



Earth's earliest forest: fossilized trees and vegetation-induced sedimentary structures from the Middle Devonian (Eifelian) Hangman Sandstone Formation, Somerset and Devon, SW England

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Abstract: The evolution of trees and forests through the Devonian Period fundamentally changed the Earth's land biosphere, as well as impacting physical environments and geomorphology by stabilizing sediments and interacting with flowing air and water. From the mid-Givetian Age onwards, lignophyte flora are known to have been key parts of the machinery in the so-called Devonian landscape factory, but the impact of earlier forests, dominated by less woody cladoxylopsids, are not as well understood. We report here evidence for a previously unrecognized cladoxylopsid forest landscape, archived within the Eifelian Hangman Sandstone Formation of Somerset and Devon, SW England. This unit has previously been considered palaeobotanically depauperate, but is here shown to contain the earliest fossil evidence for such trees in the British record, as well as the oldest known evidence globally for the relative position of standing trees: in common parlance, a fossil forest. In addition to abundant fossil material attributable to the cladoxylopsid tree *Calamophyton*, and other early Mid-Devonian flora, the sedimentary context of the plant remains sheds light on the biogeomorphic impacts of these earliest forests. The trees colonized a sizeable distributive fluvial system that was prone to seasonal disturbance events. The nature of the sedimentary system has created a bias to those facies where biogeomorphic signatures are most frequently recorded (from the distal parts of the system), but across the whole system there is evidence of plant–sediment interactions in the form of vegetation-induced sedimentary structures, rooting features and accumulations of plant debris. Plant remains are also found in nearshore facies adjacent to the distributive fluvial system, attesting to the development of a novel non-marine/marine teleconnection from the production and export of new biological sedimentary particles. The Hangman Sandstone Formation is illustrative of the revolutionary power of cladoxylopsid trees as biogeomorphic agents, forming densely spaced forests and shedding exceptionally abundant plant debris, while also impacting local landforms and sediment accumulations and profoundly changing landform resilience against flood disturbance events. These findings provide evidence that the Eifelian Stage (393.3–387.7 Ma) marks the onset of tree-driven changes to physical environments that would forever change Earth's non-marine landscapes and biosphere.

Supplementary material: Details of sedimentary facies and additional images of plant fossils are available at <https://doi.org/10.6084/m9.figshare.c.7084873>

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The Devonian Period (c. 419–359 Ma) was arguably the most crucial chapter in the evolution of the Earth's land biosphere. Non-marine environments at the end of the preceding Silurian Period accommodated nascent invertebrate communities in near-water settings (e.g. Davies *et al.* 2006; Morrissey *et al.* 2012a; Shillito and Davies 2017; Wellman *et al.* 2023), witnessed frequent invasions of freshwater bodies by jawless fish (e.g. Boucot and Janis 1983; Blom *et al.* 2001; Sallan *et al.* 2018) and hosted scattered stands of small, simple plants in coastal regions (e.g. Wellman *et al.* 2013; Gensel *et al.* 2020; Capel *et al.* 2022), but their equivalents 60 Myr later were unrecognizable.

By the end of the Devonian, the range of permanent invertebrate habitats had expanded to even the driest non-marine settings (e.g. Morrissey *et al.* 2012b; Minter *et al.* 2016; Buatois *et al.* 2022), jawless and jawed fish had become enduringly resident in lakes and rivers (e.g. Thanh *et al.* 2013; Burrow *et al.* 2016), evolutionary developments among vertebrates meant that subaerially mobile tetrapods traversed river margins and floodplains (e.g. Clack 2007; Stössel *et al.* 2016; Ahlberg 2018) and there had been an explosion in morphological disparity among plants that saw vast inland forests of multi-metre tall trees, in addition to a huge diversity of other plant

groups, including woody shrubs (e.g. Stein *et al.* 2012, 2020; Giesen and Berry 2013; Berry and Marshall 2015).

This fundamental transformation not only triggered novel interactions between different organisms, such as the rise of herbivory and detritivory (e.g. Habgood *et al.* 2003; Labandeira 2007; Buatois *et al.* 2022; Veenma *et al.* 2023), but also saw many new organism–environment interactions take shape: the diversity and disparity of burrow forms imparted into terrestrial sediments rocketed (e.g. Minter *et al.* 2016, 2017; Buatois *et al.* 2022), soils became more diverse and complex with increased biological turnover and mixing (e.g. Diessel 2010; Mintz *et al.* 2010; Morris *et al.* 2015; Xue *et al.* 2023), biologically mediated climate shifts altered regional temperature and precipitation patterns (e.g. Le Hir *et al.* 2011; Dahl and Arens 2020) and plant organic material began to accumulate biogenic sediment in the form of incipient coals (e.g. Kennedy *et al.* 2012; Blumenberg *et al.* 2018). The sedimentary rock record provides an archive of the biogeomorphic change which accompanied this evolutionary transition, as trees and other plants altered groundwater flow and surface runoff, and stabilized and sculpted geomorphic landforms, such as hillslopes, river bars and channels (the Devonian

landscape factory of [Davies *et al.* 2021](#); see also [Davies and Gibling 2010](#); [Davies *et al.* 2011](#)).

The introduction of novel biological agents to settings that were previously dominated by abiotic Earth surface processes created a distinct non-marine sedimentary rock record for the Devonian. Strata from this interval exhibit incremental facies changes reflective of the important role of burgeoning plants in sediment erosion, transport and deposition (e.g. [Davies and Gibling 2010](#); [McMahon and Davies 2018](#); [McMahon *et al.* 2023](#)). While preserved sedimentary phenomena can be seen to be analogous to modern equivalents that have been influenced by life ([Corenblit *et al.* 2015](#)), the number of ancient case studies that focus on these innovative characteristics is likely far less than the true abundance of such features in the rock record. Vegetation-induced sedimentary structures (VISS) ([Rygel *et al.* 2004](#)) are commonly documented from Carboniferous and younger strata (e.g. [Bourquin *et al.* 2011](#); [Neff *et al.* 2011](#); [Rößler *et al.* 2012](#); [Allen *et al.* 2014](#); [Davies *et al.* 2020](#); [Trümper *et al.* 2020, 2022](#); [McMahon *et al.* 2022](#); [Mottin *et al.* 2022](#); [Gastaldo *et al.* 2023](#)), but reports are more limited from the time of the Devonian plant radiation. Notably, while VISS have been recorded in association with diminutive or Early Devonian flora ([Allen and Gastaldo 2006](#); [Hillier and Williams 2007](#); [Davies *et al.* 2021](#)) and relatively established Late Devonian trees ([Bridge *et al.* 1980](#); [Davies *et al.* 2021](#); [Veenma *et al.* 2023](#)), there is a gap in such records for the Mid-Devonian, the interval that records the first forest vegetation, partly due to outcrop availability and facies constraints. For example, while [Davies *et al.* \(2021\)](#) documented the

evolution of VISS through the near-complete Devonian sedimentary record of Svalbard, their Mid-Devonian examples all came from littoral and marine-influenced facies.

This paper documents fully non-marine VISS and fossil flora from the Middle Devonian (Eifelian) Hangman Sandstone Formation of Devon and Somerset, SW England ([Fig. 1](#)). While the unit has previously been considered relatively depauperate of recognizable plant fossils, we here show it to host the earliest British evidence for small trees and likely the oldest global evidence for the spacing of growing trees. The paper first contextualizes the Hangman Sandstone Formation and reviews the limited fossil flora previously identified from the unit. New VISS occurrences are then described and interpreted, including standing and fallen cladoxylopid trees, sediment accumulations and scours around standing vegetation, and plant fossil accumulations that developed both from driftwood and suspension settling. The paper concludes by discussing the controls on the distribution of these phenomena within the different facies of the Hangman Sandstone Formation and the implications of their recognition for the development of the Devonian landscape factory.

Old Red Sandstone as an archive of land biosphere evolution

The present day North Atlantic region hosts a significant archive for the study of land biosphere evolution, by way of the Silurian–Devonian Old Red Sandstone and associated successions ([Friend](#)

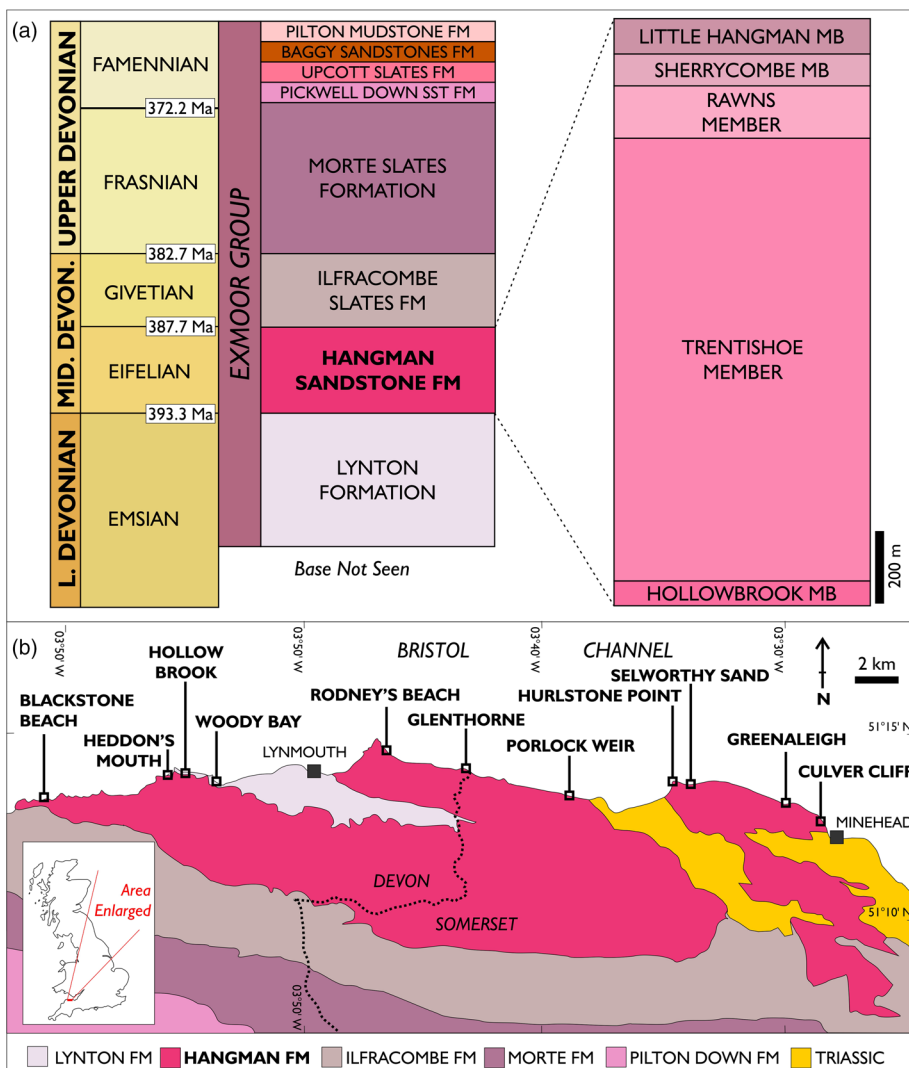


Fig. 1. Geological context of the Hangman Sandstone Formation. (a) Stratigraphy of the Exmoor Group showing the position of the Hangman Sandstone Formation and its informal members (as defined by [Tunbridge 1978](#) and [Goldring *et al.* 1978](#)). (b) Outcrop area of the Hangman Sandstone Formation in the study area, across the Devon–Somerset county boundary, showing the locations referred to in the text.

et al. 2000; Kendall 2017). Devonian-aged outcrop belts are very well represented by virtue of the mid- to late Paleozoic compressional tectonic events that affected this region of Laurussia, providing abundant sediment accommodation space in orogenic forelands during the Caledonian Orogeny, which were subsequently exhumed and/or tilted during the Variscan Orogeny (McKerrow *et al.* 2000; Etensohn 2004; Leveridge and Hartley 2006; Woodcock 2012).

In Britain and Ireland, Devonian strata are preserved and exposed in a series of basins of variable dimensions and connectivity (Figs 2, 3) and many of these strata are known to yield plant fossils reflective of the ongoing evolution of the terrestrial biome. Lower Devonian palaeobotanic records are well documented from the exceptionally preserved Rhynie Chert in Scotland (Garwood *et al.* 2020), in addition to multiple significant sites in the Anglo-Welsh Basin (e.g. Edwards and Richardson 2004; Edwards *et al.* 2022). Upper Devonian records are less abundant, but include several floras reported from Irish basins (e.g. Jarvis 2000) and the Anglo-Welsh Basin (Hilton 1999), and transported plant material in marine delta-front facies of the Famennian Baggy Sandstones Formation in Devon (Goldring 1971; Hilton and Edwards 1999). By way of contrast, Middle Devonian palaeobotanic records are relatively scarce. In part, this reflects the tectonic conditions during the

interval, when the peak of the Caledonian Orogeny resulted in uplift, erosion and the development of regional unconformities across Avalonian, and many Laurentian, parts of Laurussia (McKerrow *et al.* 2000; Woodcock 2012) (Fig. 3). Mid-Devonian subsidence and sediment accrual persisted only in the basins of SW England, the Dingle Basin of Ireland and the Orcadian Basin in NE Scotland, and only the latter of these has previously yielded significant plant fossils in the form of Givetian floras, including cladoxyloids and *Svalbardia*, from Orkney and Shetland (e.g. Allen and Marshall 1986; Berry and Hilton 2006).

The British and Irish palaeobotanic record has thus so far suffered from an Eifelian blind spot due to the paucity of terrigenous strata of this age. Across the wider region of NW Europe, this Stage is associated with significant fossil floras, with several notable palaeobotanic sites known from the Ardennes in Belgium (Nappe de Goé, Unité de la Gileppe) and the Rhenish Massif region of Germany (Mühlenberg Schichten, Brandenburg Schichten, Funkloch Schichten) (e.g. Leclercq and Andrews 1960; Streef *et al.* 1987; Fairon-Demaret and Berry 2000; Berry and Fairon-Demaret 2002; Giesen and Berry 2013; Hartenfels *et al.* 2022). The unit considered in this study, the Hangman Sandstone Formation, fills this blind spot and has much in common with the Belgian and German sites.

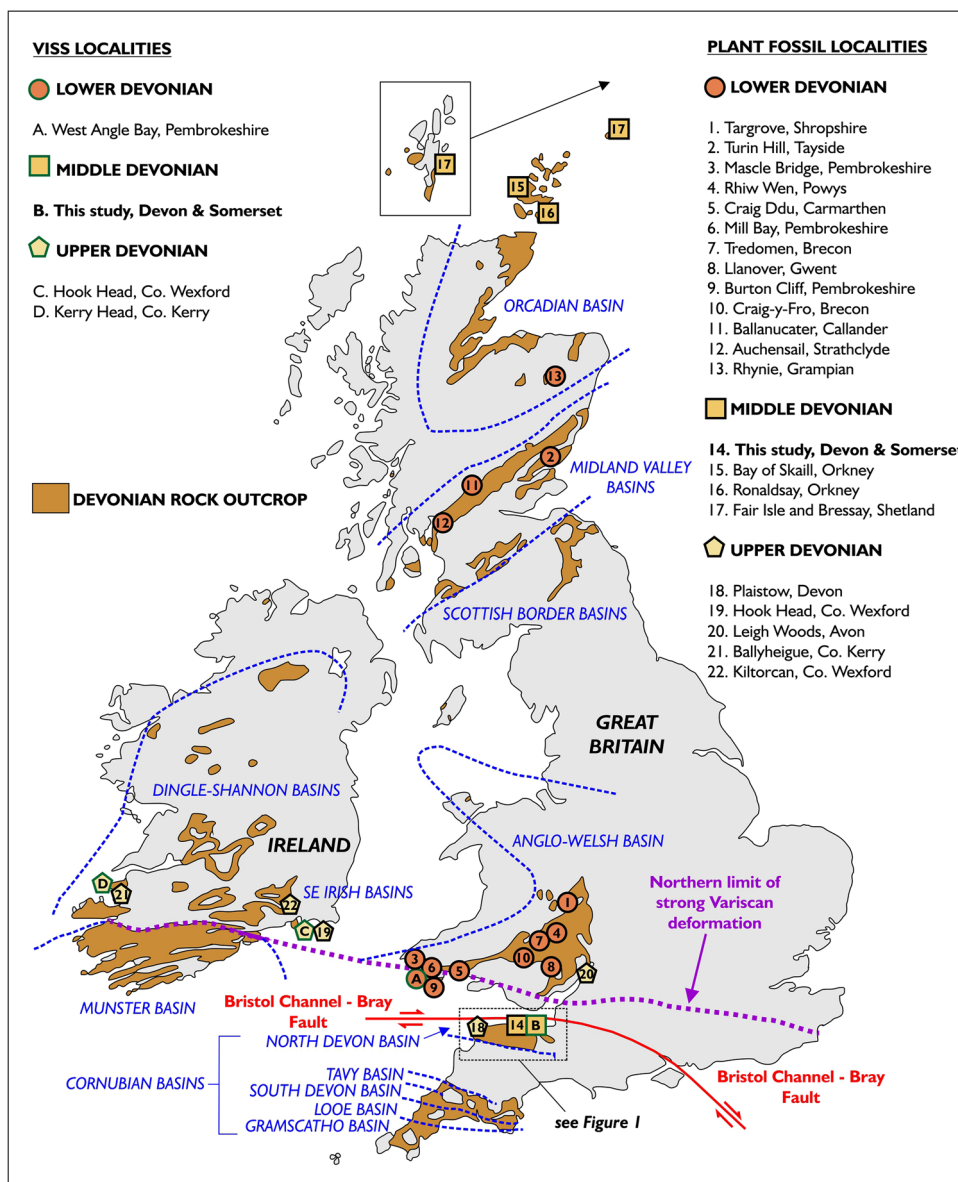


Fig. 2. Outcrop of Devonian-aged strata in Britain and Ireland showing the major depocentres and significant known locations of plant fossils and vegetation-induced sedimentary structures (VISS). Plant fossil localities compiled from Cleal and Thomas (1995) and Edwards and Richardson (2004); VISS localities referred to by Hillier and Williams (2007), Veenma *et al.* (2023) and Bridge *et al.* (1980).

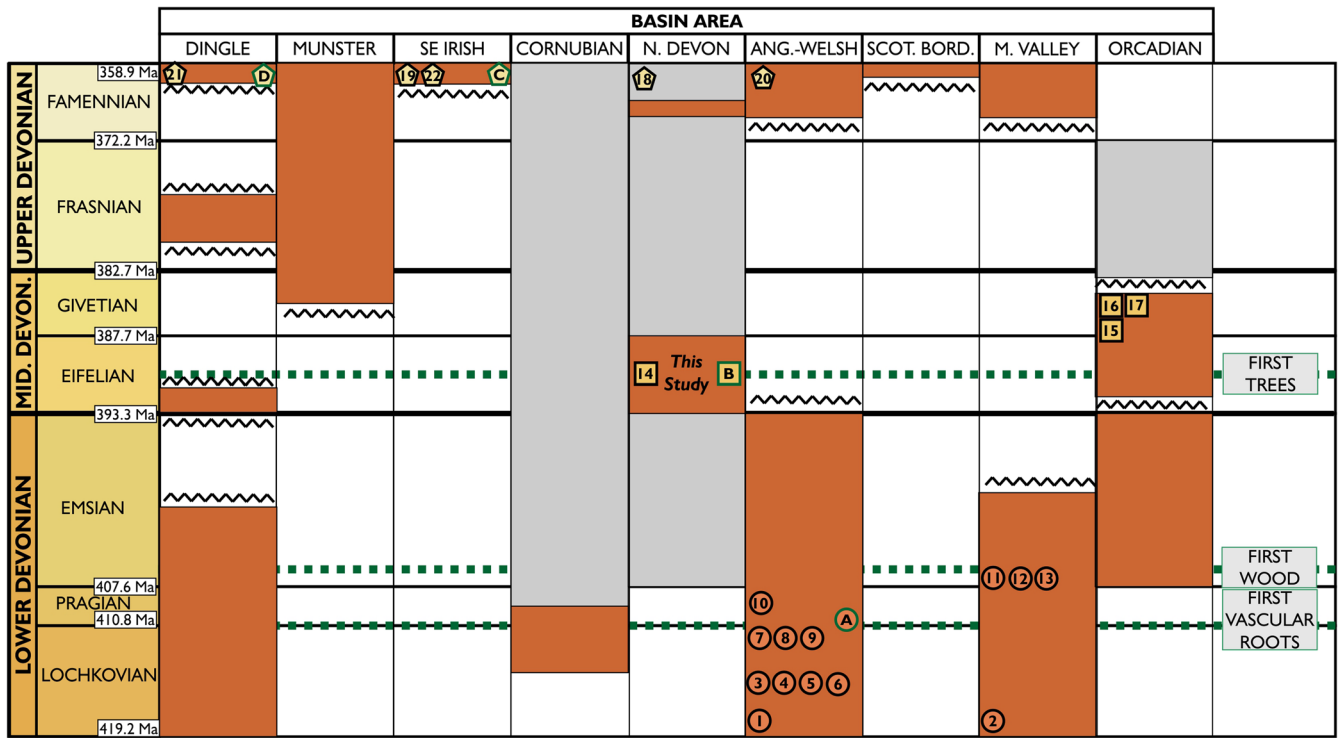


Fig. 3. Stratigraphic distribution of Devonian strata and fossil plant localities in Britain and Ireland relative to major evolutionary innovations in land plants. Brown bars show non-marine facies successions; grey bars show marine facies successions. Source: based on Friend *et al.* (2000, their fig. 3).

Hangman Sandstone Formation

The Hangman Sandstone Formation is a 1400 m thick succession of terrigenous red sandstones, with subordinate mudrocks and conglomerates, which has been palynologically dated as Eifelian in age (Knight 1990) and constitutes the second oldest unit of the Devonian–Carboniferous Exmoor Group (Webby 1965; Tunbridge 1983, 1984, 1986; Edmonds *et al.* 1985; Jones 1995; Edwards 1999; Whittaker and Leveridge 2011; Davies *et al.* 2023) (Fig. 1). The unit accrued within the North Devon Basin, the northernmost of several small, interconnected basins that developed in SW England throughout the Devonian (Leveridge and Hartley 2006; Whittaker and Leveridge 2011) (Fig. 2). Unlike the Old Red Sandstone elsewhere in the British Isles, the basins of SW England are dominated by marine sedimentary facies and the regressive interval recorded by the Hangman Sandstone Formation has frequently been excluded from being considered a ‘true’ Old Red Sandstone unit (Barclay *et al.* 2015).

Traditionally, the distinct character of this formation has been explained by the North Devon and Anglo-Welsh basins neighbouring one another as they do today, with the Exmoor Group mostly recording offshore deposition contemporaneous to the non-marine Old Red Sandstone and the Hangman Sandstone Formation being eroded sediment from the Anglo-Welsh Eifelian unconformity (Edmonds *et al.* 1975; Allen 1979; Tunbridge 1984, 1986; Tunbridge *et al.* 1987). However, several lines of evidence, including palinspastic tectonic reconstructions, stratigraphic comparison, facies correlations, basement composition and the presence of a ‘Rhenish’ trilobite fauna (Holder and Leveridge 1986; Dewey and Strachan 2003; Woodcock *et al.* 2007; Dijkstra and Hatch 2018; Rushton and Fortey 2018), show that the North Devon Basin was part of a distinct terrane, Cornubia (Leveridge and Hartley 2006; Woodcock 2012). More recent reconstructions (Fig. 4) suggest that this Cornubian terrane was displaced up to 400 km to the SE of the Anglo-Welsh Basin in the Mid-Devonian, along the Bristol Channel–Bray Fault (Holder and Leveridge 1986; Woodcock

et al. 2007; Leveridge and Shail 2011a; Whittaker and Leveridge 2011; Woodcock 2012). The unit was thus deposited along-strike of the same low-gradient continental plain as the plant-bearing Ardennes and Rhine Valley successions, south of the uplift that created a Mid-Devonian unconformity throughout most of the Devonian successions of Britain, Ireland and the North Sea (Bluck *et al.* 1988; Barclay *et al.* 2005; Belka *et al.* 2010) (Fig. 4).

Sedimentary environments

Detailed accounts of the sedimentary facies of the Hangman Sandstone Formation exist elsewhere (Tunbridge 1978, 1981, 1983, 1984, 1986; Jones 1995; Davies *et al.* 2023) and the unit can be summarized as being deposited within a suite of adjacent alluvial and lacustrine settings (see also Supplementary Material). The unit has been divided into several members (Fig. 1; Goldring *et al.* 1978; Tunbridge 1978) that have not been formally adopted by the British Geological Survey as they represent sedimentary facies assemblages rather than mappable units (Edmonds *et al.* 1985; Jones 1995; Edwards 1999). However, for the purpose of sedimentological investigation, the informal stratigraphic terminology remains useful and is followed here to aid comparison with older literature on the unit (e.g. Tunbridge 1984).

The informal members of the unit considered in the present study are the Trentishoe and Hollowbrook. The Trentishoe Member makes up the majority thickness of the Hangman Sandstone Formation (Fig. 1) and consists of parallel-laminated and subordinately convoluted red sandstones with siltstone drapes and scour surfaces, and desiccated mudrock packages with redoximorphic horizons and very rare calcretes (Tunbridge 1981, 1984). The member has traditionally been described as representative of ‘sheetflood’ deposition (Tunbridge 1981, 1984), although the use of this term as a descriptor has more recently been discouraged because of a lack of modern analogues for such phenomena (North and Davidson 2012).

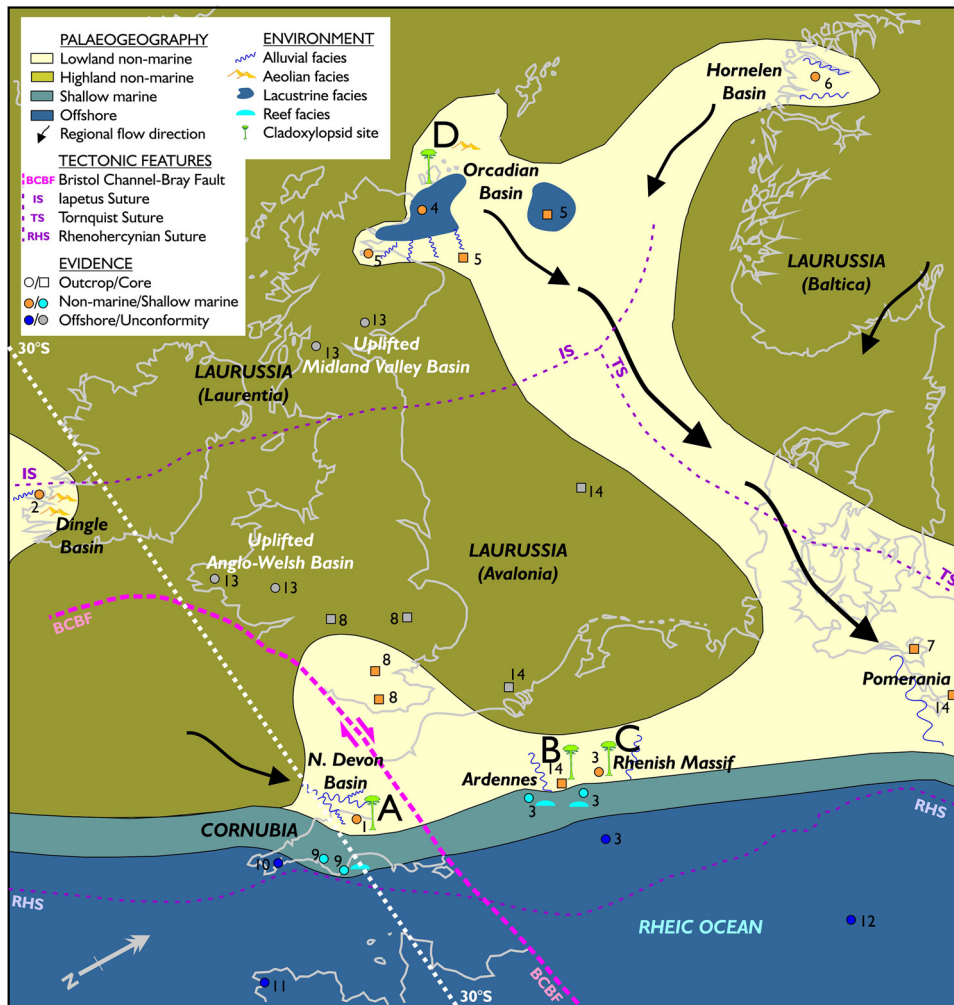


Fig. 4. Palaeogeographical map showing synthesis of tectonic and palaeoenvironmental evidence for the nature of the SE coast of the 'Old Red Continent' during the Eifelian (c. 390 Ma) and the relative location of the North Devon Basin and Cornubian terrane. Position relative to other known cladoxylopsid-bearing localities highlighted. A, this study. B and C, Belgian and German sites (see [Fairon-Demaret and Berry 2000](#)); B, Ardennes; C, Rhenish Massif. D, Younger Givetian site from the Orcadian Basin (Eday Flags, Scotland) ([Berry and Hilton 2006](#)). Extent of uplands, lowlands and marine area based on outcrop and core evidence for Eifelian continental, shallow marine and offshore sedimentary strata and unconformities, with greater uncertainty in reconstruction away from these data points. Numbers indicate references for data points: 1, this study; 2, [Morrissey et al. \(2012b\)](#); 3, [Hartenfels et al. \(2022\)](#); 4, [Marshall et al. \(2007\)](#); 5, [Whitbread and Kearsey \(2016\)](#); 6, [Steel et al. \(1977\)](#); 7, [Aehnelt and Katzung \(2009\)](#); 8, [Bluck et al. \(1988\)](#); 9, [Leveridge and Shail \(2011a\)](#); 10, [Leveridge and Shail \(2011b\)](#); 11, [Morzadec et al. \(1988\)](#); 12, [Chlupac \(1988\)](#); 13, [Barclay et al. \(2005\)](#); 14, [Belka et al. \(2010\)](#). Location of tectonic features from [Leveridge and Shail \(2011a\)](#); drainage directions from [Marshall et al. \(2007\)](#), palaeolatitudes from [Torsvik and Cocks \(2016\)](#).

The succession can more accurately be described as the deposits of a distributive fluvial system (DFS) (i.e. channel and floodplain deposits radiating outward from an apex where the river enters the sedimentary basin: [Weissmann et al. 2010](#)), sourced from the NW (see [Davies et al. 2023](#); and [Supplementary Material](#)). In this interpretation, the sandstone-dominated facies that predominate in the west of the outcrop belt, in Devon, record amalgamated alluvial channels in the proximal and medial parts of a DFS. The more heterolithic deposits in the east, in Somerset, reflect the distal parts of the same DFS, with more widely dispersed alluvial sandstones interfingering with playa lake facies ([Davies et al. 2023](#)). The Hollowbrook Member records a subordinate facies assemblage at the base of the Hangman Sandstone Formation, with only patchy exposure in Devon. The member consists of quartzitic grey sandstone with cross-lamination and local flaser bedding, indicative of nearshore or estuarine deposition at the onset of the marine regression in the area ([Tunbridge 1983](#); [Davies et al. 2023](#)).

Previous palaeobotanic reports

Despite preserving a notable thickness of non-marine strata, the Hangman Sandstone Formation has not previously been considered palaeobotanically significant ([Cleal and Thomas 1995](#)). Several studies have alluded to the presence of plant fossils without illustrating them, variably describing 'a few obscure plant remains'

([Hallam 1934](#), p. 28), 'common plant fragments' ([Lane 1965](#), p. 40), 'a few, scattered plant fragments' ([Webby 1965](#), p. 332), 'occasional carbonized plant remains' ([Tunbridge 1978](#), p. 277), 'rare plant debris' ([Tunbridge 1981](#), p. 82) and 'rare plant stems' ([Jones 1995](#), p. 8).

Other unillustrated reports of fossil plants in the unit have been made by [Evans et al. \(1914\)](#), [Evans \(1922\)](#) and [Evans and Stubblefield \(1929\)](#), who mention specimens of '*Psilophyton*' and '*Calamites cannaeformis*'. Reference to the presence of *Psilophyton* has been repeated in many subsequent studies ([Tunbridge 1978](#); [Edmonds et al. 1985](#); [Edwards 1999](#)), but is in all instances reliant on the original anecdotal report ([Edwards pers. comm.](#), in [Evans et al. 1914](#)) rather than new observations. In an earlier study, [Kidston \(pers. comm.](#), in [Ussher 1908](#)) noted the presence of material that resembled *Psilophyton*, but rejected that identification in favour of '*Ptilophyton*' based on better preserved specimens (see later). Reference to the presence of '*Calamites*' has also persisted without verification (e.g. [Edmonds et al. 1985](#)), but the specimens reported by [Evans and Stubblefield \(1929\)](#) are more likely to have been trunk fragments of *Calamophyton* (see [Giesen and Berry 2013](#)), which bear a superficial resemblance and are known to be common in the Hangman Sandstone Formation based on the present study.

Two plant fossils were illustrated by [Ussher \(1908\)](#) from [Smith's Combe](#) in the Quantock Hills, Somerset, within a detached inlier of

the Hangman Sandstone Formation east of the present study area. One specimen (Ussher 1908, fig. 2) shows a longitudinally striated stem ascribed to ‘the corduroy plant’ (Kidston pers. comm., in Ussher 1908). Examples of the ‘corduroy plant’ elsewhere are now thought to be the stem of the progymnosperm *Svalbardia* (Allen and Marshall 1986), of mid-Givetian to early Frasnian age, but in the Hangman instance, the striated stem might demonstrate the internal vascular system of a cladoxypsid, such as *Calamophyton*.

The second specimen (Ussher 1908, fig. 3) is ascribed to ‘*Ptilophyton thomsoni*’ (Kidston pers. comm., in Ussher 1908), now *Rellimia thomsonii* (Leclercq and Bonamo 1973). This identification may be correct as the illustration shows a ribbed main axis, typical of aneurophytalean progymnosperms. The most recent assessment of plant fossils in the Hangman Sandstone Formation was provided by Edwards (1999), who reported a single specimen of the bucket taxon *Hoftimella* (*sic*) sp. (Chaloner pers. comm., in Edwards 1999). Edwards (1999) also showed a photograph of a plant fragment from east of Hurlstone Point (Edwards 1999, plate 17), ascribed to a member of Cladoxyloids, possibly *Pseudosporochnus nodosus* (D. Edwards pers. comm., in Edwards 1999). This specimen is re-identified in this paper as *Calamophyton*. In addition to these scattered reports of plant macrofossils, Knight (1990) reported that the majority of the Hangman Sandstone Formation was relatively barren of palynomorphs, but that its upper strata contained over 70 different types typical of an Eifelian–Givetian age.

Plant–landscape interactions in the Hangman Sandstone Formation

Fieldwork across the Hangman Sandstone Formation outcrop belt (Fig. 1) has revealed that the unit is, in fact, rich in plant fossil material. Further, in many instances, both plant debris and standing trees are seen to exhibit a direct influence on physical sedimentary structures in the form of VISS, indicating that early Middle Devonian plants had a hydrodynamic role in shaping sediment accumulations. Three specific sites in the outcrop belt provide high-resolution windows onto plant–landscape interactions during the interval and these localities are described and interpreted as case studies to inform on archetypal Eifelian interactions. Away from these three sites, other strata within the Hangman Sandstone Formation shed light on hydrodynamic VISS associated with standing plants and both large and small plant debris as novel Middle Devonian sedimentary particles, and examples of these are also described.

Localities revealing Mid-Devonian plant–landscape interactions

Evidence for plant–landscape interactions has been identified at three sites: Culver Cliff, Selworthy Sand and Porlock Weir (Fig. 1). All these sites are located within the eastern part of the Hangman Sandstone Formation outcrop belt in Somerset (Fig. 1). As such, they are dominated by strata deposited in the distal region of a DFS, where the interfingering of alluvial sandstone facies and playa lacustrine mudrocks is common (Davies *et al.* 2023).

Culver Cliff

Culver Cliff is an isolated 30 m tall cliff that extends for *c.* 150 m along an otherwise low-gradient stretch of coast, located *c.* 1 km NW of the town of Minehead, Somerset (51° 13′ 11″ N, 03° 29′ 10″ W). The cliff provides an exposure of dominantly red heterolithic Trentishoe Member strata (distal DFS facies) within a faulted structural antiform. The oldest strata in the cliff are found in the middle of the antiform, in the centre of the cliff exposure at beach

level, and consist of grey fine- to medium-grained sandstones. The lowest visible bed surface in the cliff has only a limited extent, but is notable for containing at least 17 trunks of cladoxypsid trees of 5–10 cm diameter and up to 1.4 m in length (Figs 5 and 6a–e).

Plant fossils. The tree trunks are preserved mostly as impressions. The most abundant forms show a three-dimensional surface, consisting of longitudinal strips of slightly raised smooth matrix alternating with slightly lower relief strips in which short transverse depressions are closely arranged (Fig. 6a–d). In some instances, the non-smooth strips are found at the margins of the compressed trunks, where they can be seen to form protuberances (Fig. 6a, b) or the stubs of short acutely inserted lateral branches (Fig. 6f). Transverse depressions in the matrix are external moulds of the branch stubs. At the ends of some preserved trunks, a sandstone cast of an inner part of the trunk can be seen, which is smaller than the diameter of the complete compression (Fig. 6e).

These fossils can be immediately and, as yet, uniquely compared with fossils from Lindlar (Middle Eifelian) in Germany, and similar German fossils. Trunks from Lindlar, which show the same features in a better or clearer state of preservation, formerly named *Duisbergia* (see Schweitzer 1966, Taf. 25, 26 fig. 2, 27 fig. 1), are now recognized to be the vertical axis of a substantial pseudosporochnalean cladoxypsid tree bearing complex lateral branches, *Calamophyton* (Giesen and Berry 2013, figs 6b, 11).

The most common preservation mode of the fossil trunks at Culver Cliff represents external moulds (impressions) of vertical files of lateral branch bases separated by external trunk tissues, which may indicate a secondarily expanding trunk diameter (for discussion of probable growth modes in *Calamophyton*, and reconstruction of the tree, see Giesen and Berry 2013). It is a characteristic of *Calamophyton* v. other well-known members of the pseudosporochnales (e.g. *Pseudosporochnus*, *Wattieza*) that in *Calamophyton* abscising branches leave a short stub on the trunk, whereas branches of the other forms abscise more or less flush with the trunk surface leaving a scar (Fairon-Demaret and Berry 2000). These scars are approximately hexagonal and adjacent on the surface of the trunk, meaning that the *Duisbergia/Calamophyton* trunk with protruding branch stubs is so far distinct from other known cladoxypsid trunks.

In pseudosporochnaleans, trunk structural xylem tissues are largely restricted to a ring of numerous radially oriented plates near the periphery of the trunk. The inner part of the trunk in life is largely parenchymatous tissue, this parenchyma also occupying the volumes between xylem plates, or is possibly empty. Thus, the central region and other parenchymatous tissue might rapidly be lost and is easily cast to form a central cylinder of sediment (Fig. 6d).

Each *Calamophyton* tree, growing up to at least 2–4 m (Giesen and Berry 2013), would have shed numerous branches during growth, with only a distal crown retaining functioning photosynthetic branches. Whereas *Pseudosporochnus* and *Wattieza* branches divide into two to six equally sized daughter axes at approximately the same level (Berry and Fairon-Demaret 1997) (often referred to as digitate branching), those of *Calamophyton* divide unevenly at various, but close, levels (e.g. Leclercq and Andrews 1960; Schweitzer 1973; Fairon-Demaret and Berry 2000; Giesen and Berry 2013). Although no obvious *Calamophyton* branches have been found to date at Culver Cliff, typical branching is demonstrated in the previously reported Henner’s Combe specimen (identified incorrectly as *Pseudosporochnus* in Edwards 1999; see Fig. 6g in the present paper) and specimens from Porlock Weir (see later), which strengthens the identification of *Calamophyton* in the North Devon Basin. The specimen from Henner’s Combe is robust, *c.* 27 mm in diameter just below the dichotomy, which is large for *Calamophyton*, and more similar in size to the biggest specimen from Goé, Belgium (Leclercq and Andrews 1960) than the slightly smaller biggest trees at Lindlar (Giesen and Berry 2013).

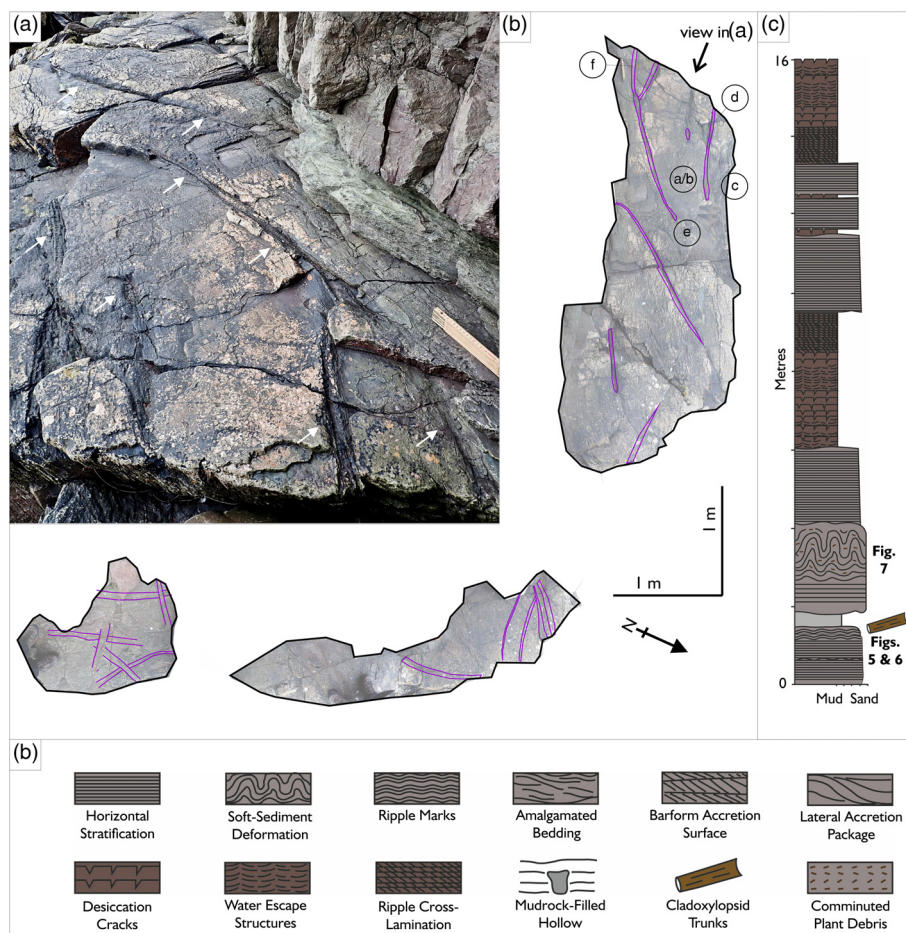


Fig. 5. Culver Cliff *Calamophyton* locality. (a) Oblique view of bedding plane showing at least 17 trunks lying on the bedding plane. (b) Annotated photomontage of discontinuous bedding plane showing plant fossils on surface. Letters in circles refer to close-up images in Figure 6. (c) Sedimentary log of the Culver Cliff site showing the stratigraphic position of later figures. (d) Key to sedimentary log in part (c).

Sedimentological context. The limited exposure of the *Calamophyton* bed precludes confident analysis of the precise environment in which the sandstone was deposited, but the reduced grey coloration may imply more waterlogged conditions than the remainder of the cliff succession, in a setting that also favoured preservation of the plant fossils (Gastaldo and Demko 2011). The plant remains rest in random orientations on top of the sandstone bed (at beach level) and there is no indication of any hydrodynamic interaction between the plant debris and sediment, such as scour marks or sediment shadows (Trümper *et al.* 2020). The debris also shows no attribute of having been a log jam deposit (see Gastaldo and Degges 2007; Gibling *et al.* 2010; Veenma *et al.* 2023) because, although there are clusters of logs, they are largely well spaced on the surface and no outsized sediment material or upwards facies shift is seen. The random orientation of the debris also differentiates the accumulation from other known Devonian woody debris accumulations (Davies *et al.* 2021) that record ancient driftcretions (Kramer and Wohl 2015), accumulations of drifted plant material organized along a strandline.

The debris thus appears to be a passive accumulation of shed woody material of uniform taxonomy on the former sediment substrate, with limited interaction with clastic sedimentary particles and having not experienced orientation by flowing water. The absence of taxonomic mixing implies that the material was not transported far (Bashforth *et al.* 2010, 2011) and the lack of preferred orientation implies that the material was subject to only weak currents before coming to rest. Similar accumulations occur in modern seasonally dry fluvial settings, where shed or snapped debris from in-channel vegetation is transported only short distances from stands of trees (Fielding and Alexander 2001).

Immediately above the *Calamophyton* horizon is a 3 m thick sandstone package (Fig. 7a, b) containing abundant comminuted

and fragmentary plant material. While the fragments are not identifiable, they are notable for their chaotic and widely spaced arrangement, rather than concentration in discrete horizons. Rod-shaped plant fragments up to 5 cm in length are seen in all orientations from horizontal to vertical and are dispersed evenly throughout the sandstone matrix (Fig. 7c–e). The unusual preservation style of these fragments can be attributed to the soft sediment deformation of the host sandstone, which exhibits large-scale active concave-up deformation of its constituent beds (*sensu* Świątek *et al.* 2023) (Fig. 7a, b). Such deformation arises from the rapid fluidization and liquefaction of the lower part of the sediment pile, usually within 2–10 m of the ground surface (Świątek *et al.* 2023). The undeformed nature of the immediately overlying beds suggests a seismogenic origin for liquefaction, rather than loading or deformation that occurred when the package was at the sediment surface. Liquefaction will have caused the upwards migration of pore fluids in the wet, unlithified sediment, repacking both loose sediment grains and any plant fragments that previously lined stratification surfaces within the sediment pile. The liquefied package does not preserve evidence of direct hydrodynamic interaction between plants and sediments, but is indicative of the heterogeneity imparted by the presence of plant remains as clasts, within sediment susceptible to liquefaction: an attribute known to influence the style and extent of soft sediment deformation (Świątek *et al.* 2023).

Other plant-related signatures at Culver Cliff include the impressions of isolated fragments of transported woody debris in fluvial channel facies (Fig. 7f) and one example of an enigmatic structure that is putatively ascribed to VISS (Fig. 7g). The latter feature consists of a 20 cm diameter circle of intraformational mud chips, hosted within a very fine-grained sandstone bed. Five poorly defined linear features of 2–3 cm width radiate from the circular

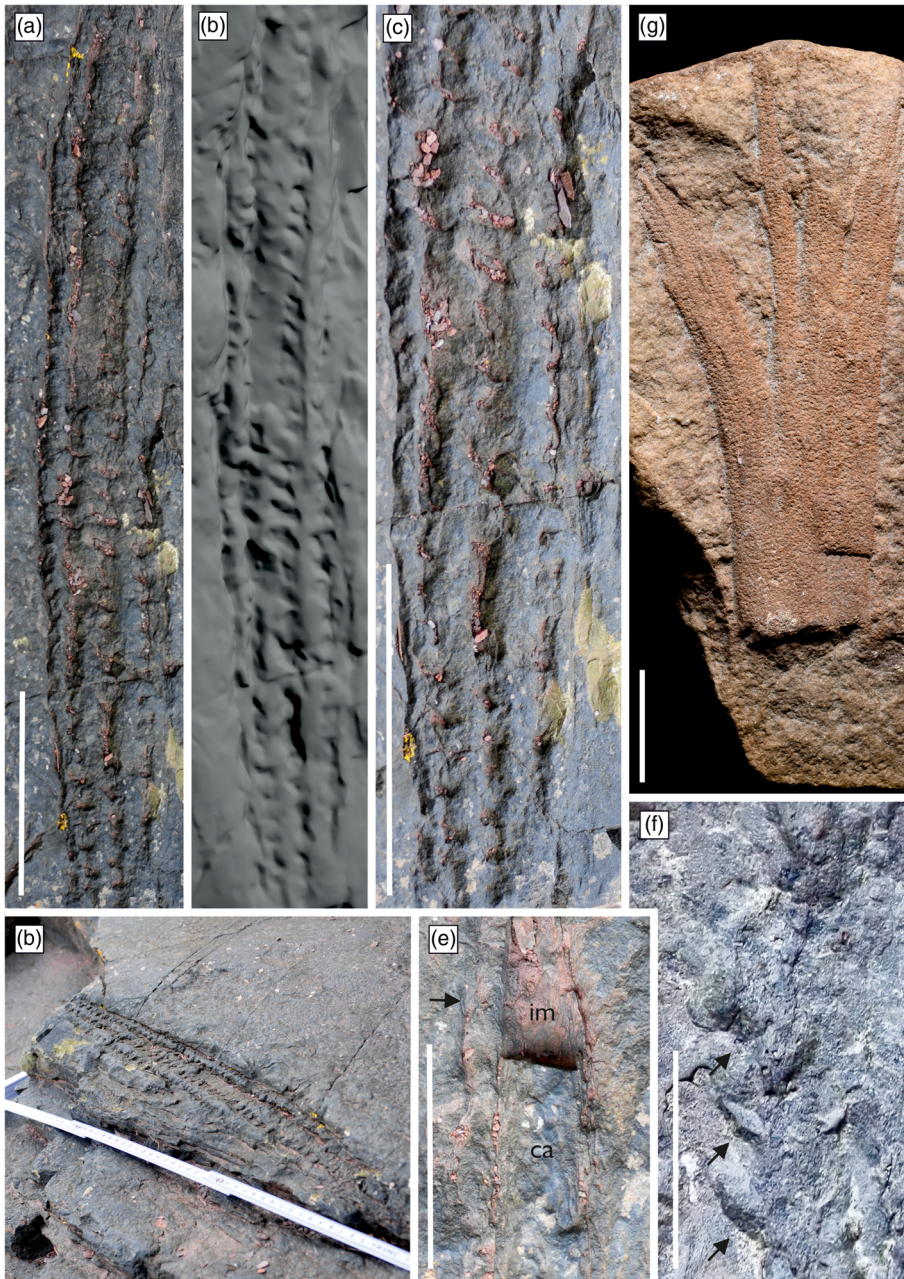


Fig. 6. (a–f) Details of the *Calamophyton* trunks at Culver Cliff. (a) Part of the best-preserved trunk impression showing four ranks of branch attachments forming depressions into the rock, with raised longitudinal strips between them reflecting the trunk surface between the ranks of branches, photographed from above. Scale bar 10 cm. (b) Photogrammetric surface model lit from top, same view and scale as part (a). (c) Close-up of the eastern end of the trunk shown in part (b). Scale bar 10 cm. (d) Oblique view of specimen shown in parts (a) and (b) looking east. Each segment of the ruler is 23 cm, width 15 mm. (e) Internal cast of another *Calamophyton* trunk (see Fig. 5). The cast (*ca*) is oval in section and stands proud of the revealed impression (*im*) where the cast has been lost. Arrow marks the left margin of the trunk, with weakly defined transverse depressions to the left of the cast representing one rank of branch bases. The internal cast is therefore narrower than the trunk diameter. Note that the dominant light direction is from the bottom of the photograph. The top of the photograph is oriented SW. Scale bar 5 cm. (f) Detail of the left margin of the trunk indicated in Figure 5, showing the still-attached branch base stubs typical of *Calamophyton* (arrows). Scale bar 2 cm. (g) *Calamophyton* branch from Henner's Coombe, as discussed in text, showing unequal branching at different levels and a typical speckled surface texture likely caused by sclereid nests in the outer tissues. Specimen UKBGS.GSM106361, grid reference SS 9141 4915. Scale bar 2 cm.

plug and preclude its identification as a burrow (such as *Beaconites* or *Taenidium*, both known from the unit; Davies *et al.* 2023). The specimen is too poorly preserved to be certain, but it is possible that the radiating spokes may preserve some aspect of a rooting system, with the mud chips recording passive decay-related infill of a former standing tree (see Rygel *et al.* 2004).

Selworthy Sand

Extensive sandstone bedding plane exposures of the Trentishoe Member occur at the western end of Selworthy Sand (51° 13' 54" N, 03° 34' 25" W) between Hurlstone Point and Minehead Bluff, Somerset. The dominant facies exposed as bedding planes is grey fine- to medium-grained sandstone, although the adjacent cliff facies contain a mixture of red sandstones and mudrock facies. The outcrops are located within the distal DFS facies belt of the Hangman Sandstone Formation (Davies *et al.* 2023), c. 1.5 km west of Henner's Coombe, from where the cladoxylopsid branch, now referred to as *Calamophyton* (see earlier), has previously been reported (Edwards 1999).

Bedding plane exposures at the locality predominantly represent true substrates: surfaces that reflect the original sediment–water/air interface from the time of deposition (Davies and Shillito 2018, 2021). The true substrate bedding planes have value in providing a short time-length scale window onto the depositional environment and can be seen to preserve multiple lines of evidence that indicate the sandstones were deposited under waning flow conditions and were subsequently emergent. In addition to these features, including ladder ripples, washover marks and washed-out ripples (Fig. 8), two prominent patches of pentagonal and hexagonal mudrock-filled hollows (individually c. 5–15 cm diameter) are also observed and are here interpreted as decay-infill of former stands of vegetation (Rygel *et al.* 2004). Evidence that the pentagons and hexagons reflect *in situ* standing vegetation (Fig. 9) includes the observation that stands of similar dimensions appear to cluster together (Fig. 9a, b), the association with flattened impressions of fallen vegetation (Fig. 9e, f) and the rare preservation of specimens preserved obliquely, rather than vertically, relative to bedding (Fig. 9g).

The relationship between the inferred standing plants and the surrounding physical sedimentary structures indicates a complex

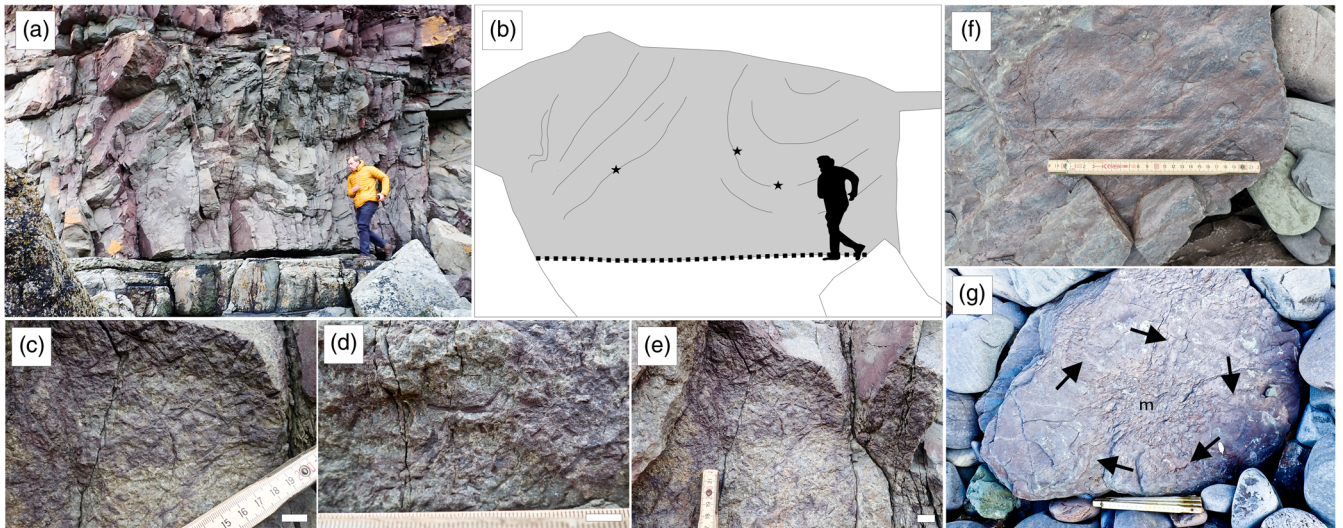


Fig. 7. Other plant material at Culver Cliff. (a–e) Extensive comminuted plant debris within 4 m thick seismogenic soft sediment deformation bed at Culver Cliff. (a, b) Photograph and sketch of the deformed bed showing plant horizon from Figure 4 (dashed line) and approximate location of images (c)–(e) (stars). Geologist for scale is 1.85 m tall. (c–e) Dense accumulations of comminuted plant debris lining upturned bedding surfaces seen in parts (a) and (b). Scale bars 1 cm. (f) Isolated impression of branch or small trunk. Scale bar 20 cm. (g) Mudchip-filled hollow (m) with five radiating arms (arrowed). Scale bar 20 cm.

depositional history because the two different stands (Fig. 8a) exhibit different levels of interaction. Stand 1 must have existed prior to the patterning of the true substrate surface with ripple marks because cusped deflections in the ripple crestlines align with the pentagons and hexagons (Fig. 9a, b). In analogous modern sparse vegetation stands (defined as where the stem spacing is less than the stem diameter; Larsen 2019), the diameter of individual stems dictates the scale at which flow disturbances develop (Tanino and Nepf 2008; Larsen 2019). Within stand 1, the scale of the ripple deflections, upstream of standing cylindrical obstacles, is broadly similar to that of the pentagonal and hexagonal features, implying that the ripples migrated while the standing obstacles were already in place.

By contrast, the pentagons and hexagons in stand 2 have a random distribution irrespective of the physical sediment patterns. Stand 2 pentagons and hexagons evenly cross-cut the main ripple crests and troughs, transverse ladder ripples and washed-out ripple

patches (Figs 8d, 9b), implying that their forms were registered into the sediment after the ripple marks. A similar relationship is seen with the flattened impressions of fallen vegetation (Fig. 9e), which can be seen to have impressed ripple crests after their formation. These observations allow the reconstruction of the sequence of events that created the main true substrate bedding plane (Fig. 8a), as follows: (1) the sediment that makes up the sandstone bed was deposited (based on facies context, as alluvial sandstone in the distal reach of a DFS); (2) after flow waned, the surface was colonized by vegetation (stand 1); (3) subsequent minor physical sculpting of the substrate (with or without new sediment), created ripple marks whose crestlines were deflected by the pre-existing stand of trees (stand 1); and (4) a second stand of trees developed on the same substrate (stand 2).

The true substrate thus records minor readjustments that developed during an interval of sedimentary stasis in between depositional events, of a duration sufficient for the growth of a small

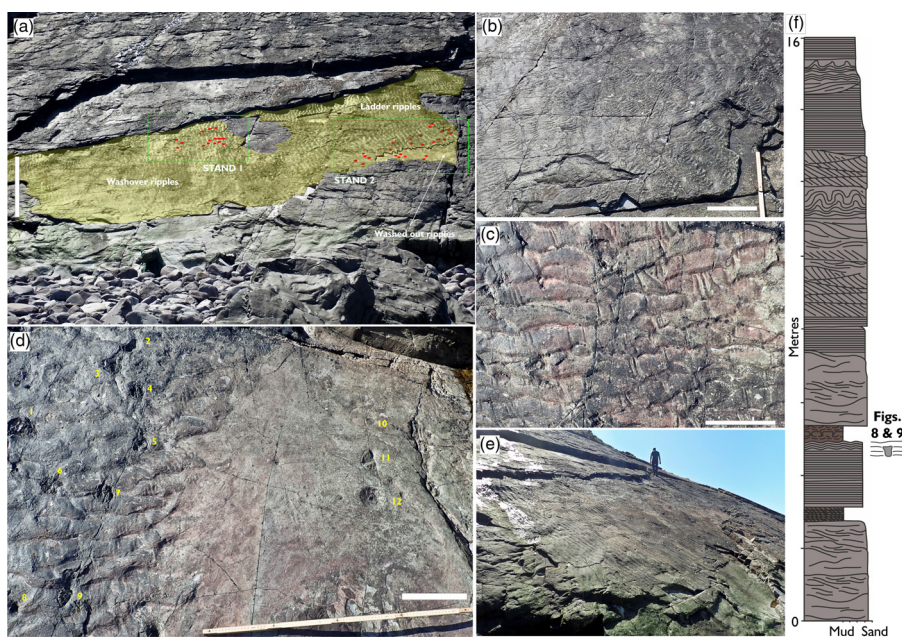


Fig. 8. Selworthy Sand standing tree locality. (a) Photograph of true substrate bedding plane yielding standing and fallen plants, annotated to show the extent of true substrate (yellow), two stands of standing plants (red) and variability in ripple mark morphology across the surface. Scale bar 5 m. (b) Ladder ripples near stand 2. Scale bar 20 cm. (c) Washover ripple marks near stand 1. Scale bar 20 cm. (d) Detail of stand 2 at washed-out margin of ripples, showing 12 standing plants passively colonizing the rippled surface (i.e. with no impact on ripple morphology). Scale bar 20 cm. (e) Oblique view of bedding plane showing gently undulose appearance. Geologist for scale is 1.85 m tall. (f) Sedimentary log of the Selworthy Sand site (key shown in Fig. 5d).

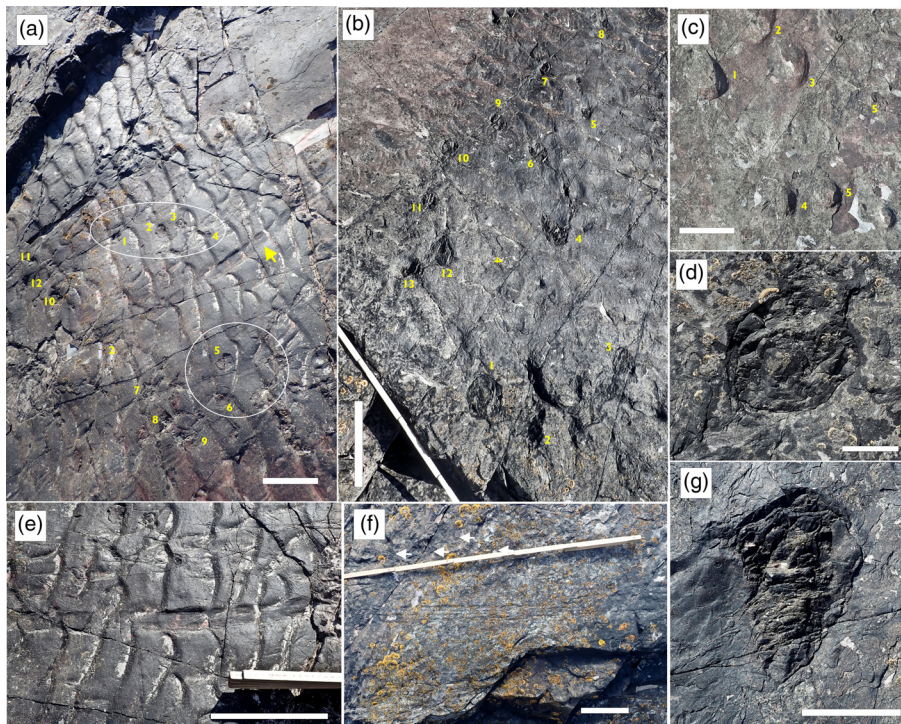


Fig. 9. Detail of the plant fossils at Selworthy Sand. (a) Detail of stand 1 showing fallen axis (yellow arrow) and 12 vertical axes. Circled areas show regions where ripples have deflected around the standing axes, indicating that the plants predated sediment deposition. Scale bar 20 cm. (b) Contrasting detail of stand 2, where the numbered vertical axes do not impact the ripple marks, implying post-deposition colonization. Scale bar 20 cm. (c) Exposed base impressions in washed-out ripples of stand 2 showing hemispherical bulbous base. Scale bar 20 cm. (d) Cross-section of mudrock-filled stem at stand 2 showing typical pentagonal form. Scale bar 20 cm. (e) Detail of fallen stem at stand 1 showing compression of ripple marks, indicating that the plant fell after ripples were cast. Scale bar 5 cm. (f) Fallen plant with longitudinal grooves (? *Calamophyton*). Scale bar 5 cm. (g) Cross-section of pentagonal stem lying obliquely in sediment, stand 1. Scale bar 5 cm.

stand of vegetation (i.e. months to years). The longevity of the ripple marks, which persisted during and after the growth of stand 2, implies that sedimentation and reworking were limited and potentially submerged (avoiding deflation by wind and explaining the grey, waterlogged(?) facies). Prolonged intervals of stasis in between depositional events would be common in the distal reaches of a DFS (Hartley *et al.* 2013), where the location of the main distributive conduit would vary, rendering some patches (at the spatial scale of this bedding plane) prone to sporadic depositional events with long intervals of stasis in between. The limited hydrodynamic disturbance in such settings would create a prime setting for plant colonization, with both an available damp sediment substrate and prolonged quiescence (e.g. Corenblit *et al.* 2007, 2015; Gurnell 2014).

Further sedimentary evidence that between-event colonization was common can be seen in the gently hummocky surface on which the ripple marks were imparted (Fig. 8e), implying that the substrate is an amalgamation of several depositional events that draped previous standing obstacles. The opportunistic colonization between events implies that this portion of the DFS experienced only weak abiotic geomorphic processes, on the timescale of the plants' lifespan, allowing biotic controls to dominate the geomorphology of the local-scale bedding plane (Corenblit *et al.* 2015; Larsen *et al.* 2021; Davies *et al.* 2022a).

Porlock Weir

A steep seaward-facing bedding plane outcrop within the Trentishoe Member, preserving abundant VISS, can be found near a cliff location known as First Rocks, 1.5 km NW of the village of Porlock Weir, Somerset (51° 13' 27" N, 03° 38' 46" W). The outcrop consists of amalgamated individual beds of limited lateral extent within the grey fine- to medium-grained sandstone facies. These beds can be divided into three discrete packages (Fig. 10): (1) an erosive concave-up surface that marks a constructed surface at the base of a channel (see Davies and Shillito 2021); (2) adjacent to this, the margins of that channel, archived as the upper surface of the amalgamated sediment package into which the channel has incised, which preserves structures that indicate the surface is a true

substrate; and (3) a package of sandstone confined to the area adjacent to the margins and above the constructed surface, reflecting the infill of sediment within the channel and capped with ripple marks indicating a surficial true substrate (at a slightly lower level to the channel margin). An entire transect of the channel can be witnessed, showing it to be a small feature of maximum 75 cm depth and *c.* 15 m width. Palaeocurrent indicators show that locally flow was in the direction upslope of the dipping bedding plane, to the south.

The channel margin package is notable for preserving six large mudstone-filled hollows, each up to 30 cm in diameter (Figs 10, 11). Unlike the mudstone-filled hollows at Selworthy Sand, the hollows show no hexagonal form, but nonetheless can confidently be identified as the boles of standing trees from two lines of evidence. First, five of the mudstone-filled hollows are located at the termination of fallen trunks, suggesting that the trees collapsed directly from these nodes, in a variety of directions (Fig. 11). Second, each hollow is seen in association with scour crescents on the channel margin true substrate, with a steep narrow incline on the stoss side of the hollow and a shallow elongate incline on the lee side of the hollow. The scours align directly with the flow of the channel form and are near-identical to modern scour marks formed by wake flow around larger standing trees, where the approaching flow is deflected downwards on meeting a pillar-like obstacle, inducing an erosional horseshoe vortex and a reduced wake zone flow in the lee of the obstacle (Allen 1982; Fielding and Alexander 2001; Nakayama *et al.* 2002; Rygel *et al.* 2004; Schlömer *et al.* 2020). As the toppled trunks overlie the scour marks (Fig. 11), the trees persisted as standing obstacles poking through the loose sediment after the scouring event occurred. The scours most likely formed when flowing water overtopped the confines of the small channel and was deflected around the adjacent standing trees.

Further evidence for the contemporaneity of the channel and trees can be seen in the fallen trunks that extend from the mudrock-filled hollows. Two of the channel-adjacent trees have toppled, such that their impressions extend from the channel margin package, down the gentle channel-side slope and onto the ripple-marked channel infill (Fig. 11). The interactions between the *in situ* vegetation and physical sediments thus reveal another timescale of intermittent

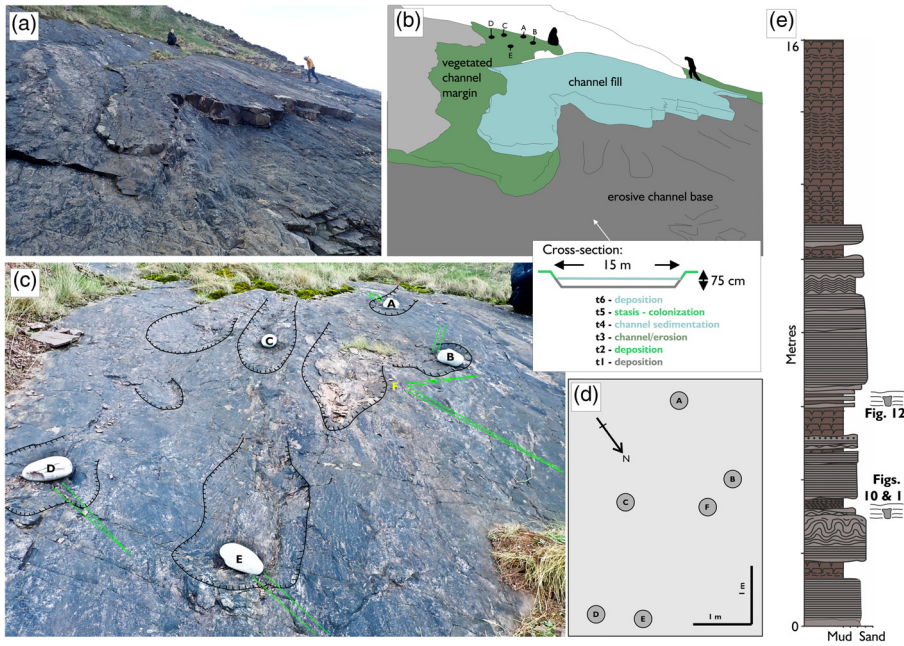


Fig. 10. Porlock Weir *in situ* tree locality. (a, b) Photograph and interpreted sketch of mudstone-filled hollows on margin of channel, infilled with sand (channel infill predates colonization because some elongate ridges extend over both surfaces; see Fig. 11). Mudstone-filled hollows marked with stones. (c) Association of mudstone-filled hollows with scours (marked). Stones marking hollows labelled A–E. F is a fallen tree preserved in convex epirelief (see Fig. 11). Green lines show the position of the associated elongate ridges or impressions, interpreted as fallen trees. (d) Measured plan map of relative spacing of the hollows on the bedding surface. (e) Sedimentary log of the Porlock Weir site (key in Fig. 5d).

sedimentation episodes: (1) the formation of a small channel in the outer reach of the DFS; (2) colonization of the channel margins during an interval of limited flood disturbance; (3) intermittent local overbank flooding from the channels, scouring hollows around the standing plants; and (4) the death of the trees and toppling into the channel.

The preservation of anatomical detail on the tree impressions at Porlock Weir is poor, so there is some uncertainty as to the tree species that were present. Given the other plant remains in the succession, and known globally, the most likely candidate for the

trees here are cladoxylopsids such as *Calamophyton*. These had a 2–4 m narrow monopodial trunk, an expanded unlobed rounded base up to 20 cm diameter and small roots (Giesen and Berry 2013), characters that cannot be attributed to any other plant type at the time, excepting the closely related *Pseudosporochnus* (Berry and Fairon-Demaret 2002). However, whatever the taxonomic affiliation of the vegetation, this outcrop provides the oldest known evidence globally for the relative position of standing trees, in common parlance a fossil forest, even though the trees are fallen so their exact dimensions cannot be established.

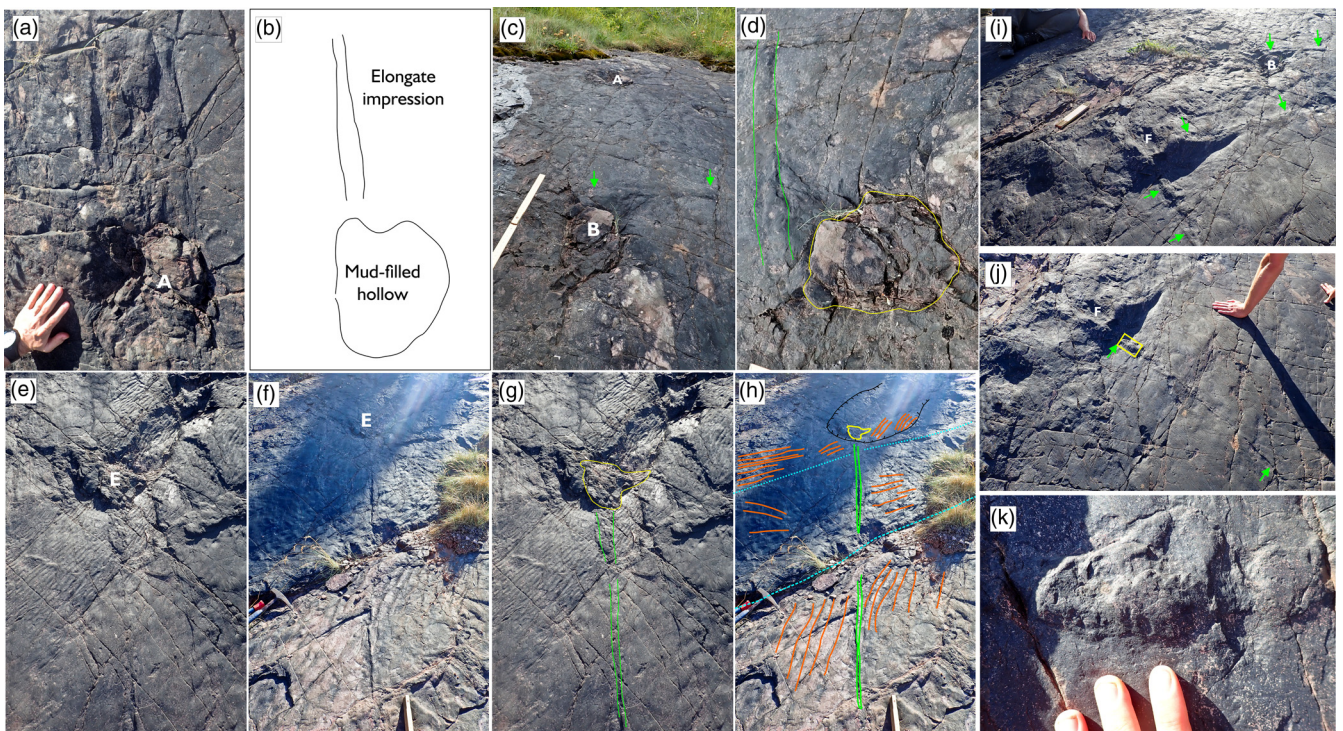


Fig. 11. Detail of the plant fossils at Porlock Weir (plants labelled as in Fig. 10). (a, b) Detail and sketch of hollow A (see Fig. 10) showing association with elongate impression. (c) Hollow B with elongate ridge (green arrows). (d) Detail of hollow B showing mud infill (yellow) and elongate ridge (green). (e, f) Detail of hollow E showing 273 cm elongate ridge extending away from hollow. (g, h) Interpreted images from parts (e) and (f) showing mudstone-filled hollow (yellow), elongate ridge (green) extending down convex (blue dotted line) and concave (blue dashed line) break of slope onto the channel sandstone fill (see Fig. 6). Note that the deflection of the ripple marks the crestlines (orange). (i) Raised mound F showing two elongate ridges extending from it (green arrows) at near 90° angle. (j) Continuation of one ridge for 208 cm. (k) Ornamentation of ridge, enlarged from yellow box in part (j).

Immediately overlying the main VISS surface, a package of grey, thin-bedded sandstones and siltstones is exposed at outcrop, with several true substrate bedding plane exposures visible. Isolated pentagonal and hexagonal mudrock-filled impressions are present throughout this package, with one bedding plane yielding *c.* 120 such specimens (Fig. 12). The features resemble those observed at Selworthy Sand, interpreted as the mudrock-filled decay voids of standing plants, but are generally smaller in diameter (<5 cm) and with tighter spacing (although still considered a sparse stand; Larsen 2019). The surface that they have colonized is patterned by ripple marks in several directions (Fig. 12a, b), implying the disruption of flowing water through the stand, as occurs in situations of bleed-flow through vegetation patches (Schnauder and Moggridge 2009).

Further evidence of the pentagonal and hexagonal features being the decayed bases of standing vegetation is seen by the development of sediment rims around them (Fig. 12c, d), indicating the deposition of sediment around a standing obstacle with minimal scour, forming small sediment mounds (Rygel *et al.* 2004). The pentagonal/hexagonal morphology suggests that the standing plants were most likely individuals of *Calamophyton*, which, because of their vertical ranks of branches, may have a trunk that is not entirely cylindrical, but is rather faceted. Near ground level, this might appear to have a low number of ranks of abscised branches because of the small size of the growing apex early in the plant's development (Giesen and Berry 2013).

A second plant fossil locality is also recognized in the Porlock Weir area, located 600 m east of the VISS bed at First Rocks. At this second locality (Fig. 13), two packages of reddened fine-grained sandstone are separated by a 30 cm thick siltstone unit, rich in parautochthonous plant fossils.

The plant-bearing siltstone caps a 1 m thick sandstone, interpreted as an amalgamated channel bar deposit. The high degree of channel bar amalgamation within this facies is a result of overall high aggradation rates (favouring the preservation of supercritical bedforms elsewhere in the succession; see Supplementary Material), in addition to a high channel return frequency (see Hajek and Straub 2017). While this autogenic reorganization has muted distinctive barform accretion surfaces, and the high dip of the outcrop (into the subcrop) limits the vantage of the original geomorphic structure, formation as an in-channel bar rather than a 1 m thick splay is considered most reasonable. Such facies are rare within the Trentishoe Member where scour has most often eroded the uppermost parts of bars, but in this fortuitous

instance the siltstone records the draping of the bar with fine sediment and plant material during receding flood conditions.

Most of the plant material is fragmentary and not identifiable, but a few specimens are complete enough to be worthy of comment. These include compressions and some rare limonite encrustations and permineralizations that preserve cellular detail, but steles prepared so far are quite broken up (Fig. 13b), potentially indicating dead plant material that had become desiccated in the semi-arid setting before burial. Where limonite is prevalent the compressions respond well to preparation, but other plant fragments are chloritized, replaced by a deep blue–green platy mineral, and preparation is problematic.

Small digitate branches of probably *Calamophyton* are *c.* 10 mm wide at their first branching point and have three or four unequal daughter branches (e.g. Fig. 13c). The branches are approximately one-third of the size of the Henner's Coombe specimen and so probably represent the early stages of growth of the plant, as demonstrated by Giesen and Berry (2013). No appendage has been found attached to the branches. The second well-preserved taxon at Porlock cannot be identified with certainty. As presently uncovered, it consists of small, regularly isodichotomizing main axes up to 2 mm diameter with a slight zigzag between branching points (Fig. 13d, e). This main axis includes a narrow strand of partially permineralized vascular tissue; however, the surface of parts of the axis are ribbed, suggesting that the complete stele may have been lobed. Some distal branching points are anisodichotomous and give off smaller axes, which are not completely preserved (Fig. 13d, e). The precise affinity of the plant is uncertain without further morphological or anatomical detail and it might be part of a much larger plant. Such material, with dominantly dichotomizing narrow naked axes, might account for previous records of both *Psilophyton* and *Hostinella* engrained in the literature for North Devon (see earlier section on previous palaeobotanic reports). The fragile nature of this plant debris implies limited transport, with the remains settling out on the bar-top during waning flood conditions.

Other plant and VISS examples from the Hangman Sandstone Formation

Away from the three main sites described, plant fossils and VISS occur in isolation throughout the Hangman Sandstone Formation. They are most common in reduced grey alluvial facies in the east of

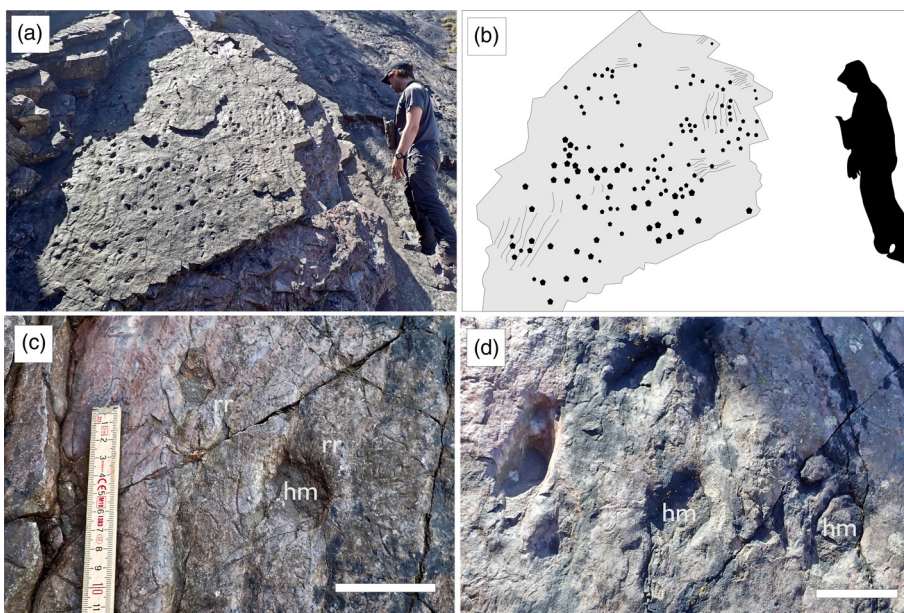


Fig. 12. True substrate bedding plane at Porlock Weir hosting a stand of 120 mudstone-filled former standing plants. (a, b) Photograph and sketch of the bedding plane showing the distribution of stems and variable ripple direction due to interference with the stand. Geologist for scale is 1.75 m tall. (c, d) Detail of the mudstone-filled hollows showing the hexagonal form (hm) and raised rims of sand (rr) around obstacles. Scale bar 5 cm. Note that photographs of this surface were taken between May 2021 and December 2022. A return visit in September 2023 revealed that much of the right-hand half of the bedding plane had been eroded in winter storms.

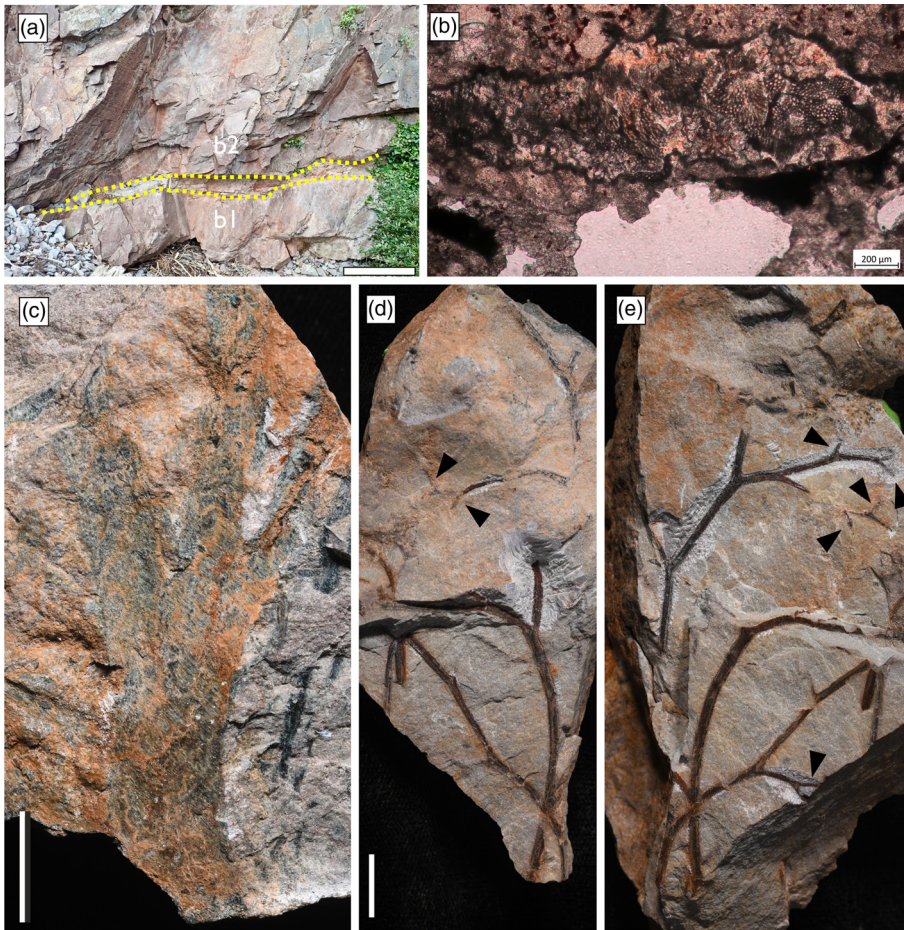


Fig. 13. Parautochthonous fossil plant material preserved in bar-top mudrocks, Porlock Weir. (a) Bar-top mudrock package (highlighted) on top of sandstone bar (b1), overlain by second bar (b2). Scale bar 1 m. (b) Degraded cellular detail in prepared stele from limonitized plant fragment within the assemblage. Scale bar 200 μm . (c–e) Selected parautochthonous plant material preserved within the bar-top mudrock (for description, see text). (c) Small unequally digitately branching axis, likely from *Calamophyton*. Scale bar 10 mm. (d, e) narrow, isodichotomously branching axes with some anisodichotomies apparently bearing narrower laterals (arrows), part and counterpart. Scale bar 10 mm.

the study area, representing the distal portion of the DFS, but examples are also known from playa lake mudrocks and from the marine-influenced Hollowbrook Member at the base of the formation in the west. Evidence for both standing vegetation and plant debris have been observed.

Evidence for standing vegetation

Two types of evidence for standing vegetation are recognized: (1) rooting structures; and (2) hydrodynamic VISS, with or without associated vegetation. Rooting structures in the Hangman Sandstone Formation (Fig. 14) have been observed at three localities in the east of the study area. Unlike the three main VISS localities, hosted within distal DFS facies, almost all known instances of rooting occur within playa lacustrine mudrock facies. Both vertical (Fig. 14a, b) and horizontal (Fig. 14d) structures have been recognized in emergent mudrocks (containing desiccation cracks) or within very fine-grained sandstone representing lake margin sedimentation.

Traces of rooting structures are also recognized in some of the redoximorphic horizons that typify the Hangman Sandstone Formation in the east (Fig. 14c). These mottled red and white textures, which often follow primary sedimentary fabrics such as cross-bedding, consist of deep red iron precipitates that were likely sourced from the host sediment. Similar redoximorphic horizons have previously been described as forming as a result of fluctuating groundwater tables in seasonally wet environments under semi-arid climates (Wright *et al.* 1992; Hillier *et al.* 2011). As the main signature of the Hangman redoximorphic horizons is one of low chroma patches in red horizons, it is likely that localized changes in sediment chemistry were imparted in two ways: (1) fluctuating water tables, which introduced oxygen through desiccation cracking

or along ped surfaces; and (2) through the decay of organic material in the vicinity of the roots (Hillier *et al.* 2011). The low chroma root traces in the Hangman Sandstone Formation (Fig. 14c) appear to cross-cut cross-bedding structures in the playa lake facies, implying groundwater recharge of sediment laid down during seasonally wet conditions.

Root structures are rare within fully alluvial facies of the formation (even in instances where *in situ* standing plants (e.g. the mudstone-filled hollows) record the penetration of substrates by upright stems) (Figs 9, 12). Aside from the putative rooting structure at Culver Cliff (Fig. 7g), one other instance has been recognized in distal DFS facies from near Hurlstone Point (Fig. 14e), where cross-cutting horizontal traces are seen, with branching characters and dimensions that differentiate them from animal burrows in the succession (Davies *et al.* 2023). The absence of evidence for rooting in the alluvial facies, despite the presence of standing plants, is most likely a taphonomic bias because the most readily recognized rooting structures occur as reduction patches in very fine sandstones (Fig. 14). The coarser grain size and fully reduced nature of many of the standing plant horizons appears to have rendered any rooting structures unidentifiable.

By contrast, in the playa lake facies where sedimentary stasis was of a longer duration, with a greater opportunity for decay, standing plant fossils tend to be absent, with their presence only indicated by root structures. Additionally, muddy substrates in the distal playa lake facies appear to have been unfavourable for plant colonization, potentially due to waterlogging or non-porous substrates. A continuous succession of >10 m of redoximorphic mudrocks is present in the Porlock Weir area, but lacks any of the vertical root structures seen in the redoximorphic very fine sandstones (instead archiving cross-sections of desiccation cracks and microbial mat structures; Davies *et al.* 2023). The only potential root structures

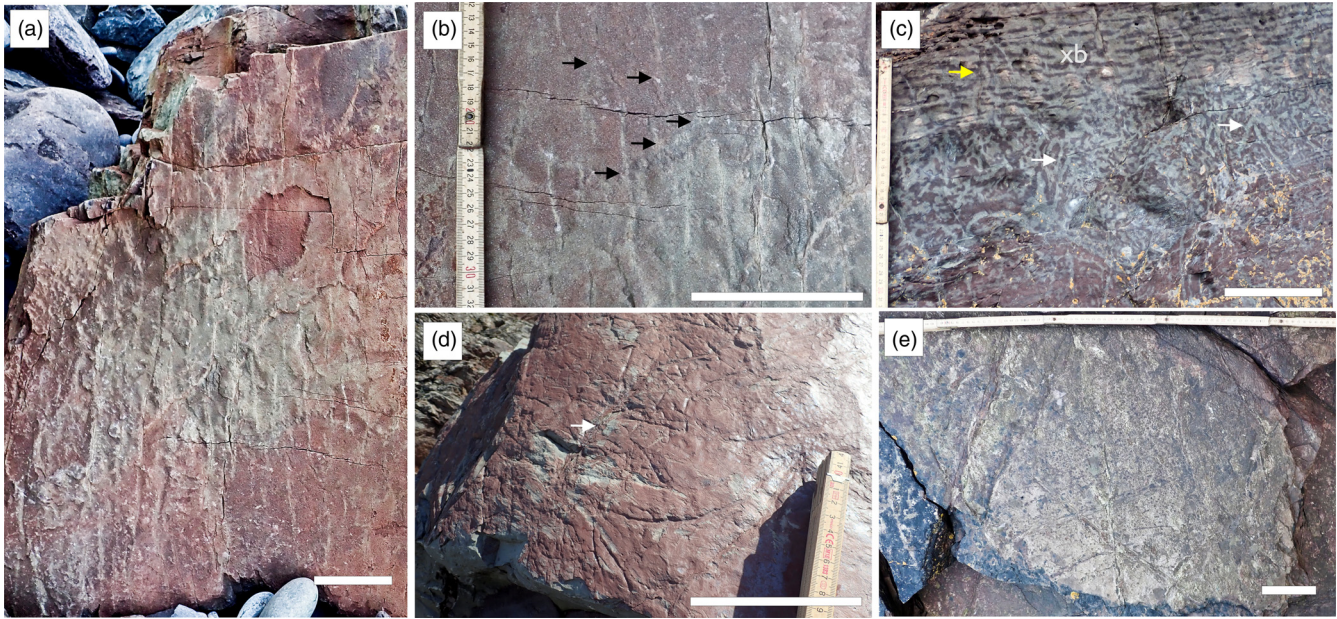


Fig. 14. Root structures in the Hangman Sandstone Formation. (a) Reduced downwards-bifurcating vertical root structures in very fine-grained sandstone, Greenaleigh. (b) Detail of part (a), with bifurcations arrowed. (c) Groundwater ferricrete that has picked out the structure of a cross-bedded sandstone (xb) overlying a rooted horizon recorded by acutely downwards-bifurcating V-structures (white arrows). Yellow arrow shows vertical structures cross-cutting the overlying sandstone, possibly also related to *in situ* plants. Hurlstone Point. (d) Horizontal arcuate rootlet(?) impressions branching from a straight central root(?) structure (arrowed), Porlock Weir. (e) Cross-cutting horizontal structures of variable width; possibly horizontal roots or poorly preserved plant debris, Greenaleigh. All scale bars 10 cm.

identified in mudrock facies in the unit are a single example of horizontal, apparently bifurcating structures at Porlock Weir (Fig. 14d).

Several isolated instances of hydrodynamic VISS also attest to the presence of standing vegetation (Fig. 15). These include

examples not recognized at the main sites (see section, Localities revealing Mid-Devonian plant–landscape interactions) and include teardrop- and horseshoe-shaped mounds of sediment surrounding mudrock-filled hollows recording small vertical plant axes. Such mounds are typical of reduced turbulence and velocity during bleed-

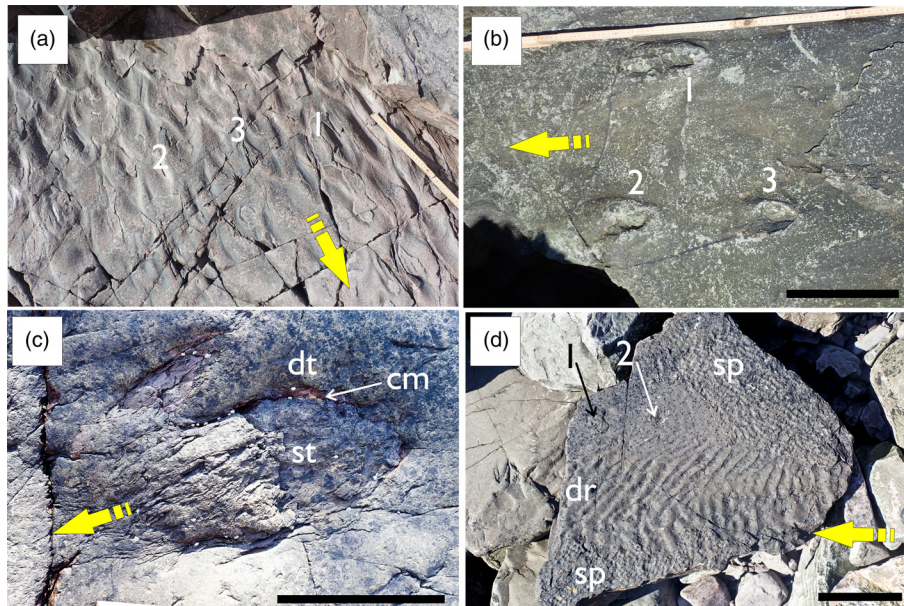


Fig. 15. Hydrodynamic vegetation-induced sedimentary structures around standing plants, with direction of flow in each instance shown by yellow arrow. (a, b) Teardrop- and horseshoe-shaped mounds of sediment around vertical plant axes, typical of reduced turbulence and velocity during bleed-flow through a stand of obstacles. (a) Image shows several chevrons, some (numbered) showing a mudstone-filled void in their centre that may have influenced their formation, Porlock Weir. (b) Image shows horseshoe-shaped mounds on the stoss side of three obstacles (not preserved), Rodney's Beach. (c) Cross-section of standing plant (st), decayed and infilled with sediment, but with carbonaceous material (cm) preserved around rim. Sediment bedding plane is downturned (dt) on the stoss side of the obstacle and the oblong shape of the obstacle suggests that the plant grew its trunk under sustained flow into the direction indicated, Rodney's Beach. (d) Diverted ripples (dr) around patch of standing plants revealed by two trunk impressions (numbered) within V-shaped patch lacking bedding plane structures. Stippled impression (sp) surrounding ripples resembles rain-impact microtopography, Hurlstone Point. All scale bars 20 cm.

flow through a stand of vertical obstacles (Hillier and Williams 2007; Davies *et al.* 2021) and ripple deflection around plants. One example of a downturned bed (the upstream part of a current scour) turns inwards towards a downstream-tilted trunk (Fig. 15c), implying that the plant was growing under at least seasonally submerged conditions, affected by local flow. While most of these examples come from distal DFS facies, two instances are recorded from the western part of the outcrop belt at Rodney's Beach, Devon (Fig. 15b, c). Such examples may only be uncommon in the proximal and medial DFS facies because their identification relies on the discovery of rare true substrates, within an environmental setting where most bedding contacts are amalgamated or erosional.

Distal red bed DFS facies of the Hangman Sandstone Formation in the Porlock Weir area also host putative examples of hydrodynamic VISS with no accompanying evidence for standing vegetation (Fig. 16). Examples include both possible centroclinal scour (Fig. 16a) and concavo-convex mounded topography (Fig. 16b). Both such phenomena are recognized VISS (Rygel *et al.* 2004) and, while confident diagnosis of these specific examples is not possible without the presence of standing tree fossils, the abundance of verifiable VISS elsewhere in the local succession renders such an interpretation probable. The absence of directly associated standing plants does not negate the interpretation because modern analogues show that substrates can develop an irregular topography inherited from upstream or cross-stream obstacles, where floodwaters flow over vegetated surfaces (Reesink *et al.* 2020).

Plant debris accumulations

In addition to parautochthonous bar-top plant debris (Fig. 13) and accumulations of large trunks (Fig. 5), isolated fragments of woody plant debris are common throughout all the DFS facies of the formation, contrary to previous assertions that such material is rare (Hallam 1934; Webby 1965; Tunbridge 1981; Jones 1995). A few pieces of debris can be identified and support the idea that the largest plants in the environment were cladoxyloids. The ubiquity of the debris attests to dense forests of these plants colonizing much of the DFS setting and its hinterland and suggests that the Mid-Devonian saw the advent of a novel sedimentary–geomorphic agent in the form of large woody debris (i.e. abundant particles of plant material greater than 1 m in length or 0.1 m in diameter: Harmon *et al.* 1986; Braudrick *et al.* 1997). In other Devonian successions, the onset of such sedimentary particles also occurs in Eifelian strata (Davies *et al.* 2021), suggesting that this Stage records a major sedimentological change reflective of a revolution in non-marine environments and landscapes. While many of the Eifelian particles are not true wood in a palaeobotanic sense and may have lacked the rigidity of equivalent fragments from lignophyte plants that became more common in the later Devonian and Carboniferous (Davies and Gibling 2013), they would have been an acutely abundant by-product of cladoxylopid forests.

Reconstructions of *Calamophyton* (e.g. Giesen and Berry 2013, fig. 1b) indicate a multi-branched plant with numerous lateral branches up to 50 cm long. To reach a mature state of growth, any one plant would need to shed 700–800 branches during its lifetime, resulting in forest floors littered with thick piles of plant detritus (Giesen and Berry 2013). This abundant woody debris would have had profound environmental consequences, representing the inception of a novel sedimentary particle that has subsequently played a major part in habitat creation, nutrient distribution and landform development within fluvial environments up to the present day (Gastaldo 1994; Gurnell 2012; Wohl 2017).

Other notable plant debris accumulations occur in sandstones within the playa lacustrine facies at Greenaleigh, Somerset (Fig. 17). At this locality, a 1 m thick package of sandstone contains plant debris

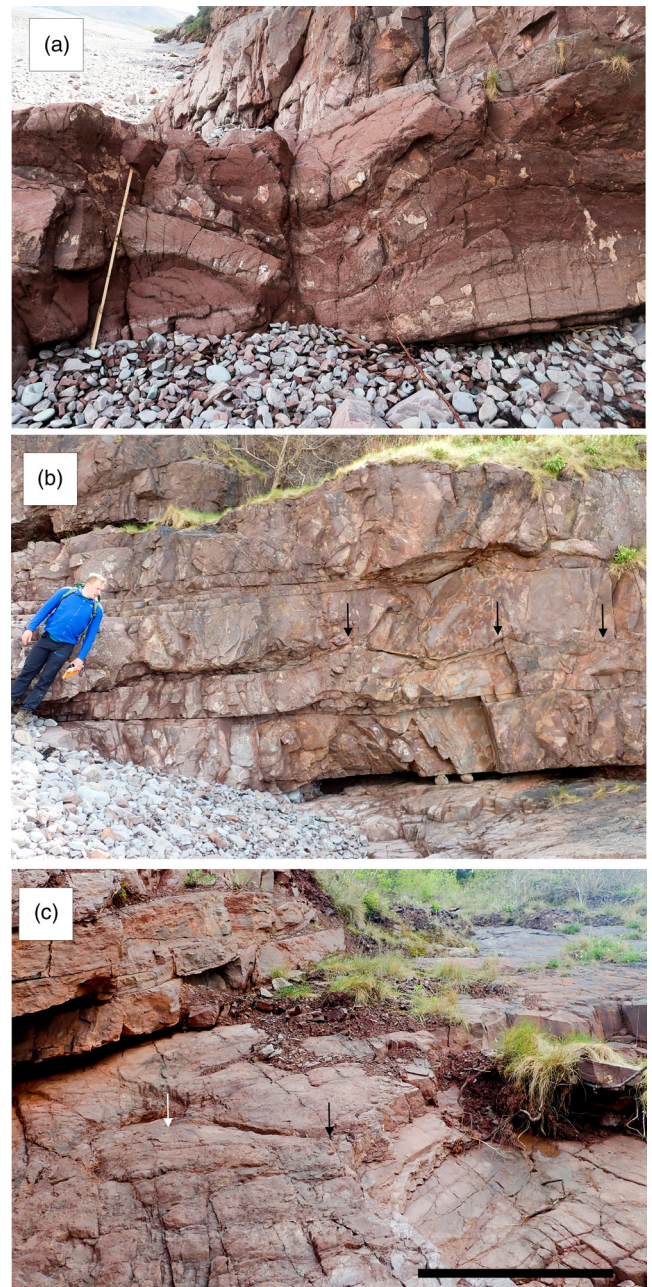


Fig. 16. Probable hydrodynamic vegetation-induced sedimentary structures preserved as synoptic topography without associated standing plants. (a) Possible heterolithic centroclinal cross-strata formed adjacent to standing tree, Porlock Weir. Measuring stick is 1 m long. (b) Closely spaced mounds (arrowed) potentially formed around standing plants, Porlock Weir. Geologist for scale is 1.85 m tall. (c) Same horizon as part (b), seen in plan view with synoptic scour-and-mound topography revealed by raised mounds (white arrow) and concave depressions (black arrow), Porlock Weir. Scale bar 1 m.

lining all the inclined surfaces that comprise its interior. The context of the package, adjacent to shallow lacustrine mudrocks, implies that the inclined surfaces represent the clinofolds of a small delta feature at a shallow lake margin. The inclined plant-debris-linings have analogies in modern lacustrine delta environments where debris is derived from the lake margin. In these settings, plant and sediment debris mixtures are swept over the rollover point on the delta, but settle at different rates, creating clinofold slopes with alternating compositions of plant debris and sand (Spicer and Wolfe 1987).

The largely comminuted nature of the plant material makes the identification of plant species impossible, but the abundance of stick-

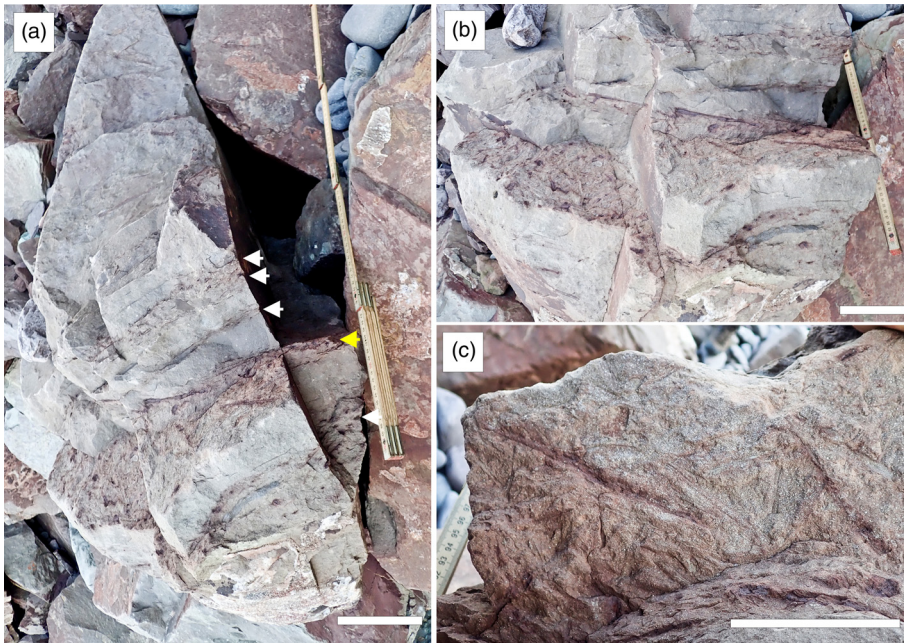


Fig. 17. Clinoforms of cross-bedded sandstone, lined with plant debris, within lacustrine facies at Greenaleigh.

(a) Oblique view of loose block of cross-bedded sandstone showing plant-debris-lined clinoforms (arrowed). (b) Detail of clinoform shown with yellow arrow in part (a). (c) Detail of randomly oriented plant debris lining a clinoform. All scale bars 10 cm.

like debris of different dimensions may imply that a succession of relatively high-velocity flow events were responsible for the deposition of each clinoform (Spicer and Wolfe 1987; Davies *et al.* 2022b). Such a hydraulic character aligns with other sedimentological traits in the Hangman Sandstone Formation that are indicative of wet-dry seasonality (e.g. the redoximorphic horizons).

Plant debris is less common within the basal Hollowbrook Member of the Hangman Sandstone Formation, which crops out in the western part of the outcrop belt in Devon and reflects marine-influenced deposition in a nearshore or estuarine setting at the onset

of the transgression that presaged non-marine conditions in the region (Tunbridge 1983; Davies *et al.* 2023). Drifted plant debris has been recognized in such open water facies at the transition between the underlying marine Lynton Formation and Hollowbrook Member at localities including Hollow Brook, Woody Bay and Heddon's Mouth (Figure 18), attesting to a vegetated landscape prior to the non-marine sedimentary record in the area. Large woody debris is absent from these facies, but drifted material includes rafted mats of plant detritus, some of which have possible *Calamophyton* digitate branching (Fig. 18a, b, e), as well as more

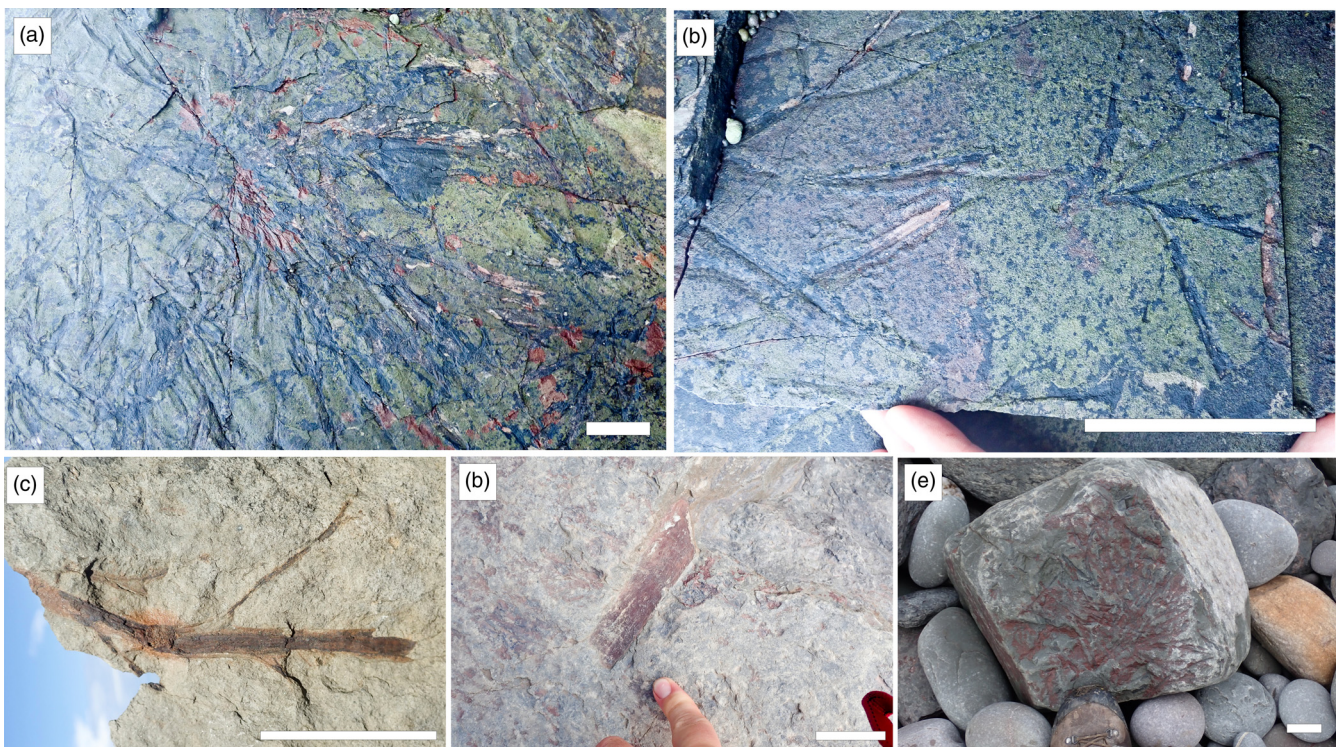


Fig. 18. Drifted plant material preserved in estuarine/shallow marine facies of the Hollowbrook Member. (a, b) Image and detail of stranded dense raft of drifted plant material preserved on rippled bedding plane of grey sandstone including possible *Calamophyton* branch, Woody Bay. Scale bar 10 cm. (c) Discrete piece of drifted woody debris, likely aneuphyte, within sandstones also exhibiting marginal marine trace fossils, Hollow Brook. Scale bar 5 cm. (d, e) Wood and matted plant debris in marine facies at transition of underlying Lynton Formation and Hollowbrook Member, Heddon's Mouth. Scale bar 5 cm.

woody axes with significantly smaller laterals that may represent branches of aneurophytes (Fig. 18c, d). The delivery of plant material to the marine realm suggests proximity to a densely vegetated land surface and is demonstrative of how the Devonian evolution of the Earth's land biosphere would have had impacted teleconnections with the marine realm, increasing the export of novel nutrients and resources through sediment transport pathways.

Distribution of plant–sediment interactions

The Hangman Sandstone Formation is rich in standing plant fossils, cladoxylopsid logs and branches, VISS, rooting traces and plant debris accumulations, all preserved within sedimentary strata that were deposited in a DFS and adjacent nearshore settings (Davies *et al.* 2023). The Eifelian age of the unit means that many of these phenomena are among the earliest known examples globally and have potential to shed light on the co-development of plant life and biogeomorphology during the Devonian revolution in the Earth's non-marine biomes. However, while some examples preserve high-resolution snapshots of local-scale features, extrapolating the significance of these to the wider regional environment or to a global context requires cautious reading of their distribution. The sedimentary record that hosts these signatures is subject to several biases that mean that it cannot be taken as a literal archive of all plant–sediment interactions in the environment, with some parts of that environment being more favourable to the preservation of plant fossils or strata in which plant fossils may be stored. The collection of plant–sediment interactions that can be observed today in the Hangman Sandstone Formation are survivors of these taphonomic hurdles and the extent to which they are representative samples must be assessed prior to attempting to elucidate the biogeomorphic and habitat characteristics of the formation. The distribution of plant-related signatures in the unit are summarized in Figure 19, and the influences on this distribution are discussed in the following sections.

Influence of the ‘stratigraphy machine’

Any stratigraphic formation is an amalgamation of sedimentary signatures, created by physical and biological processes, and deposits at a multitude of spatiotemporal scales (Kleinhans *et al.* 2005; Miall 2015; Holbrook and Miall 2020; Davies and Shillito 2021; Miall *et al.* 2021; Davies *et al.* 2022a). In the Hangman Sandstone Formation, these signatures include features that formed over both very short (e.g. ripple marks) and long (e.g. rare calcrites) timescales, and both small (e.g. individual burrows) and large (e.g. channel bases) length scales. The surviving signatures and sedimentary beds that have been archived are a fragmentary sample of all such iterations that existed during the time of deposition and their storage to the present day has been determined by the processes of the so-called stratigraphy machine – the interplay of reworking and accommodation that determines survivorship (Miall 2015; Holbrook and Miall 2020; Miall *et al.* 2021).

The precise operation of the stratigraphy machine is specific to a setting because different environments and sub-environments have variable propensities for sediment reworking and particular accommodation limitations. In the case of the Hangman Sandstone Formation, the dissipation of flow and energy through a distributive fluvial system would have meant that the proximal apex of the DFS experienced more frequent reworking, while distal and DFS-adjacent regions would have witnessed only intermittent high-energy conditions (Hartley *et al.* 2010, 2013). Direct sedimentary evidence indicates that flooding events would have been relatively common, as suggested by the abundant redox-imorphic horizons implicit of a fluctuating groundwater table, wetting and drying cycles in the playa lake facies, and the absence of well-developed palaeosols, cumulatively implying that even DFS-adjacent regions frequently aggraded. Together, these factors suggest that the relative time-completeness of the DFS sedimentary record increases away from its apex, with proximal facies dominated by scoured and amalgamated sandstones indicative of much of the

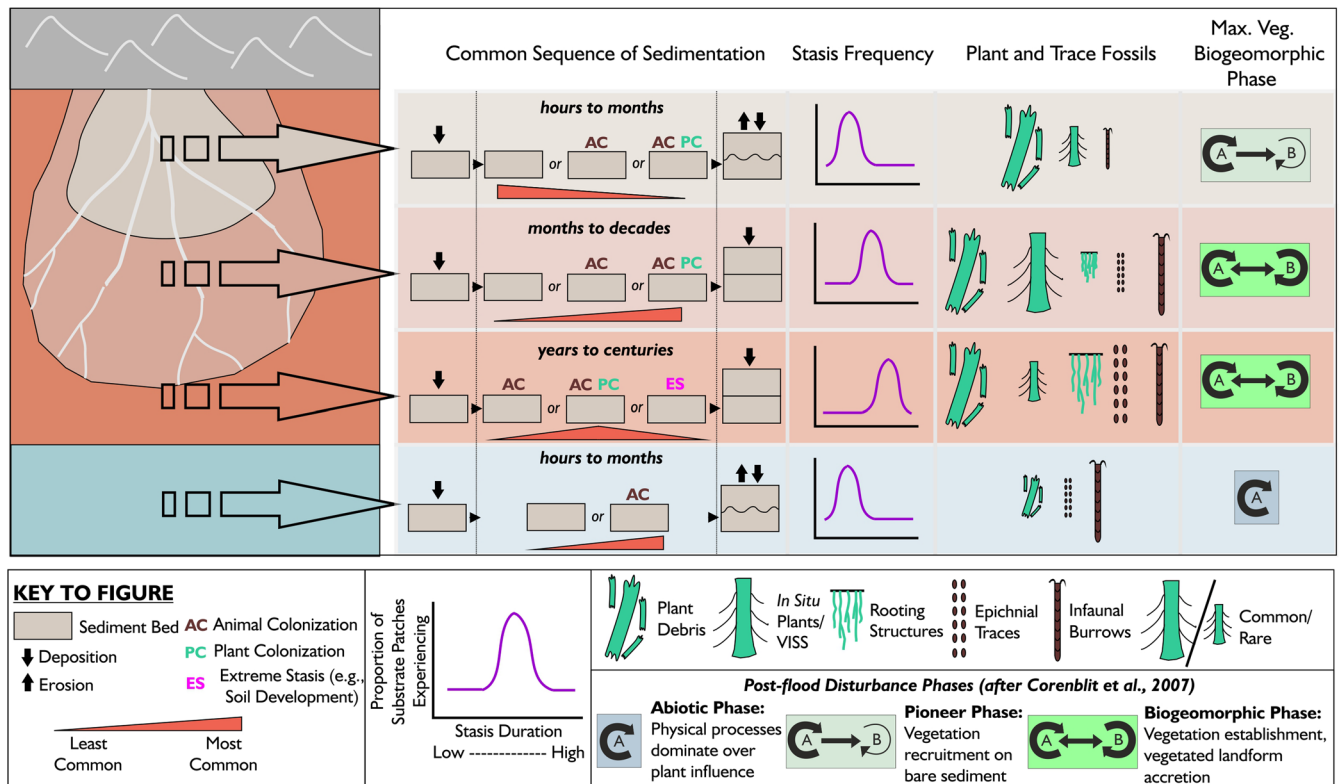


Fig. 19. Summary of the sedimentary and palaeoecological controls on plant and trace fossil distribution across the sub-environments of the Hangman Sandstone Formation distributive fluvial system. See text for details.

record having been lost to erosion. The fragmentary nature of the proximal facies, and the concomitant erasure of true substrates, has biased the fossil record of life in this sub-environment, with only very rare plant–sediment interactions having been preserved (Fig. 15b, c) and a paucity of surficial trace fossils relative to infaunal burrows (Davies *et al.* 2023).

Role of sedimentary stasis and vegetation succession

The focusing of erosion and deposition at the DFS apex resulted in a markedly different style of sedimentary record in the distal DFS and the DFS-adjacent playa lake facies. In these areas, flood disturbance events were less frequent and often of less intensity as energy had been lost through radial dissipation. Erosional surfaces are more scarce, true substrates more abundant, and plant fossils and VISS more common (Davies *et al.* 2023). While fewer strata appear to have been reworked in such settings, the deposition of new sediment occurred in erratic intervals, meaning that the sediment was less mobile and a greater proportion of the elapsed time was spent in sedimentary stasis. Stasis is a sedimentation state during which neither deposition nor erosion occurs, leading to no change in the elevation of the lithic surface at a site (Tipper 2015), and is increasingly recognized as an important factor in determining the fabric and time-completeness of the sedimentary–stratigraphic record (e.g. Tipper 2015; Straub *et al.* 2020; Davies and Shillito 2021). The palaeoecological role of sedimentary stasis has less frequently been remarked on, but is known to be of importance in biogeomorphology and ecology. In such fields, sedimentary stasis is equivalent to the interval between hydrogeomorphic disturbance events during which vegetation succession can progress from a bare substrate to pioneer herbs and shrubs, to post-pioneer forests, to mature forests (Van Andel *et al.* 1993; Corenblit *et al.* 2007). The biogeomorphic effectiveness of vegetation increases with the duration of the interval between disturbance events (Corenblit *et al.* 2007, 2015). A rapid recurrence means that the primary geomorphic processes are abiotic (abiotic stage); a longer recurrence interval means that pioneer vegetation, with some stabilizing and flow-dampening effects, has a chance to colonize (pioneer stage); even longer allows a balance of abiotic and vegetation-induced landforms (biogeomorphic stage); and extremely prolonged intervals between events may allow landforms to enter an ecologic stage, whereby landforms vegetated by mature plant communities are disconnected from hydrogeomorphic disturbances (Corenblit *et al.* 2007, 2015).

Sedimentary stasis allows plant communities to take hold, and those parts of successions where sedimentation events were less frequent (such as the distal Hangman DFS) preserve a greater number of *in situ* plant fossils and VISS. The wide spectrum of timescales recorded by a sedimentary rock succession means that different stages of vegetation and biogeomorphic succession may be archived, dependent on the specific duration of stasis between two beds. However, for the Hangman Sandstone Formation, there may have been evolutionary limitations because the flora required for a mature ecologic stage may not have evolved by the Eifelian.

The notion that the maximum attainable biogeomorphic stage has changed with plant evolution has been discussed previously. Small herbaceous plants in the Ordovician and Silurian likely could not attain more than the pioneer phase of succession (i.e. being at risk of reworking during moderate flood events) (Corenblit *et al.* 2015; Brückner *et al.* 2021) and previous applications of post-flood biogeomorphic stages to other Devonian successions have suggested that the ecologic stage was not attained until the Givetian expansion of lignophyte vegetation (Davies *et al.* 2021; Veenma *et al.* 2023). The distal DFS and playa lake facies of the Hangman Sandstone Formation contain several examples of plants reaching the biogeomorphic stage, whereby standing plants could resist

erosion by moderate floods (e.g. Figs 9, 10 and 15), but no evidence of very dense stands of vegetation or organic matter accumulations that might indicate the attainment of the ecologic stage. Whether this is a result of local environmental conditions (e.g. flood frequency) or the age of the unit predating later Mid-Devonian adaptations, is presently uncertain.

A further factor that determines the maximum attainable biogeomorphic stage is the duration of stasis in between events. This can be estimated for the Hangman Sandstone Formation because true substrates in the distal DFS and DFS-adjacent playa facies contain both animal and plant traces, likely imparted during stasis intervals on the order of months to decades (Fig. 19). Only in the proximal DFS facies was stasis recurrence likely too short for the advanced stages of biogeomorphic succession to develop (the alternative explanation related to minimal vegetation resistance in this sub-environment can be discounted based on rare VISS (Fig. 15b, c).

Taphonomic limitations

A limitation to the record of plant–sediment interactions from deep time arises because of the taphonomic filters that may have affected the succession. Plant material may decay at the surface or be destroyed after burial by processes such as pedogenesis (Gastaldo and Demko 2011). In the Hangman Sandstone Formation, plant fossils are dominantly found within grey sandstones and shales (e.g. Fig. 13), suggestive of locally reducing conditions preferable for preservation, even though most of the sedimentary succession consists of red sandstones and mudrocks. (The alternative possibility that the grey coloration is diagenetic seems implausible given the correlation with plant fossil presence.) However, these fossils should be considered a fortuitous sampling of a flora that was widespread across sedimentary surfaces archived as both red and grey strata. Red strata in the unit do preserve putative VISS (Fig. 16), which are physical structures unhindered by taphonomic decay, as well as rooting structures (Fig. 14) that attest to a vegetated landscape at the time of deposition.

Decay may theoretically limit the extent to which biogeomorphic succession phases can be identified because, among the spectrum of timescales recorded by a sedimentary rock succession, some phases can be of greater longevity than the historicity of evidence attainable from modern biogeomorphic studies (Larsen *et al.* 2021; Davies *et al.* 2022a). In such situations, a fully mature vegetation succession (ecologic phase) could have existed, but subsequently diminished or disappeared due to other long timescale factors (e.g. climate change), and weathering may have degraded the former surface, rendering both fossil and VISS evidence opaque. However, the duration of stasis in the Hangman Sandstone Formation distal DFS deposits rarely seems to have been of this extent, as signatures of long-term stasis (e.g. palaeosols, calcretes) are extremely rare.

Plant fossils and VISS in the Hangman Sandstone Formation

Figure 19 summarizes the facies distribution of plant fossils and VISS in the Hangman Sandstone Formation and the controls that have impacted these distributions. Plant debris is common throughout all the non-marine facies, and present in the marine facies of the Hollowbrook Member, indicating that vegetation was widespread, from areas upstream of the proximal DFS facies to the shoreline, and exported out at sea as debris. VISS and *in situ* plants are most common in the distal DFS facies, where intervals of stasis between depositional events lasted months to decades, enabling increasingly mature plants to colonize substrates and progress through varying stages of succession. As such phenomena require the preservation of the upper part of a sediment pile, and as the proximal facies are

dominated by erosional bounding surfaces, this limited sampling is likely a preservational bias and suggests that whatever biogeomorphic stage was attained, the intensity of disturbance events was great enough to eradicate most plants colonizing the DFS apex.

VISS and *in situ* plants are also rare in the DFS-adjacent playa mudrock facies, with only one putative example known (Fig. 7g). As rooting structures are common in these facies, standing plants were clearly present, but may have been smaller stature organisms that have thus far not yielded a macrofossil record from the succession, but may account for some of the >70 palynomorphs known (Knight 1990). All instances of standing *in situ* vegetation in the Hangman Sandstone Formation are observed in sandstone, which is limited in extent in these mudrock-dominated facies. If the standing vegetation records cladoxylopsid flora, as suggested by large debris of a similar diameter, then it is possible that these larger Eifelian plants preferred sandy substrates, which would have been well aerated and more porous substrates than muds (in which biological mixing and aeration were still limited and extreme waterlogging of the surface was common).

The distribution of plant fossils and VISS in the Hangman Sandstone Formation thus appears to reflect taphonomic filters, the propensity for sedimentary substrates to be reworked, and the longevity and frequency of sedimentary stasis, all across different sub-environments. These characteristics were specific to the Hangman Sandstone Formation and the summary shown in Figure 19 has several variables that would differ in other settings (e.g. the duration of stasis in different sub-environments, the rates of vegetation succession that may be different with floras from different geological intervals, and the intensity of flood disturbance events).

Taking the preservational biases in the formation into account, a reconstruction of the plant–sediment interactions in the Hangman DFS is shown in Figure 20. Vegetation must have been abundant across the DFS, rendering it the earliest example of a fossil forest from Britain. Cladoxylopsids likely colonized the whole region, rarely including in-channel settings, but most commonly colonizing fresh sediment surfaces laid down at channel margins after flood events. Even when small, these plants had the capacity to withstand sporadic low-intensity flooding, and sometimes grew to maturity to become more effective biogeomorphic engineers. Away from the sandy substrates of the DFS, trees were apparently less widespread, but rooting attests to the possible presence of other small vegetation. The influence of this Mid-Devonian early forest extended beyond the local landscape, as plant material was exported into the marine realm as driftwood and floated vegetation mats.

Comparison with other Devonian forests

According to the palaeogeographical reconstruction (Fig. 4), the vegetation in the North Devon Basin was probably the most southerly area of a strip of lowland cladoxylopsid-dominated landscape that also encompassed well-known Eifelian localities in Belgium (Goé, Ardennes; latest Eifelian) and Germany (including Lindlar, Rhennish Massif; mid-Eifelian) at about 30° south of the equator. At Lindlar, coastal facies, which include crinoid ossicles mixed into the plant assemblages, are dominated by cladoxylopsids, including *Calamophyton*, *Weylandia* and *Hyenia* (Giesen and Berry 2016). The landscape reconstruction of Lindlar (Giesen and Berry 2016, their fig. 4) is based on transported accumulations only; no *in situ* plants have been found. As the potential understory, a small number of specimens of the aneurophyte *Rellimia*, the herbaceous lycopsid *Leclercqia* and the enigmatic, possibly zosterophyll, spiny herbaceous plant *Thursophyton* (Giesen and Berry 2016) were recovered. At Goé, there are also three cladoxylopsids (*Calamophyton*, *Pseudosporochnus* and *Lorophyton*), with a single specimen of each of the zosterophyll *Serrulacaulis* and the lycopsid *Leclercqia* (Berry and Fairon-Demaret 2001). No *in situ*

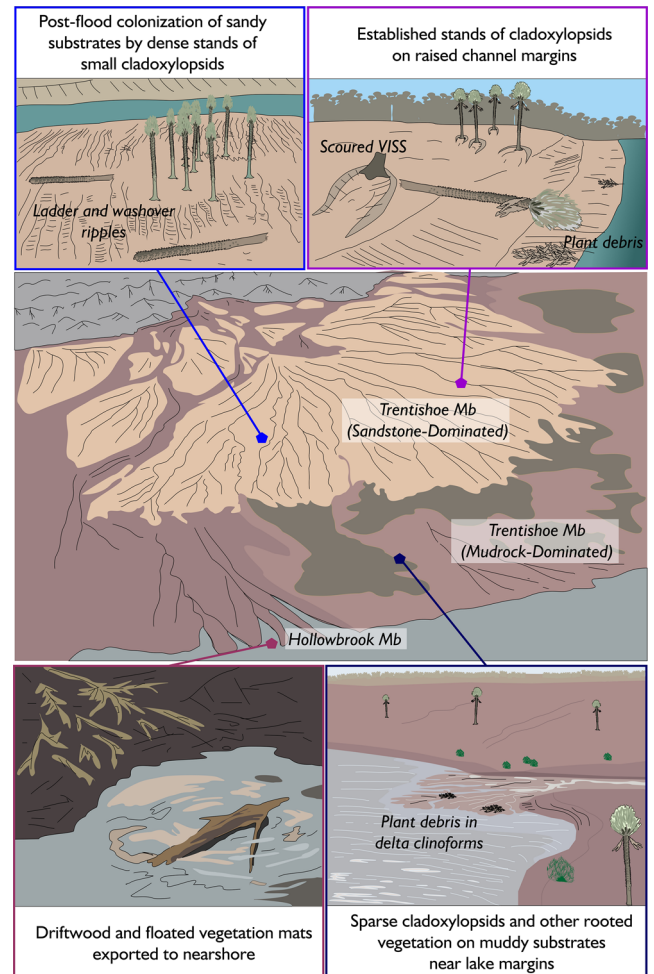


Fig. 20. Palaeoenvironmental reconstruction of the depositional environment of the Hangman Sandstone Formation, summarizing vegetation–landscape interactions across a transect of a distributive fluvial system to marginal marine setting.

plants are known from Goé and the environment has also been interpreted as nearshore marine (Streele 1964). The main difference between Goé and Lindlar is that the aneurophytes *Rellimia* and *Aneurophyton* are locally common in the former. In comparison, the North Devon Basin is taxonomically impoverished, but this may relate to the taphonomic conditions. For example, no appendages are preserved on the cladoxylopsids, which would have allowed the identification of different genera based on fragments. The Porlock Weir bedding plane exposure is therefore the only known exposure where this early cladoxylopsid vegetation can be related directly to a terrestrial sedimentary environment and the spacing of individuals evaluated (Fig. 10).

The well-known middle to upper Givetian fossil forests of New York State show the later development of vegetation at about 30° south of the equator. At Gilboa, a forest largely composed of giant cladoxylopsid trees, with basal diameters of up to 1 m, heights of at least 8 m and foliage attributed to *Wattieza*, demonstrates the climax of the evolution of these plants (Stein *et al.* 2007). As demonstrated by plan mapping, recumbent woody rhizomes and attached branch systems of aneurophytes were the main components of the understory (Stein *et al.* 2012, 2021). The carbon-rich, pyritic, dark grey–black horizon with horizontal roots indicates an ever-wet soil. This contrasts with Cairo, New York, where large cladoxylopsid bases are mixed in with large radial branching root systems that mark the presence of early forms of the *Archaeopteris* tree, a leafy lignophyte, likely with heights much greater than the cladoxylopsids (Stein *et al.* 2020). At Cairo, the soils are patchy,

with some dark surface soils, but also large areas where red, well-oxygenated soils dominate, and shallow boreholes demonstrate mostly red soils with small vertical roots down to depths of at least 1.5 m (Morris *et al.* 2015; Stein *et al.* 2020). In early Frasnian deposits in Svalbard, lycopsids are the dominant plant in wet soils, growing in dense stands near the equator, where cladoxyloids have not been discovered (Berry and Marshall 2015).

The Porlock Weir tree bases therefore mark the beginnings of an understanding of pseudosporochnalean cladoxylopid vegetation, which drove competition for light and other resources, shed large amounts of discarded branches, and contributed significantly to, or in some places dominated, terrestrial vegetation for the next 10 Myr.

Conclusions

Original fieldwork has shown that the Mid-Devonian (Eifelian) Hangman Sandstone Formation of Devon and Somerset, previously considered to contain only rare plant fossils, in fact archives a rich array of standing plant fossils, cladoxylopid logs, VISS, rooting traces and plant debris accumulations, preserved within sedimentary strata that were deposited in a DFS and adjacent nearshore settings. These phenomena occur throughout the succession, but are most common at three sites in the eastern part of the outcrop belt – at Culver Cliff, Selworthy Sand and Porlock Weir – where high-resolution windows on the landscape impacts of Britain's earliest forests can be observed. These *Calamophyton*-dominated forests were likely palaeogeographically contiguous with similar vegetation across Belgium and Germany. Early Mid-Devonian trees are seen to have enabled landscapes to enter the biogeomorphic phase of post-flood succession. Distal DFS facies, where event recurrence was less frequent, are well suited to identifying the evidence for this. The Hangman Sandstone Formation provides another case study that shows how the non-marine sedimentary environments of the Devonian Period evolved (Davies *et al.* 2021; Veenma *et al.* 2023). While not as developed as Givetian or younger settings, non-marine settings in the Eifelian had, for the first time, the potential to be densely forested with arborescent cladoxyloids, with individual trees producing vast amounts of shed litter as sedimentary debris and acting to influence the flow of water across the landscape. This interval marked a key stage in the development of fluvial systems that operated fundamentally differently from those that preceded them, and fundamentally similarly to many that followed.

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Data availability All data generated or analysed during this study are included in this published article (and if present, its supplementary information files).

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