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A calamitalean forest preserved in growth position in the Pennsylvanian coal measures of South Wales: Implications for palaeoecology, ontogeny and taphonomy

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ABSTRACT

A newly discovered fossil forest is reported from Lower Pennsylvanian (late Langsettian) strata in the classic Amroth to Wiseman's Bridge section of Pembrokeshire, South Wales. It comprises nearly two hundred sediment-cast *Calamites* axes and putative groundcover ferns, preserved in growth position in the deltaic mouth bar deposits of a marine-influenced coastal plain. Vegetation-Induced Sedimentary Structures developed around upright axes imply that dense *Calamites* thickets promoted localized patterns of sedimentation, and ultimately, stabilized substrates, paving the way for the establishment of mire vegetation. Not long after initial colonization, a short-lived brackish incursion resulted in dieback of the *Calamites* thickets; however, a few axes survived to recolonise the delta front through adventitious regeneration, implying that calamitaleans were, to a limited degree, saline tolerant. A remarkable feature of the fossils is that many examples preserve an internal pith-cast embedded *within* a stem-cast. Preservation of both pith- and stem-casts for the same plant allows inference of an ontogenetic growth-series, and shows that these clastic-substrate *Calamites* were much more substantially 'woody' than previously conjectured. This raises the possibility that plastic developmental traits like growth rate and longevity may have been what mainly distinguished these opportunistic *Calamites* in disturbed clastic settings from their much larger, and even more woody, cousins in adjacent mires. Analysis of the fossils also contributes to taphonomic debates, supporting the hypothesis that upright *Calamites* axes are mostly preserved as stem-casts (rather than pith-casts, as traditionally believed). As such, the newly discovered fossil forest sheds light on the ecology, ontogeny, and taphonomy of *Calamites* – an iconic, familiar, yet, insufficiently understood Pennsylvanian plant.

1. Introduction

Calamitaleans are the most common type of tree to be preserved in growth position in the Pennsylvanian strata of tropical Pangaea (Gastaldo, 1986, 1992; Pfefferkorn et al., 2001; Gastaldo et al., 2004; DiMichele and Falcon-Lang, 2011, 2012). Two general growth-forms, partitioned by environment and ecology, are inferred to have existed. The first form comprises peat-forming calamitaleans (preserved in coal balls or more rarely as silicifactions), which were large, woody trees, up to 0.6 m diameter (Eggert, 1962; Rößler and Noll, 2006; Rößler et al., 2012a). This form is infrequently preserved as upright trees (e.g., where abruptly buried by volcanic tuffs; Rößler et al., 2012b) because the slow rate of peat accumulation means that stems decay away before they can be buried upright (DiMichele and Falcon-Lang, 2011); however, horizontally-disposed remains are fairly commonly in parautochthonous assemblages above abruptly flooded peat mire (coal) deposits (DiMichele et al., 2007).

The second form comprises calamitaleans that are rooted and entombed in clastic facies (Gastaldo, 1992). In contrast to the mire-type, this form has been interpreted – in the absence of preserved cellular anatomy – as a reed-like plant with relatively small radii of secondary xylem (DiMichele and Falcon-Lang, 2012). These latter trees are very commonly preserved as upright sediment-cast axes, typically 50–100 mm diameter, showing a distinctive 'rib and node' structure (Kidston and Jongmans, 1917; DiMichele and Falcon-Lang, 2012). This paper focuses, solely, on the palaeoecology and taphonomy of the latter form of calamitalean (hereafter referred as 'upright *Calamites*'), and also considers the ontogenetic distinction between them and their mire-based cousins.

Being one of the few fossil plant types reliably recognised by most sedimentologists, upright *Calamites* have been frequently reported in Pennsylvanian clastic sediments (e.g., Fielding, 1982; Hartley, 1993; Browne and Plint, 1994; Davies and Gibling, 2003). Occurrences range right across the edaphic spectrum from well-drained to poorly-drained soils (Falcon-Lang, 2003a,b), with entombing facies including in-channel bars, levees, and crevasse splays in freshwater fluvial floodplain settings (e.g., Scott, 1978; Gradzinski and Doktor, 1995;

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Martín-Closas and Galtier, 2005; Calder et al., 2006; Falcon-Lang, 2006; Bashforth et al., 2010; Thomas, 2013), and also wave- and tide-dominated delta mouth-bars, estuaries, and shorelines in, possibly, somewhat marine-influenced coastal environments (e.g., Gastaldo, 1986, 1992; Gastaldo et al., 2004; Falcon-Lang, 2005; DiMichele et al., 2009).

Two features common to all occurrences are: (1) typically high localised tree densities of up to 17 stems per m^2 (though usually <5 stems per m^2), almost to the exclusion of other taxa (Gradzinski and Doktor, 1995; Falcon-Lang, 1999, 2006; Calder et al., 2006; Thomas, 2013); and (2) entombing sediments with evidence for rapid and/or episodic aggradation (DiMichele and Falcon-Lang, 2011, 2012; Bashforth et al., 2014), and typically showing a variety of Vegetation-Induced Sedimentary Structures (VISS) developed around upright trees (Rygel et al., 2004). While these observations are consistent with *Calamites* being a disturbance-adapted, clonal plant like extant *Equisetum*, its close relative (Husby, 2013), direct evidence for *Calamites* palaeoecology, based on geological case studies (e.g., Gastaldo, 1992; Gradzinski and Doktor, 1995; DiMichele et al., 2009; Thomas, 2013), remain limited.

A second insufficiently understood aspect of upright *Calamites* axes is the mode of preservation. Calamitaleans were characterised, in life, by a hollow, partitioned pith surrounded by a secondary xylem cylinder (Eggert, 1962; DiMichele and Falcon-Lang, 2012). The idea that upright *Calamites* axes, entombed in clastic facies, represent sediment-cast piths was first proposed by J.D. Hooker in 1854 (Darwin Correspondence, Letter 1581, www.darwinproject.ac.uk), and has been entrenched in the literature ever since (Taylor et al., 2009). However, recent critical re-evaluation has highlighted flaws in this taphonomic concept, and suggested that, in many, if not most cases, fossils represent stem-casts, with the familiar structure of 'ribs and nodes', reflecting the external ornament of the stem, rather than the internal structure of the pith (DiMichele and Falcon-Lang, 2012). This hypothesis has not met with universal acceptance (Thomas, 2013), however, and as I hope will be obvious, the debate has implications that go well beyond *Calamites* taphonomy, with ramifications for understanding architecture (Spatz et al., 1998) as well.

The aim of this current paper is to improve knowledge of upright *Calamites* based on a newly discovered fossil forest in the Lower Pennsylvanian coal measures of South Wales. This forest is of special significance because trees occur in very high numbers in three-dimensional coastal outcrop and, unusually, individual stems preserve some of their internal structure. Qualitative and quantitative analysis of this fossil forest in a detailed facies context sheds new light on the palaeoecology, ontogeny, and taphonomy of this group of plants.

2. Geological setting

The fossils, reported here, occur in the section between Amroth and Wiseman's Bridge, near Saundersfoot, Pembrokeshire (South Wales), southern Britain (51°43′38″N; 4°40′32″W; Fig. 1A, B). At this locality, gently WSW-dipping strata are superbly exposed in near-continuous, 30 m-high sea-cliffs, ~1.5 km long, and extensive, wave-cut platform exposures (George and Kelling, 1982). Although long-studied (De la Beche, 1826, 1846; Goode, 1913; Strahan et al., 1914; George and Trueman, 1925; Davies and Trueman, 1927; Dix, 1933, 1934; Keunen, 1948; Jenkins, 1954, 1960, 1962; Williams, 1966, 1968, 1969; Kelling and George, 1971; Kelling, 1974; Fielding, 1982; George and Kelling, 1982), there has been a dearth of recent publications dealing with this "classic section". De la Beche (1846, p. 162–167) was the first to note "vertical stems of *Calamites*", but such trees occur at many horizons, and given the very active cliff-erosion that has occurred over the past century and a half, it is unlikely that he refers to the same fossil forest described here.

2.1. Stratigraphy and age

The ~230 m thick section (re-measured as part of this study) between Amroth and Wiseman's Bridge may be confidently correlated

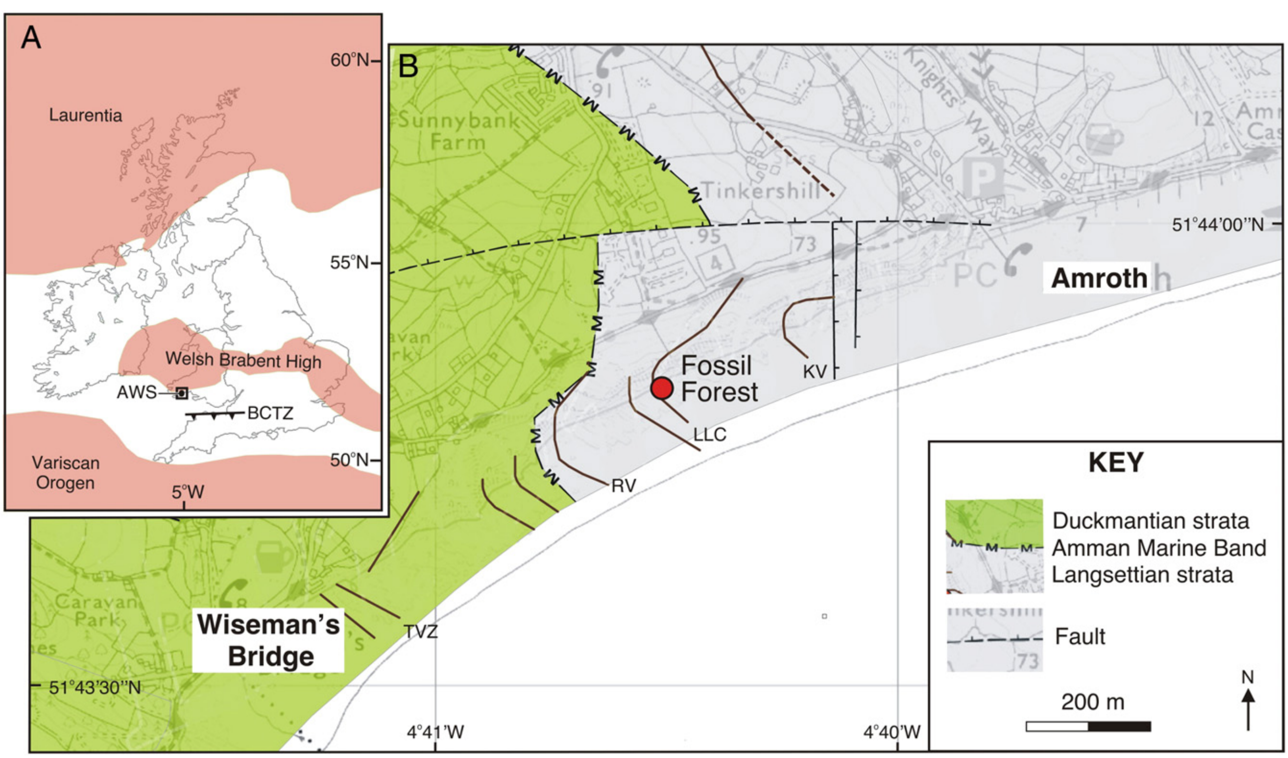

Fig. 1. Location maps and geology. (A) Pennsylvanian palaeogeography of the British Isles showing the location of the Amroth to Wiseman's Bridge section (AWS), Pembrokeshire, Wales, and the Bristol Channel Thrust Zone (BCTZ); (B) Geological map of the Amroth to Wiseman's Bridge section, southeast Pembrokeshire, Wales (© Crown Copyright/database 2011. An Ordnance Survey (Datacentre) supplied service) showing the location of the fossil forest reported here. The Amman Marine Band marks the Langsettian-Duckmantian boundary in this area. Abbreviations of named coal seams, from base to top, are KV, Kilgetty Vein; LLC, Lower Level Coal; RV, Rock Vein; and TVZ, Timber Vein Zone.