (2)</td>
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<tr>
<td>P. dayi</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GOR 1478 NHM</td>
<td>Juvenile</td>
<td>30–61 (44)</td>
<td>n.d.</td>
<td>2–43 (14)</td>
<td>1–6 (3)</td>
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<tr>
<td>P. primaeva</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>KID 210/211 HM</td>
<td>Mature</td>
<td>61–75 (69)</td>
<td>68</td>
<td>2–63 (16.4)</td>
<td>1–8 (3.5)</td>
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<td>GOR 1386 NHM</td>
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<td>49</td>
<td>2–58 (14.4)</td>
<td>2–10 (3.4)</td>
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<td>P. withamii</td>
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<td></td>
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<tr>
<td>KID 485 HM</td>
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<td>68–88 (79)</td>
<td>69</td>
<td>2–78 (14)</td>
<td>1–3 (1.6)</td>
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<tr>
<td>SCO 9319 NHM</td>
<td>Mature</td>
<td>50–70 (58)</td>
<td>56</td>
<td>2–53 (14)</td>
<td>1–4 (1.7)</td>
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<tr>
<td>This paper</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BRSUG28884</td>
<td>Mature</td>
<td>37–74 (61)</td>
<td>35–68 (59)</td>
<td>1–55 (11.7)</td>
<td>1–12 (4.4)</td>
</tr>
<tr>
<td>BRSUG28886</td>
<td>Juvenile</td>
<td>15–59 (42)</td>
<td>–</td>
<td>1–53 (12.3)</td>
<td>1–3 (2.3)</td>
</tr>
</tbody>
</table>


n=100; Fig. 3H). Rays are typically 1.5–2.4 mm long (mid-value: 1.95 mm) and separated by 2–9 (mean 4.13, n=100) rows of tracheids. Ray parenchyma cells locally show profuse circular pits on transverse walls (Fig. 3I). Growth rings, or subtle growth interruptions, are entirely absent.

Branch wood

Branch wood is only seen in BRSUG28886, where a lateral branch, 14 mm in diameter, is embedded within a 0.14 m diameter specimen of trunk wood (the original diameter of the trunk is estimated to have been c. 0.19 m). The branch comprises pith, xylem and phloem (Fig. 4A, B). The pith, 7 mm in diameter, is exclusively parenchymatous. Pith parenchyma cells are equidimensional, 58–106 µm diameter, and include three types: thin walled cells with empty lumen, thick-walled cells with empty lumen, and secretory cells filled with opaque material (Fig. 4A, C–D).

In one thin section, two, possibly three, mesarch primary xylem bundles are embedded in the pith, c. 1 mm from its edge (Fig. 4E). Primary xylem tracheids, 11–20 µm diameter (mean: 14.2 µm), show scalariform-thickening. Secondary xylem is similar to that seen in mature trunk wood, differing in having smaller tracheids, 15–59 µm radial diameter (mean: 42.2 µm), and narrower rays, 1–3-seriate (mean: 2.3), of greater density (16 mm², n=1). One notable feature of the secondary xylem in TS is the presence of irregular, closely spaced growth interruptions (*sensu* Falcon-Lang 2003). These are defined by narrow zones (2–3 cells) of smaller than average tracheids (15–20 µm diameter; Fig. 4B) and typically spaced 0.25–0.46 mm apart (mean 0.34 mm, n=8). Where seen departing through the secondary xylem, leaf traces bifurcate a short distance from the pith (Fig. 4B).

The secondary phloem is locally present, up to 1 mm wide, shows poor preservation, and comprises a complex structure of parenchyma, rays, fibres and sieve cells. Very poorly preserved tissue, interpreted as periderm, lies outside the phloem layer (Fig. 4F).

Systematics

Secondary xylem is generally classified as either manoxylic, as in calamopityans, lyginopteridaleans, and medullosan pteridosperms (tracheids >150 µm diameter and multiseriate rays >200 cells high), or pycnoxylic (tracheids <50 µm diameter and short, uniseriate rays) as seen in conifers (Galtier 1992). In this system, our woods would be considered transitional showing both pycnoxylic and manoxylic characteristics. Fossil trunks showing secondary xylem similar to our material include several Mississippian pteridosperms such as *Archaeopitys*, *Cauloxylon*, *Erystphoton*, *Faironia*, *Megaloxylon*, *Pitus* and *Pycnoxyylon* (Galtier et al. 1998; Galtier & Meyer-Berthaud 2006; Decombeix et al. 2006, 2008). However, the occurrence of primary xylem bundles embedded within the pith (as seen in our specimens) is a feature only present in *Archaeopitys* and *Pitus*. Of these morphogenera, *Pitus* shows the closest match in terms of secondary xylem.

Four morphospecies of *Pitus* are known: *P. antiqua* Witham, *P. dayi* Gordon, *P. primaeva* Witham and *P. withamii* Lindley and Hutton (Arnold). A quantitative description of type material of these morphospecies was made by one of us (JG) and summarized in Table 1. For each morphospecies, both juvenile wood, being tissue within a few millimetres of the pith, and mature wood, being tissue more than a few centimetres from the pith, were studied, the exception being *P. dayi* for which only juvenile wood is known (Gordon 1935). Based on secondary xylem alone, only ray width and height allow discrimination between morphospecies (Gordon 1935) and these characters are highly dependent on ontogeny (Falcon-Lang 2005). *P. primaeva* bears closest resemblance to our material, having rays up to 63 cells high (up to 55 cells high in our material) and up to 10 cells
wide (up to 12 cells in our material). In mature specimens of *P. antiqua*, rays are of greater height and lower density, and in *P. withamii* are substantially narrower (Table 1). Several qualitative characters of uncertain systematic value support assignment to *P. primaeava* including the occurrence of pith parenchyma of three types, and the terminal curvature of tracheids.

**Palaeoecology**

One of the most notable features of the branch of *Pitus primaeava* from Montford is the occurrence of growth interruptions. Similar growth interruptions have been previously observed in Mississippian gymnosperms from the Midland Valley of Scotland and surrounding areas (Falcon-Lang 1999a, b). These occur in certain specimens of *Pitus primaeava* (Gordon 1935), *P. withamii* (Galtier & Scott 1994), *P. antiqua* (Galtier et al. 1994) as well as in *Bilignea*, *Endoxylon*, *Eristophyton*, *Stanwoodia* and *Stenomyelon* (Scott et al. 1994b; Falcon-Lang 1999a, b). Growth interruptions are only found in small diameter axes suggestive of branches or a position close to the stem apex. This is most clearly shown by our material where growth interruptions are absent in ontogenetically mature wood in a trunk but present in the juvenile wood of an attached branch.

The factors that give rise to growth interruptions include temporary disturbances to growth such as fires, frosts, floods, droughts, wind damage, insect defoliation and leaf flushes (Falcon-Lang 2003). Twigs and branches tend to preferentially develop growth interruptions (as seen in our material) because their peripheral position means they are more sensitive to subtle environmental changes (Falcon-Lang 2005). The British Isles lay close to the equator on the SE coast of Laurasia during Mississippian times. Growth interruptions in the Montford fossil trees and those found elsewhere most likely reflect monsoonal seasonality with occasional droughts leading to aperiodic water stress. This is consistent with the occurrence of vertic and calcrete paleosols (Wright 1990; Andrews & Nabi 1998), and schizohaline lagoon deposits (Leeder 1974), all of which point to pronounced seasonality in tropical rainfall.

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