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Stigmaria Brongniart: a new specimen from Duckmantian (Lower Pennsylvanian) Brymbo (Wrexham, North Wales) together with a review of known casts and how they were preserved

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Abstract – *Stigmaria* is one of the iconic plant fossils of the Carboniferous and fragments of the narrower parts of the rhizomorph are found in most museum collections. However, very few almost entire specimens have been found and preserved. A new specimen of *Stigmaria* from Brymbo, North Wales is described and compared with other preserved examples from Europe and North America. The Brymbo specimen shows a large portion of trunk still attached to the large stigmarian base, which is a rare find, and this specimen supports our ideas of how these impressively large casts were formed. Stigmarias were preserved by the deposition of minerals around them following a sediment inundation, which gave sufficient support while the tissues rotted and filled with sediments. Remnants of the outer tissues were compressed to form a thin surrounding coal layer.

Keywords: Carboniferous, lycophytes, preservation, rhizomorph.

1. Introduction

Stigmaria Brongniart is the large dichotomizing rhizomorph base of Carboniferous arborescent lycophytes, such as *Lepidodendron* Sternberg, *Lepidophloios* Sternberg and *Sigillaria* Brongniart, that bears spirally distributed roots or circular scars where the roots had once been.

Specimens referable to *Stigmaria* had been figured in early literature (Petiver, 1704; Volkmann, 1720; Woodward, 1729; Martin, 1809), although they were given various names and interpreted in different ways. There was much early debate on the nature of the stigmarian axes and Brongniart (1822) first used *Stigmaria* as a generic name for a type of cast that had been included by Sternberg (1820) in his genus *Variolaria* (a name already given to an extant lichen). Brongniart (1828) later gave a more detailed description of specimens of *Stigmaria ficoides* (Sternberg) Brongniart and made the first proposal for a relationship between *Stigmaria* and the extant quillwort *Isoetes* L., but it was Brown (1848) who demonstrated the relationship between *Lepidodendron* and *Stigmaria*.

The internal structure of *Stigmaria* was first published by Lindley & Hutton (1837) from a specimen that showed both external features and internal anatomy. Anatomical studies were described by many others including Brongniart (1839), Göppert (1841), Binney (1844) and Corda (1845), but it was Williamson (1887) that gave the first comprehensive study of large casts and of anatomy from petrifactions.

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The extensive literature that followed on *Stigmaria* has been summarized to some extent by Jongmans (1936), Chaloner (1967) and Frankenberg & Eggert (1969). Here we describe a new specimen of a virtually complete *Stigmaria* rhizomorph from Brymbo, north Wales that has a sizable trunk attached, which is rather unusual for this iconic Carboniferous plant fossil. We also show that preserved *Stigmaria* fossils are actually rarer than thought and few are well preserved; using this new find, we also summarize how these impressive rhizomorphs became preserved as fossils.

2. Geological setting

The Denbighshire Coalfield is on the southern margins of the Pennine Basin, with a relatively condensed succession of Pennsylvanian (upper Carboniferous) strata (Fig. 1). The succession (Fig. 2) consists in the lower part of grey coal-bearing beds (Lower and Middle Coal Measures) that pass upwards into barren red beds of the Etruria Formation. Recent opencast mining after the closure of the steelworks at Brymbo, Wrexham in north Wales revealed sediments from the Main Coal to the Two Yard Coal (middle–upper Bolsovian, Fig. 2). The Brymbo exposure shows the uppermost *c.* 14 m of the Coal Measures which are associated with two coal seams, the Crank Coal and the Two Yard Coal (Fig. 2). The lower part of the sequence is buried where there is a palaeosol with *Stigmaria*, some of which were removed for storage. The largest basal stump is *c.* 850 cm tall and 105 cm broad at its base, and is covered with

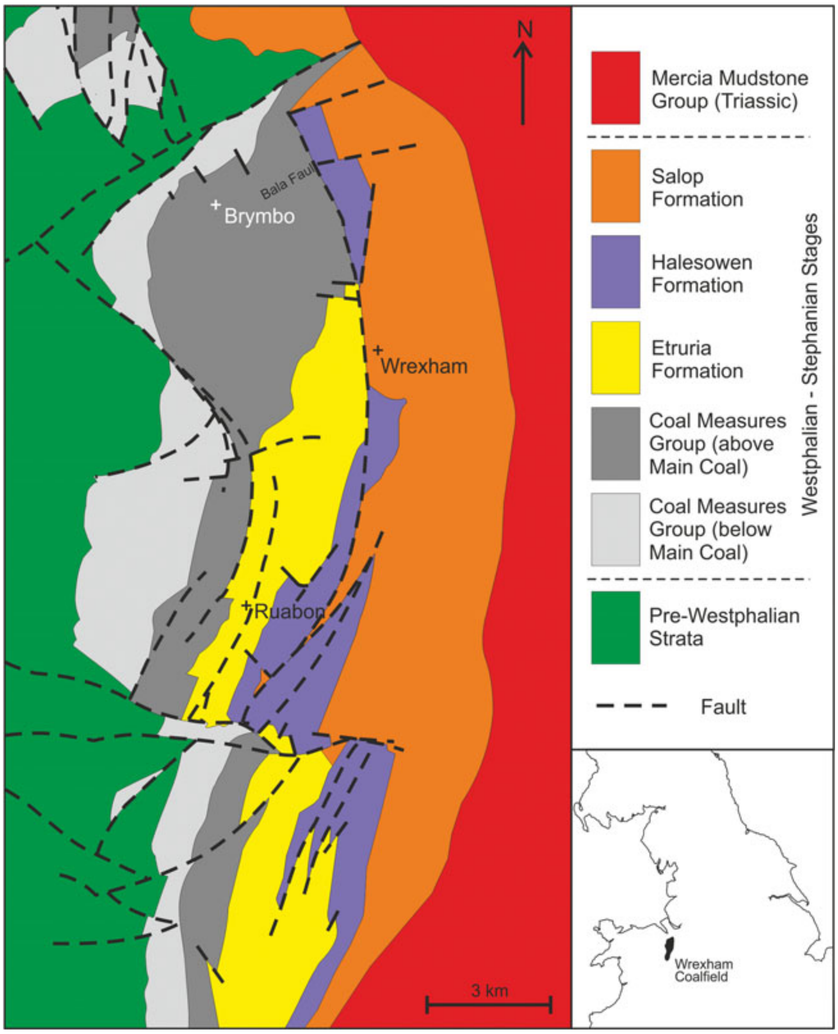

Figure 1. (Colour online) Geological map of the Denbigh Coalfield. Inset shows location of the coalfield in Britain. Figure reproduced with permission from Appleton *et al*. (2011).

vertical ridges suggesting that it was probably the base of a *Sigillaria*. These trunks broadened at their bases, but none had *Stigmaria*.

The Crank Coal is *c.* 0.8 m thick and is overlain by an essentially coarsening sequence of laminated carbonaceous mudstones, within the lowest metre of which is a thin band of ironstone. The succeeding 2 m unit grades from a mudstone to a siltstone with 'inter-tonguing' shallow sandstone lenses. This is overlain by a thin nodular mudstone, which in turn is overlain by a massive sheet-like sandstone. The next 1.5 m is a sequence of four interbedded sandstones with mudstones, which underlies the thin Two Yard Bench Coal. The Two Yard Bench Coal is separated from the Two Yard Coal at the top of the sequence by 70 cm of a mudstone palaeosol (Fig. 2). The sequence at Brymbo has been interpreted by Appleton *et al.* (2011) as a vegetated swampy floodplain (which produced the Crank Coal) that was flooded, and a lake formed (mudstones). As a fluvial delta encroached (coarsening sandstones) the lake shallowed and the floodplain emerged and became re-vegetated (eventually forming the Two Yard Coal).

3. The Brymbo lycophytes

A small area of exposed Carboniferous rocks at Brymbo was saved from opencast mining when a well-preserved assemblage of plant fossils was found. Most importantly, there were both arborescent lycophyte and calamite stems found in growth position at several horizons (Appleton *et al*. 2011; Thomas, 2014).

About 20 erect trunks have been found at the site with most being rooted in a thin 1–2-cm-thick coal parting *c.* 1.25 m above the Crank Coal. The trunks range up to 1.5 m in diameter and 2.5 m in height with their casts being formed either in sandstone or less durable mudstone, but there are no recognizable *Stigmaria*. The erect stems are therefore enclosed in the succeeding 2 m unit that consists of mudstone grading upwards to a siltstone with inter-tonguing sandstone lenses (Fig. 2). The basal part of one of the trunks was filled with yellow clay, composed dominantly of fluorapatite (calcium halophosphate) with some goethite, which gave it a yellow colour. We have no explanation for this preservation as no other deposit of this clay has been found on the site.

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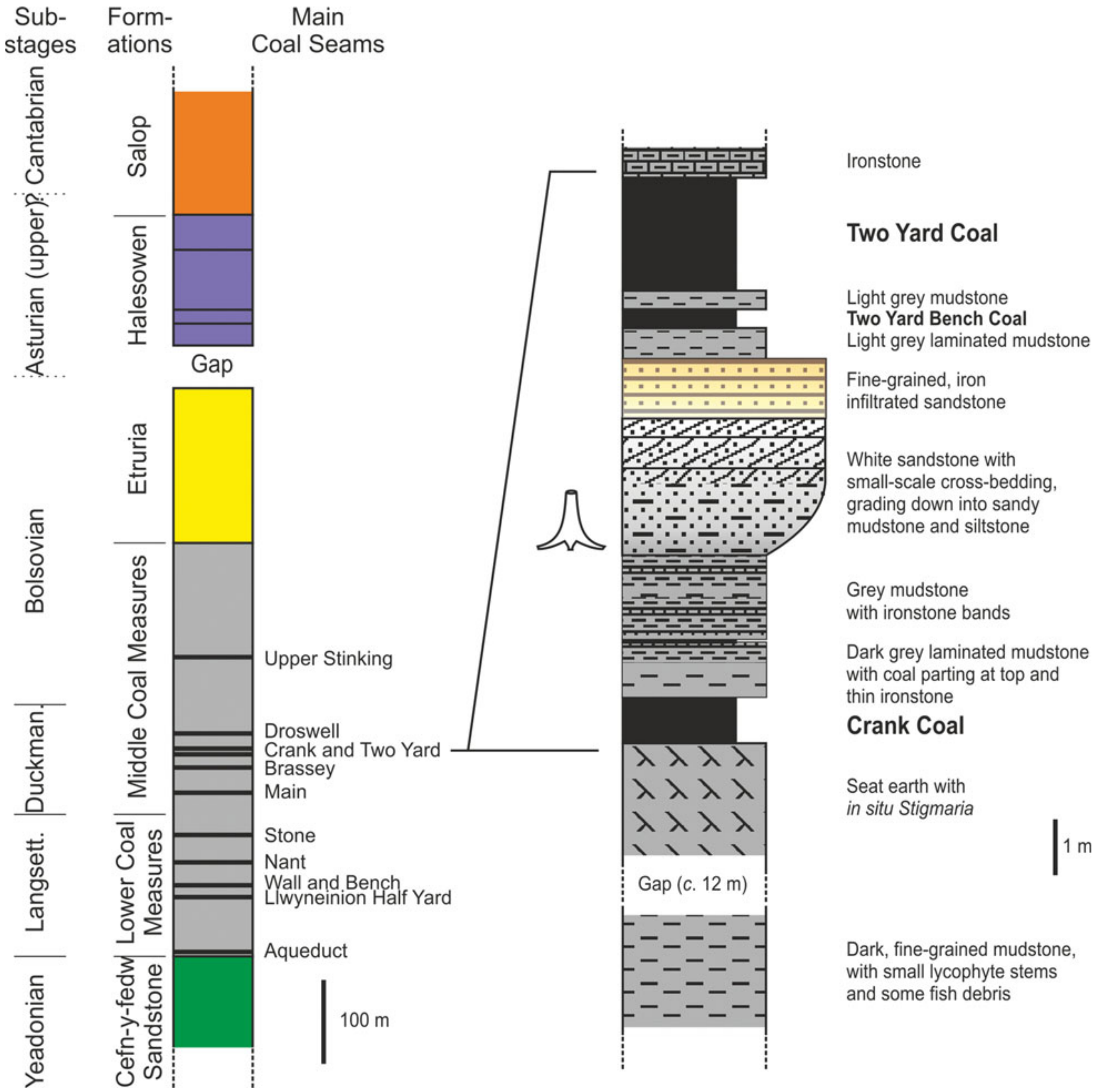

Figure 2. (Colour online) A generalized sequence through the Denbigh Coalfield succession showing the main coal seams, together with a detailed graphical log of the sequence exposed at Brymbo. Langsett. – Langsettian; Duckman. – Duckmantian. The stump indicates the position of the *Stigmaria* removed for study. Figure adapted with permission from Appleton *et al.* (2011).

Several more or less flattened casts of prone trees have been found in the upper part of the unit. An exceptionally well-preserved trunk was found in this sandstone horizon and its *Stigmaria* was excavated to show it spreading out beneath the trunk (Fig. 3a), along with other casts of sigillarian tree stumps with small bases (Fig. 3b) and large fragments of *Stigmaria* (Fig. 3c).

The complete spread of the dichotomizing stigmarian base is nearly 5 m and the amount of drop of the final *Stigmaria* ends from the base of the stem is *c.* 150 mm (Fig. 3a). This *Stigmaria* has a vertical stem cast that is 1.7 m tall, tapering slightly from a diameter of 540 mm to 480 mm (Fig. 3a). The outer surface shows some vertical striations but no other details. This *Stigmaria* and its trunk was removed from the exposure and safely stored with the intention of reconstructing it when the opportunity arises. Lithologically the cast is a siltstone, similar to the surrounding sediments.

In the upper part of this unit there was an isolated length of *Stigmaria*, 8 m long, that shows no tapering at all.

4. Other notable *Stigmaria*

There have been many descriptions of *in situ* lycophyte trunks in the literature (Buckland, 1840; Brown, 1846, 1848, 1849; Young, 1868; Balfour, 1872; Brongniart, 1828; Kidston, 1891; Lyell, 1843; Dawson, 1853, 1859, 1882; Lyell & Dawson, 1853; Ferguson, 1988; Scott, 1998; Falcon-Lang & Calder, 2004; Thomas, 2005), but there are fewer accounts of *in situ Stigmaria*.

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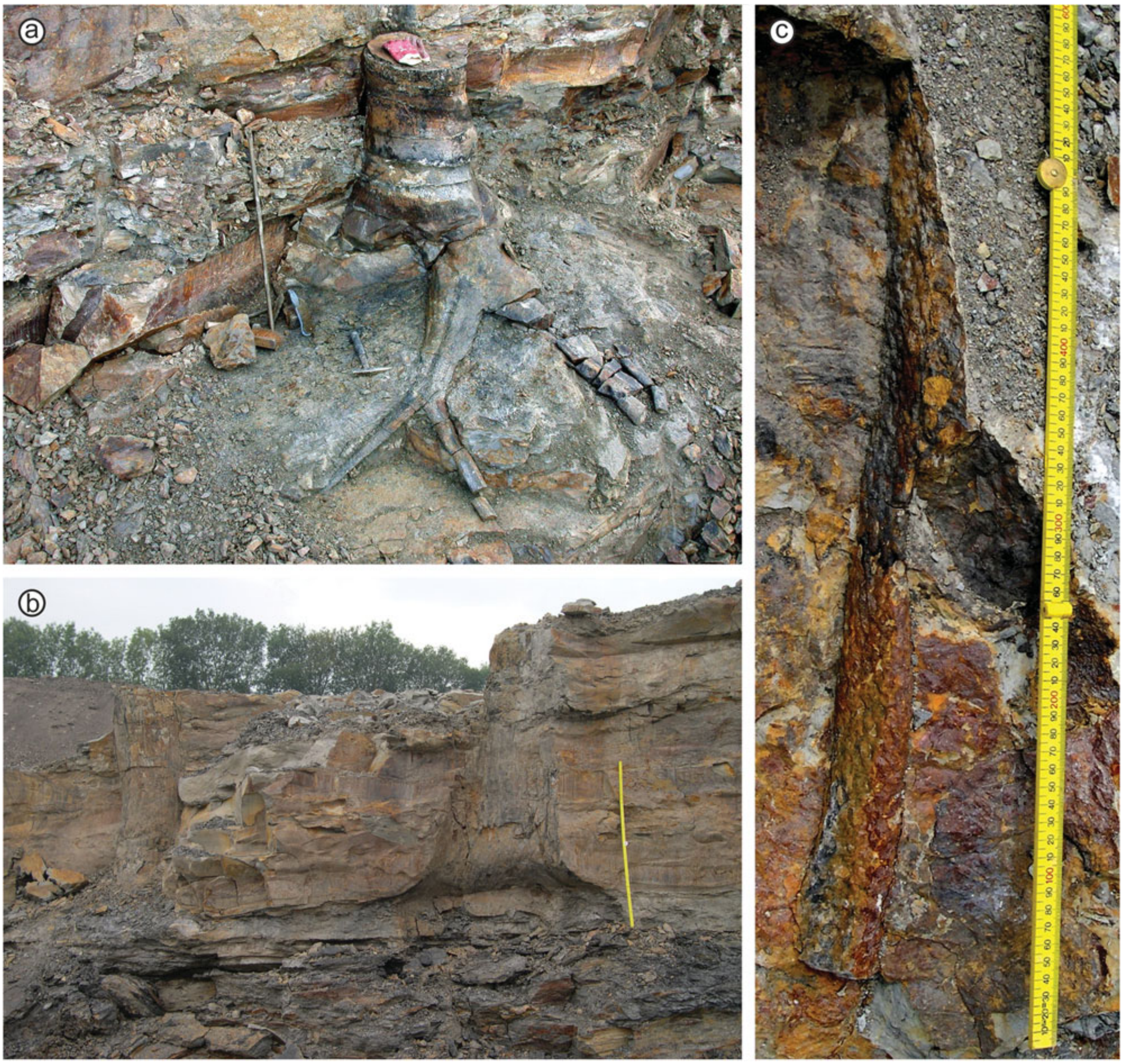

Figure 3. (Colour online) *Stigmaria in situ* at Brymbo, North Wales. (a) *Stigmaria* and trunk *in situ* (photograph by author BAT, *c.* 2010). (b) Exposure face with a stem cast with stigmarian base (left) and the mould of another (right), both rooted in the same level. Yellow measure 1 m long (photograph by BAT, *c.* 2010). (c) Distal tapering fragment of an isolated portion of *Stigmaria* (photograph by BAT, *c.* 2010).

Hawkshaw (1839) reported erect trees preserved with their basal parts and Binney (1844) described Sigillarian fossil trees with their root-organs showing the characteristics of *Stigmaria*. Hooker (1848) described some Bolton Railway trees from which *Stigmaria* extended outwards for "upwards of 20 feet" (over 6 m). In 1873, excavations for new buildings in the grounds of the Wadsley Asylum (later Middlewood Hospital and now a housing development) in Sheffield uncovered a group of lycophyte stumps with short lengths of *Stigmaria* rhizomorphs attached. Sorby, who was Professor of Geology at Sheffield at the time, ensured that special buildings (Fig. 4a) were constructed to protect several of them (Sorby, 1875). Unfortunately the buildings were left to deteriorate and collapsed sometime after the 1960s exposing the *Stigmaria* (Fig. 4b), which started to disintegrate (Fig. 4c).

The new housing developments at Middlewood provided the opportunity to excavate more of the site revealing remains of many stigmarian bases and fallen stems. After charting the remains, the site was covered over to preserve the remains from weathering (Boon, 2004).

Soon after the Wadsley *Stigmaria* were found, another specimen was excavated from a railway cutting near Chappeltown. It was first taken to the contractor's garden at 'High Hazels', Darnall in 1875 where it remained for over 100 years. In the early 1980s it was transferred to the Sheffield Botanic Gardens (Hunter, 2013). The trunk is *c.* 80 cm in diameter and the total span is *c.* 2 m (Fig. 5).

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Figure 4. (Colour online) *Stigmaria in situ* at Sheffield, England: (a) former building housing a *Stigmaria* (photograph by BAT, *c.* 1964); (b) a second *Stigmaria* exposed after the collapse of its building (photograph by BAT, *c.* 1964); and (c) the same *Stigmaria* shown in (b), after weathering (photograph by BAT, *c.* 2002).

Figure 5. (Colour online) *Stigmaria* in the Botanic Gardens, Sheffield, England. Courtesy of J. Hunter.

In 1886 William Crawford Williamson, the Professor of Natural History in Manchester, obtained a *Stigmaria* from a quarry at Clayton (Fig. 6a) near Bradford (Williamson, 1896). It was 28 feet (*c.* 9 m) across when uncovered (Fig. 6b) and the discovery was just in time for Williamson to include a photograph and measurements of it in his monograph on *Stigmaria* (Fig. 6c; Williamson, 1887). He purchased the *Stigmaria* and paid for its removal to Manchester. Now mounted in the Manchester Museum, it is only 6 m across with the furthest extensions of the system not included in the reconstruction because of space constraints (Fig. 6d). This is probably the most well-known and often figured *Stigmaria* (e.g. Frankenberg & Eggert, 1969; Cleal & Thomas, 2009; Stewart & Rothwell, 1993, fig. 11.12). What is not so widely known is that two further specimens of complete *Stigmaria* were taken from the same quarry at Clayton and reconstructed in two Bradford parks. They are still there, with one in Whitfield Park (Fig. 6e) and the other in Lister Park (Fig. 6f).

In 1887 a group of 11 *Stigmaria* (Fig. 7a, b) was uncovered during excavations of Namurian sandstone in the new Victoria Park in Glasgow, opened to honour Queen Victoria's Jubilee (Young & Glen, 1888). The Scottish palaeobotanist Robert Kidston had been involved in the excavation and played a crucial part in persuading Glasgow Council to construct the glass-roofed building to protect this world-famous 'Fossil Grove' (Fig. 7c). Interestingly, these *Stigmaria* are incomplete with only short lengths of the rhizomorphs (Fig. 7c). Preservation by incursion of sediments into the rhizomorphs must have been curtailed with none reaching the more distal parts. For further information on this site and the stigmarias see McGregor & Walton (1948, 1972), McLean (1973), Lawson & Lawson (1976), Gastaldo (1986*a*), Cleal & Thomas (1995), Thomas & Cleal (2005) and Thomas & Warren (2008).

A similarly curtailed stigmarian base with a length of trunk attached was uncovered in 1915 and then reconstructed in the 1960s in a gap in a wall at St Thomas' Church, Stanhope, County Durham, UK (Fig. 8). The original specimen was found at a quarry near Edmundbyers Cross just north of Stanhope. Two other similar specimens were also recovered, formerly on display at the Hancock Museum (now the Great North Museum, Hancock).

In Germany there are two *Stigmaria* currently on display. Both were recovered from the Westphalian (Middle Pennsylvanian) Piesberg colliery; one now stands in the Museum Am Schölerberg in Osnabrück (Fig. 9a), the other at the Deutsches Bergbau-Museum in Bochum (Fig. 9b). There was however a third specimen that was first reconstructed to stand outside the shaft of the Piesberg colliery (Fig. 10), but then was moved to the Berlin Bergakademie. Potonié (1899), copied by Gothan & Remy (1957) and Remy & Remy (1977), figured this large *Stigmaria* with the base of a trunk that was thought to be *Sigillaria*. This specimen was lost in the bombing of Berlin in the Second World War because it was too large to be moved to safety. Interestingly, perhaps reflecting their apparent rarity, there is a reproduction cast of the *Stigmaria* that is currently displayed at the Museum Am Schölerberg, Osnabrück in the Senckenberg museum, Frankfurt am Main.

There is a somewhat curtailed *Stigmaria* on display in the Smithsonian Institution National Museum of Natural History, USA (Fig. 11a, b) from the Lower Freeport coal bed (late Desmoinesian in age, early Cantabrian) from the Stanley Mine, Sykesville,

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Figure 6. (Colour online) *Stigmaria* from a quarry at Clayton, Bradford, England: (a) view of the quarry with a party of visiting geologists (*c.* 1880s), (b) *in situ Stigmaria* from Williamson (1887); (c) dismantling the *Stigmaria* for removal to Manchester; (d) the *Stigmaria* after removal and reconstruction in the Manchester Museum (photograph courtesy of Dr Joan Watson); (e) a Clayton quarry *Stigmaria* reconstructed in Whitfield Park, Bradford (photograph by BAT); and (f) a Clayton quarry *Stigmaria* reconstructed in Lister Park, Bradford (photograph by BAT).

Pennsylvania which was purchased by the museum in 1915 after it had been given to Mr M. W. Harvey from a roof fall in the mine and displayed at his Sunday school.

There is a *Stigmaria* on display at the campus of the University of Kentucky (Fig. 12a, b). It came from above the Pennsylvanian Harlan Coal Seam, Pikeville Formation of the Clover Fork Coal Company at Kitts, Harlan County in Eastern Kentucky. The manager of the mine, Mr George Whitfield, brought it to the surface in a special car after widening the mine's passageways and it remained on display at Kitts from the late 1930s to 1961 when it was donated to the University of Kentucky (Anon, 1967). Another is on display at the West Virginia Geological and Economic Survey (Fig. 13) from Consol's Itmann No. 1 Mine in 1974 Wyoming County West Virginia (Base of the Pottsville Formation, Namurian B). The Pocahontas No. 3 Coal was mined extensively at this mine, so the *Stigmaria* most probably came from above or below this seam.

There are reports of *Stigmaria* finds across Alabama. *In situ* lycopod forests are preserved across the Plateau Coal Field, Blount County, Alabama (upper Namurian – lower Westphalian), some trees as trunks, others as stumps with *Stigmaria* attached, or isolated stigmarian fragments (Gastaldo, 1986*b*). From the Mary Lee coal cycle (Upper Pottsville Formation,

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Figure 7. (Colour online) *Stigmaria* at Victoria Park, Glasgow, Scotland: (a) excavation of the Victoria Park *Stigmaria* (1887); (b) the exposed *Stigmaria* (1887); and (c) the *Stigmaria* within the specially constructed building (recent photograph by BAT).

Langsettian) of the Black Warrior Basin, Walker County, Alabama, Gastaldo, Stevanovic-Walls & Ware (2004) also reported upright trunks and *Stigmaria*.

5. Significant finds of lycophyte trunks without *Stigmaria* attached

There are significantly more finds of lycophyte trunks published than those of large *Stigmaria*, and here we briefly summarize key finds to highlight the difference in the numbers of finds between the stumps and *Stigmaria*.

5.a. UK

Fossil tree stumps were recorded in a sandstone quarry at Balgray, three miles north of Glasgow (Buckland, 1840). Another small group of five or six stumps was uncovered in a nearby sandstone quarry (Young, 1868). Balfour (1872) described many stems near Morpeth (in Northumberland) as “standing erect at right angles to the planes of alternating strata of shale and sandstone” and varying “from 10 to 20 feet in height, and from one to three feet in diameter”. There were 20 portions of these trunks within half a mile, with all but four or five being upright. Brongniart (1828) also mentioned similar erect stems near St Etienne in France. Kidston (1891) described some standing fossil trees from a marl pit near Hanley in Staffordshire whose outer surfaces only showed longitudinal striations. He detailed their dimensions but thought that it was impossible to say if they belonged to *Lepidodendron* or *Sigillaria*. The maximum height shown by these trunks was given as 18 feet (5.48 m) and maximum diameter was 7 feet 3 inches (2.2 m) on an 8-feet-tall (2.4 m) trunk.

5.b. Canada

There have been descriptions of other stands of lycophyte stems such as the cliffs at Joggins on the west coast of Nova Scotia, Canada (Lyell, 1843; Dawson, 1853, 1859, 1882; Lyell & Dawson, 1853; see also Ferguson, 1988; Scott, 1998; Falcon-Lang & Calder, 2004; Thomas, 2005). A second lepidodendroid forest in Nova Scotia was reported by Brown (1846, 1848, 1849) on the coastal section at Sydney Mines, Cape Breton where there were standing trees both above and below the Sydney Main (Harbour) seam (Asturian). More details of the forest were given by Calder *et al.* (1996) who described approximately 30 trees of mixed diameters within one of the clastic splits of the Harbour

Figure 8. (Colour online) *Stigmaria* found at a quarry near Edmundbyers Cross, reconstructed in 1915 at Stanhope's St Thomas' Church, County Durham, England (photograph by BAT).

seam, where they were rooted in the No. 4 seam. This could have been the result of different ages of the same species or a mixture of species.

5.c. USA

DiMichele, Eble & Chaney (1996) reported over 800 upright trunks above the Mahoning coal (lowest Conemaugh/Asturian) in Ohio. DiMichele *et al.* (2009) detail five–six upright sigillarian trunks with basal lobes only of their *Stigmaria* attached, rooted in top of the middle coal bed, from the Miller Creek Mine Jenlin Pit (Desmoinesian/early Asturian) in Indiana.

Figure 10. (Colour online) One of the *Stigmaria* from the Piesberg colliery, Osnabrück, Germany (photograph courtesy of Prof Dr Hans Kerp), reconstructed at the quarry site, before it was moved to Berlin where it was subsequently destroyed during World War II.

This summary highlights a bias in the fossil record of lycophyte tree remains preservation towards trunks rather than large *Stigmaria*, but the way the trunks are preserved does have a bearing on how we believe *Stigmaria* were also preserved.

6. Preservation of *Stigmaria*

The general view is that *Stigmaria* and/or trunk casts are assumed to have been filled by sediments deposited above or around them. The specimen exposed as a section in a quarry face near Sheffield (Fig. 14) clearly shows that the shale from the upper bed has infiltrated the *Stigmaria* in the lower sandstone layer. We believe that there are two key factors to the preservation of *Stigmaria.*

The critical limiting factor in preserving either *Stigmaria* or trunks is the amount of sediment that is brought into the lycophyte forests. This will determine how much of the plant is encased before the plant dies and decays. The decay rate would have been relatively rapid because, unlike conifer and angiosperm trees,

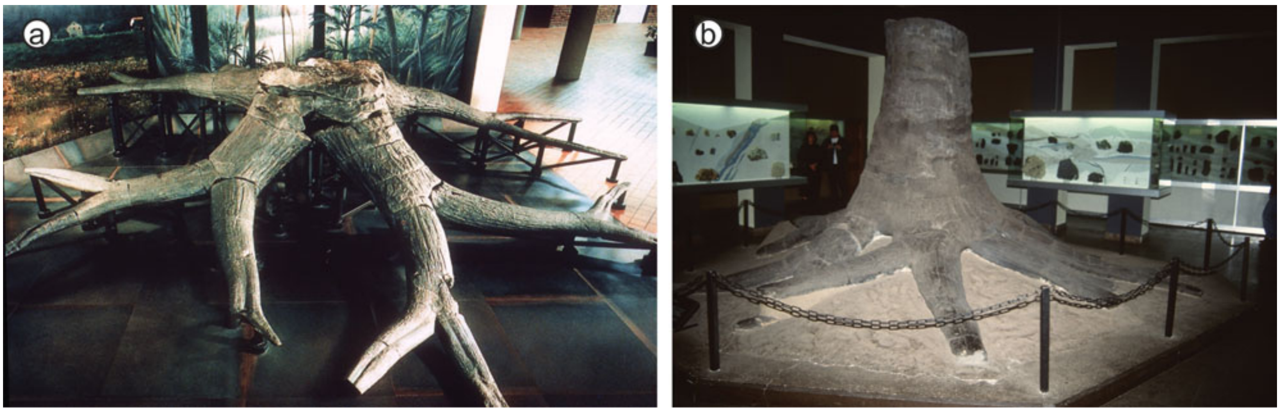

Figure 9. (Colour online) Two surviving *Stigmaria* from the Piesberg colliery, Osnabrück, Germany: (a) specimen currently on display at the Museum Am Schölerberg in Osnabrück; and (b) the specimen currently on display at the Deutsches Bergbau-Museum in Bochum.

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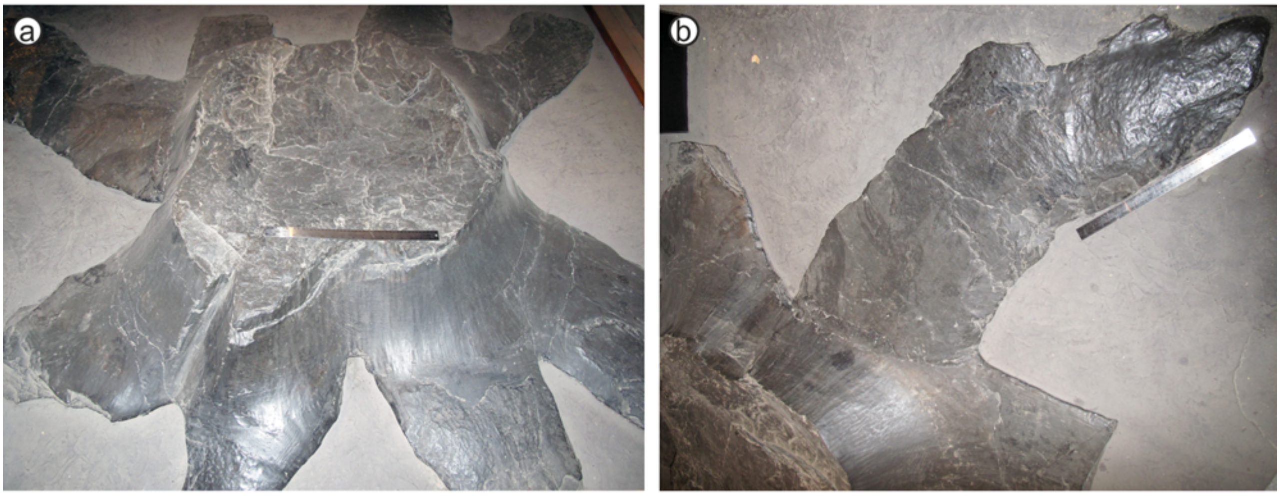

Figure 11. (Colour online) *Stigmaria* (specimen number 34989) on display at the Smithsonian Institution National Museum of Natural History (both photographs courtesy of Dr W. A. DiMichele, 2014): (a) the spread of the specimen with clear dichotomizing axes; and (b) this specimen has a smooth outer surface as seen here on the longest axis of this *Stigmaria* (from the upper left portion of (a)). Measure in both photographs is 45 cm.

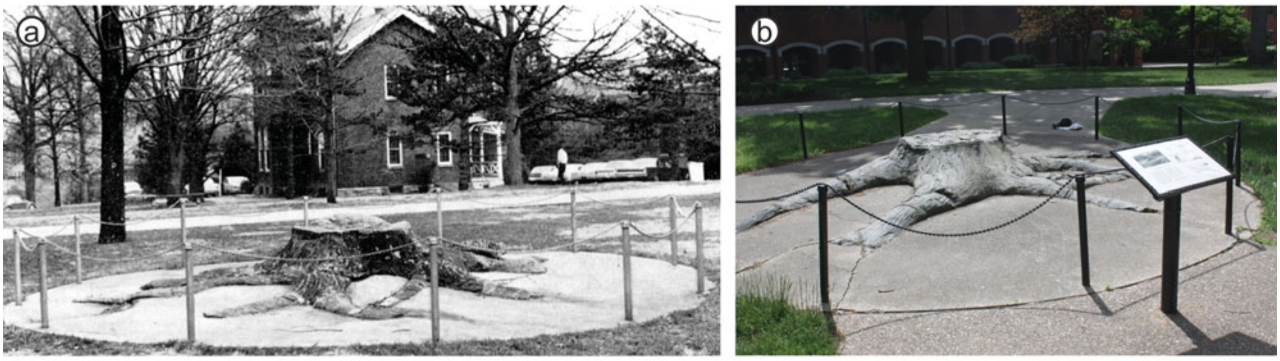

Figure 12. (Colour online) *Stigmaria* from the Harlam coal seam, Clover Fork Coal Company pit, Eastern Kentucky, USA now on display at the campus of the University of Kentucky: (a) soon after its reconstruction at the University (early 1960s), courtesy Carolina Tips; and (b) recent photograph supplied by Dr F. R. Ettensohn.

Figure 13. (Colour online) *Stigmaria* at the Geological Survey for West Virginia.

Figure 14. (Colour online) Specimen exposed in a quarry face near Sheffield, where the shale from the upper bed has infiltrated the *Stigmaria* in the lower sandstone layer (photograph by BAT, 1966).

they had comparatively little vascular tissue. The outer periderm, not the vascular tissue, was the main supporting tissue. The other limiting factor in preserving the *Stigmaria* at Brymbo was their position in the sedimentary sequence. It was only those growing as pioneers on open mud or silt that were preserved. Those growing in thin swamp peats that were covered by an inrush of sediments may have had their stems preserved, but their *Stigmaria* appear to have been incorporated into the peat and converted with it into coal. Those lycophytes

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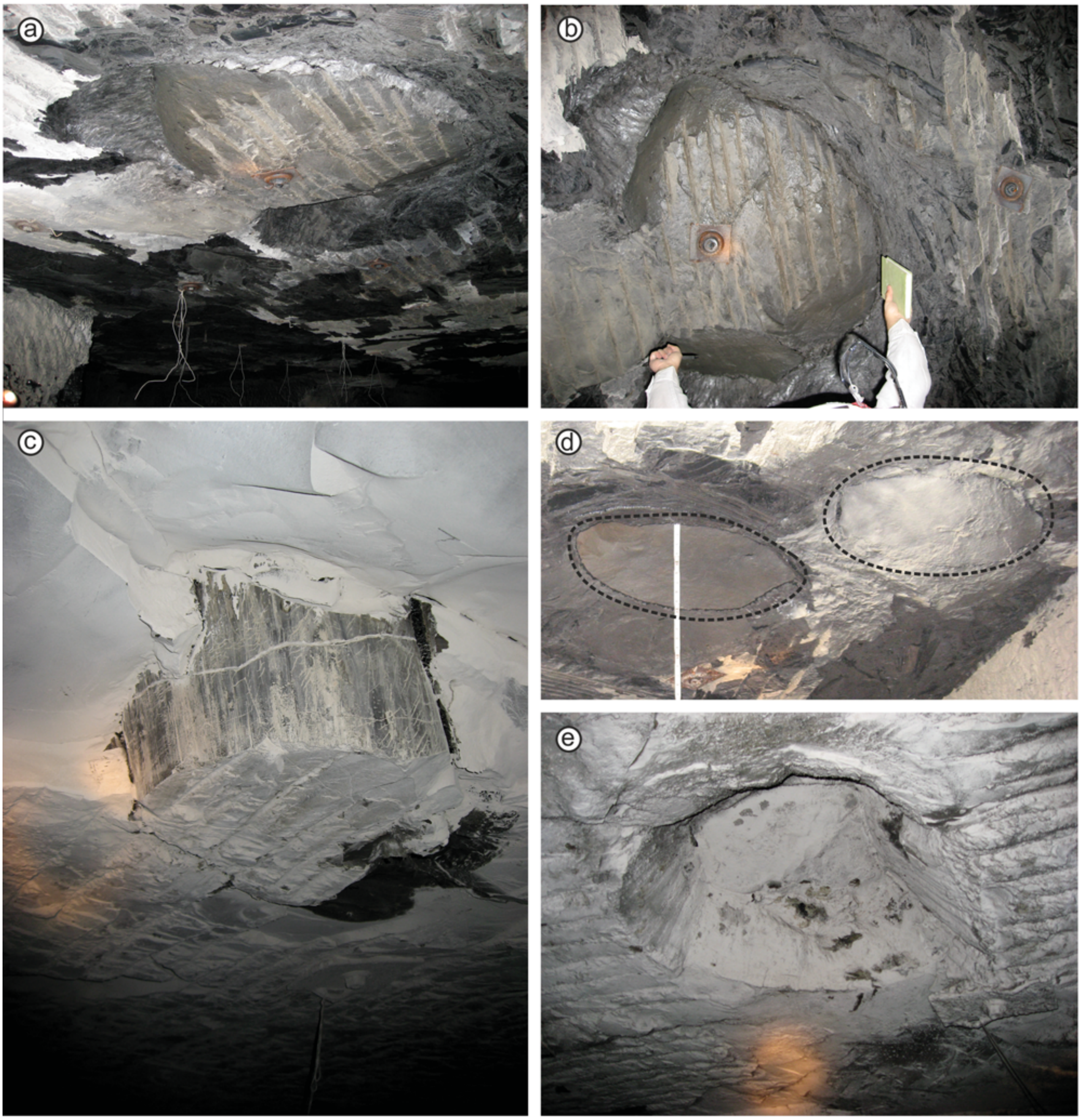

Figure 15. (Colour online) Large fossilized plant remains can be hazardous structures in coal mines, in particular kettle bottoms which are stumps that are slickensided and liable to fall out of the mine roof. Examples from the Springfield (No. 5) Coal (late Desmoinesian age, early Cantabrian, Middle Pennsylvanian), USA (all photographs courtesy of Dr W. A. DiMichele): (a, b) a bolted stump in the roof of the Prosperity Mine, Illinois, (a) looking along the gallery and; (b) looking directly up at the stump in the roof (both photographs taken in 2007); (c) a tree trunk protrudes from the roof of the Galatia North Mine (2006); (d) two *in situ* kettle bottoms (inside dashed ellipses) side by side in the roof of a mine in Indiana (note the thin coalified layer surrounding each stump base, just inside dashed ellipses); and (e) space left after a kettle bottom has come out of the roof of the Galatia North Mine, Illinois (2006).

growing on deep swamp peat may have had the basal portions of their stems preserved as casts that were eventually situated immediately above the coals. Sometimes the bases of such stumps are visible in the roofing shale after the underlying coal has been removed, and they can be a major hazard if they suddenly fall out of the roof. They are variously called kettle bottoms, bells, coal pipes, pots, caldron bottoms, tortoises or camelbacks and their surfaces are highly slickensided with a thin layer of coalified bark separating them from their casts in the surrounding sediments. Cohesion between the mould and the cast is weak and it is only the tensile strength along the bedding planes that prevents them from falling out of the roof (Fig. 15a–e).

Chase & Sames (1983) made a study of kettle bottoms in the eastern United States which was primarily conducted in the Dunkard and Pocahontas coal basins. Those in the Dunkard Basin were usually rare, less than 2 feet in diameter and extending less than 2 feet into the roof. In contrast, some of the seams in the Pocahontas

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Basin had gained notoriety because of the numerous and unstable, large kettle bottoms that were 3–8 feet in diameter and extending 4–8 feet into the roof. Chase & Sames (1983) made the observation that sediments found on top of the coal within a kettle bottom often correspond to those deposited several feet above that same horizon. This suggests that the first inrush of sediment killed the trees, but it was later sediment that infilled the rotting stumps.

The amount of sediment infilling of the *Stigmaria* can also vary. Some, like the Brymbo, Manchester, Barnsley, Osnabrück and Kansas specimens, are virtually complete except for the apices which would have consisted of softer meristematic tissue (Rothwell, 1984) and would therefore have been unlikely to be infilled with sediment. Others, like the Sheffield, Glasgow and West Virginia specimens, only have the larger parts of their dichotomizing axes preserved. The ends of the axes in these incomplete specimens appear as though they were broken, presumably resulting from the sedimentary infilling not reaching the more distant and smaller branches, possibly through complete tissue collapse.

The question remaining to be answered is how is the shape of the *Stigmaria* was retained while tissue rotted before it could be filled by the overlying sediments. Close examination of the Brymbo specimen showed it to be covered in a thin brown layer of an iron-bearing oxide mineral (FeO(OH)), the most common diagenetic iron oxyhydroxide frequently occurring on the bottom of lakes and smaller creeks (van der Zee *et al*. 2003) and the basis of gossan and bog iron. This precipitation would have been initiated through the water coming into contact with oxygen-rich cells of the *Stigmaria*, similar to the red ferric hydroxide that can be seen today in water emerging from springs or flowing from old underground workings. This precipitation would have resulted in a thin but hard layer surrounding the Brymbo *Stigmaria* that would have retained its shape while the tissues were rotting and breaking down and overlying sediment was entering the cavity.

Similar precipitation of ferric hydroxide has been reported in a study of *Calamites* pith casts from Brymbo (Thomas, 2014) while modern leaves have been shown to acquire a similar encrustation within a few weeks after entry into a stream or lake (Spicer, 1977). It is almost certain that similar analytical studies on other plant fossil remains will reveal that iron oxides play a much greater role than is recognized at present.

7. Ecological interpretations

Stigmaria give an insight to the arborescent lycophytes that dominated the Carboniferous palaeoequatorial regions of the world, and their presence shows the type of sediments in which they grew. Gastaldo (1986*a*) interpreted the silty mudstone in which the *Stigmaria* in the Glasgow Fossil Grove were growing as a palaeosol. The fact that *Stigmaria* are preserved suggests some catastrophic event, such as storm damage to the river levees, which allowed rapid ingress of large amounts of water-borne sediments such as crevasse-splay deposits to entomb them.

Stands of *Stigmaria* permit an estimation to be made of their abundance. For example, an extrapolation from the 11 *Stigmaria* in the Glasgow Fossil Grove gives an estimate of about 4500 trees per square kilometre. This suggests a dense coverage of arborescent lycophytes, possibly with overlapping crowns that would have prevented any regeneration from sporelings. The rate of growth and the lifespans of the trees are unknown, although their anatomy suggests a much more rapid growth rate and shorter lifespan than those of woody conifers and angiosperms. Clearly the plants would have produced vast numbers of spores but only in open areas, maybe after such catastrophic events outlined above, which would permit waterborne sexual reproduction (swimming of sperm from microspore antheridia to reach the archegonia formed by megaspores). Surfaces of some shales at Brymbo show large numbers of such lycophyte megaspores (up to a maximum density of c. 6 cm^{-2}) which, given appropriate succeeding conditions, would have produced the next crop of arborescent lycophytes with their own *Stigmaria*.

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Declaration of interests

The authors declare no competing interests.

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