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The Devonian Landscape Factory: plant-sediment interactions in the Old Red Sandstone of Svalbard and the rise of vegetation as a biogeomorphic agent

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ABSTRACT

The Devonian Period was a crucial interval in the evolution of plants. During its 60 myr duration, it witnessed the successive evolution of roots, wood, trees and forests, and many of the biogeomorphic phenomena that operate in modern terrestrial environments came online for the first time. The Old Red Sandstone (ORS) of Svalbard consists of a near-continuous Silurian to Late Devonian record of land plant-colonized sedimentary environments and provides a perfect natural laboratory to aid understanding of the facies signatures and evolution of these phenomena. Here we describe and illustrate a catalogue of ORS features that provide evidence for the stepwise appearance of novel plant-sediment interactions,

including: preserved plant material and rooting structures, early large woody debris accumulations, cannel coal deposits, and the oldest known vegetation-induced sedimentary structures, in addition to vegetation-influenced motifs of elevated mudrock content and complex alluvial sand bodies. These characteristics are combined to reconstruct changes to non-marine environments in this Devonian ‘landscape factory’. In addition to tectonic and climate influences, plant evolution first served as an allogenic geological control on the construction of the sedimentary record during this period, and has persisted as a fundamental influence on Earth surface processes and landforms ever since.

1. Devonian Vegetation and Sedimentation

Land plants are some of the most effective biogeomorphic agents on Earth today, modifying physical processes and landforms by complex and diverse means that include: roots increasing substrate shear strength and resistance to erosion; canopies and litter reducing the efficacy of raindrop impact and surface runoff; plant- and fungal symbiont-induced weathering and modification of the critical zone, soils and regolith; the provision of organic matter that can change sediment properties such as cohesiveness; baffling and binding of sediment to promote the accretion of landforms; or acting as obstacles to flowing air and water, changing turbulence properties through friction and drag effects (e.g., Corenblit et al., 2007, 2015, 2020; Phillips, 2016; Horton et al., 2017; Kleinhans et al., 2018; Larsen, 2019). Trees in particular are effective ecosystem engineers, promoting landscape heterogeneity not only through their physical presence, but also due to the hydrodynamic resistance of their arborescent form and deeper rooting systems, their role in the hydraulic redistribution of groundwater, their propensity for uprooting release of sediment and creation of microhabitats, and the production of large woody debris that can modify landscapes through island formation or log-jamming of streams (e.g., Harmon et al., 1986; Jones et al., 1994; Gurnell et al., 2002; Gurnell, 2003; Wohl, 2013, 2017; Gurnell, 2014; Davidson et al., 2015; Kramer and Wohl, 2015; Pawlik et al., 2016; Sullivan et al., 2016).

These contributions to the operation of continental landscapes were absent for most of the planet's history, and establishing a timeline for their origin and radiation is essential for understanding the mechanistic evolution of the Earth system. A consensus of hypotheses has arisen that it was the Devonian Period (419-359 Ma) that was the critical interval for the initiation, expansion and development of land plant controls on climate, landscape and terrestrial biodiversity (e.g., Algeo and Scheckler, 1998; Davies and Gibling, 2010a,b; Gibling and Davies, 2012; Corenblit et al., 2015; Morris et al., 2015; Pawlik et al., 2016, 2020; Boyce and Lee, 2017; Dahl and Arens, 2020). This mirrors the Devonian palaeobotanic record, which shows a rapid transition from small leafless plants at the start of the period (Kenrick and Strullu-Derrien, 2014), through the evolution of fully vascular plant roots, with meristems, around 411 Ma (Matsunaga and Tomescu, 2016; Hetherington and Dolan, 2018), the earliest wood at 407 Ma (Gerrienne et al., 2011; Strullu-Derrien et al., 2014), the earliest trees at 390-388 Ma (Berry and Fairon-Demaret, 1997, 2002; Giesen and Berry, 2013), and the earliest forests by 385 Ma (Stein et al., 2012, 2020).

The physiologies and life habits that originated at this time are all fundamental to the role of plants as biogeomorphic agents in modern landscapes, yet there is little reported direct evidence for Devonian plant-sediment interactions. In this paper we rectify this omission with examples from the late Silurian- to Devonian-aged "Old Red Sandstone" strata that crop out across northwest Spitsbergen, in the Svalbard archipelago of Arctic Norway (Figs. 1 and 2). Here we: 1) introduce the constituent stratigraphic units of the Spitsbergen ORS; 2) describe and illustrate a catalogue of features that provide tangible geological evidence for plant-sediment interactions; and 3) demonstrate how the local stratigraphic distribution of these features reflects the global onset and development of plant-related biogeomorphic processes. The Spitsbergen ORS is shown to be an archetypal case study that yields insights into the 'Devonian landscape factory': a key interval of Earth history when plants first came online as biogeomorphic agents, influenced terrestrial surface processes in ways analogous to modern flora, and sculpted still-familiar landforms, landscapes and habitats.

2. The 'Old Red Sandstone' of NW Spitsbergen

The 'Old Red Sandstone' (ORS) is an informal term used for successions of dominantly terrigenous strata that crop out around the north Atlantic region, and whose deposition was contemporaneous with mid-late Palaeozoic orogenic events in Laurussia (e.g., Friend et al., 2000; Kendall, 2017). The Spitsbergen ORS is one of a number of near-contemporaneous Silurian-Devonian successions of non-marine-dominated sedimentary strata across Scandinavia and Greenland (e.g., Marshall and Stephenson, 1997; Anderson and Cross, 2001; Davies et al., 2005a,b; Astin et al., 2010), and has been the subject of intermittent but significant geological investigations for over 120 years (e.g., Nordenskiöld, 1892; Holtedahl, 1914). It was an instrumental case study in the development of non-marine sedimentary facies models that later found global application (e.g., Friend, 1965; Moody Stuart, 1966), and has proved to be particularly rich in fossil plant material. The earliest geological expeditions to the region collected abundant and well-preserved megafossils (see summaries in Høeg 1942; Schweitzer, 1999; Berry 2005), the palynological record of the succession has been studied for over half a century (Vigran 1964; Allen 1965, 1967), and, more recently, fossil forests of lycopsids and archaeopterids have been discovered in the youngest units of the succession (Dallman et al., 2004; Berry and Marshall, 2015). The succession is exceptionally well-suited for tracking the onset of plant-sediment interactions not only because of its fossil content, but also because it provides a well-exposed and near continuous record of non-marine and coastal sedimentation between the latest Silurian and early Frasnian (early Late Devonian).

2.1. Geological Setting

Formally, the Spitsbergen ORS consists of three groups: the upper Silurian Siktefjellet Group, the Lower Devonian Red Bay Group, and the Lower to Upper Devonian Andréeland Group (Wood Bay, Grey Hoek, Wijde Bay formations and Mimerdalen Subgroup) (Figure 2; Friend, 1961; Murašov and Mokin, 1979; Harland, 1997**;** Piepjohn and Dallman, 2014). The succession was deposited during the development of the Ellesmerian Orogeny to the west (McCann 2000), and the groups are bounded by unconformities resulting from drainage reorganization during intervals of renewed strike-slip faulting (Beranek et al., 2020). As a result, there is some discordance between their tectonic dips, and the younger units can contain reworked clasts from the older strata (Friend, 1961; McCann, 2000; Piepjohn, 2000). Regional variations in syn- and post-depositional uplift have meant that the oldest preserved deposits (Silurian and Lochkovian) are restricted to small extensional basins in the north, the youngest deposits (Frasnian) are restricted to fragments of foreland basin fill in the south, and there is also north-south palaeoenvironmental and age variation in Middle Devonian strata (Figs. 1 and 2) (Friend, 1961; Manby and Lyberis, 1992; Piepjohn, 2000; McCann, 2000; Piepjohn and Dallman, 2014; Beranek et al., 2020). The Old Red Sandstone across the region is capped by a regional unconformity, associated with uplift during the Late Devonian Svalbardian event (Manby and Lyberis, 1992; Piepjohn, 2000; McCann, 2000; Bergh et al., 2011; Piepjohn and Dallman, 2014; Beranek et al., 2020).

Palaeogeographically, Spitsbergen formed part of western Laurussia and occupied an equatorial location for the entire duration of ORS deposition, migrating only 5° of latitude during the Devonian (from c. 10° S to c. 5° S) (Torsvik and Cocks, 2017). Despite the stable tropical location, long-term climatic variability is recorded through the succession by evidence of either seasonal semi-arid (calcretes, vertisols: Friend and Moody-Stuart, 1970; Blomeier et al., 2003a) or humid conditions (coals: Vogt, 1941; Harland et al., 1976;

Blumenberg et al., 2018). Red bed strata are also partitioned within the succession, attesting to long-term variability in levels of drainage (Sheldon, 2005).

2.2. Constituent Units

Each of the constituent units of the Spitsbergen ORS (Fig. 2) were visited in this study, in order to characterize the stratigraphic distribution of evidence for plant-sediment interactions throughout the Devonian. Localities visited are shown in Figure 1, representative outcrop style of the units is shown in Figure 3, and their lithologies, palaeoenvironments and fossil flora are summarized in Tables 1 and 2, and outlined briefly below:

2.2.1. Silurian (Siktefjellet Group)

The Siktefjellet Group is the least well-understood unit of the Spitsbergen ORS: it crops out only the far northwest of the region (Gjelsvik and Ilyes, 1991**)** and exposure is poor due to internal faulting (with shales acting as shear planes), scree coverage and frost-weathering, which renders confident architectural analysis of the strata impossible (Figure 3A). Further, although the unit has previously been interpreted as recording braided fluvial, and possible lacustrine, deposition (Friend et al., 1997), the strata contain few unambiguous indicators of depositional environment and a marine influence cannot be ruled out (Gjelsvik and Ilyes, 1991). At Siktefjellet they consist of fine- to medium-grained light grey sandstones and dark grey shales, and the only sedimentary structures observed in this investigation were climbing ripple lamination and two indistinct horizontal burrow traces. The succession has been reported to contain plant macrofossils (Murašov and Mokin, 1979), but only comminuted carbonaceous debris was witnessed in this study. Analyses undertaken for this study reveal the palynological assemblages are very poorly preserved and much more thermally mature than elsewhere in the Spitsbergen ORS. The assemblages are dominated by phytodebris (cuticles, tubes, etc.) and the few spores are present are mostly indeterminable, except for rare cryptospore tetrads. In addition no marine chitinozoans or acritarchs are present, and the unit yields no other reliable age indicators. Despite this a Silurian age is most likely based on the general palynological motif, and because the Siktefjellet Group lies tilted and unconformable below the base of the Red Bay Group (Friend et al., 1997).

2.2.2. Lower Devonian (Red Bay Group and Wood Bay Formation)

Two units comprise the Lower Devonian strata of Spitsbergen: the Lochkovian-aged Red Bay Group, restricted to the north of the region, and the more widely-distributed Pragian- to Emsian-aged Wood Bay Formation.

The Red Bay Group is an overall-fining upwards succession. The conglomerate-dominated lower half of the group consists of the Wulffberget Formation, syn-tectonic alluvial fan deposits that rest directly on basement marble (Fig. 3B), followed by a poorly exposed shale unit (Rabotdalen Formation), and then further alluvial fan deposits (Prinsesse Alicefjellet Formation) (Murašov and Mokin, 1979; Harland, 1997; Friend et al., 1997; McCann, 2000). These coarse-grained facies lack plant macrofossils and are dominated by physical sedimentary structures of high-energy debris-flow and stream-flow, rendering them unsuitable for assessing early Lochkovian plant-sediment interactions. The upper Red Bay Group comprises three finer-grained units. 1) The Andréebreen Formation comprises grey-green fine- to medium-grained sandstones with subordinate interbedded dark grey shales and pebble-lag conglomerates. The unit yielded newly discovered macrofossils of small shrubby plants (cf. *Zosterophyllum*) during this study (Fig. 4). Observed downstream accretion elements (Miall, 1985), allied with reworked calcretes and *in situ* plant material, supports previous explanations of the strata as braided river alluvium (Friend et al., 1997). 2) The Frænkelryggen Formation comprises archetypal ORS alluvial facies (Fig. 3C): predominant red bed mudrocks (overbank deposits) with recurrent fine sandstone horizons (in-channel deposits). It has previously yielded abundant small plant macrofossils, in addition to enigmatic (*Pachytheca*) and possible fungal (*Prototaxites)* fossils (Høeg, 1942; Schweitzer, 1999). 3) The topmost unit of the Red Bay Group, the Ben Nevis Formation, marks a return to grey-green strata, dominated by fine- to coarse-grained cross-bedded sandstones of probable braided fluvial origin (Fig. 3D) (Friend et al., 1997). It is not known to contain any plant fossils.

The Wood Bay Formation rests unconformably on top of the Red Bay Group: it is the most widely-distributed Devonian unit in Spitsbergen, and also one of the most well-studied from a sedimentological perspective (Friend, 1961, 1965; Moody-Stuart, 1966; Friend and Moody-Stuart, 1970, 1972; Blomeier et al., 2003a,b; Wisshak et al., 2004a,b). The formation is divided into the Austfjorden (basal), Dicksonfjorden (middle), and Verdalen (upper) members, defined by fossil fauna (Murašov and Mokin, 1979). Lithologically, there is little variability between members beyond a general fining-upwards: throughout, the Wood Bay Formation is a heterolithic red bed succession, dominated by calcrete-bearing fluvial overbank, palaeosol and lacustrine mudrocks (Blomeier et al., 2003a,b). Outcrop of the unit is superficially excellent, with large-scale architecture apparent in extensive mountainside exposures (Fig. 3E): however, these can comprise frost-shattered and scree-covered recessive mudrocks on the ground (Fig. 3F), with accessible *in situ* outcrop limited to intermittent ledges of sandstone. The succession has long been known to contain fossils of a small shrubby flora (e.g., *Psilophyton, Bucheria*) (Høeg, 1942), and further discoveries were made in this study.

2.2.3. Middle Devonian (Grey Hoek, Wijde Bay and Tordalen formations)

Middle Devonian strata exhibit pronounced regional variability in northwest Spitsbergen.

In the north of the region, dark grey and grey-green heterolithic strata of the Eifelian Grey Hoek Formation grade conformably out of red mudrocks of the upper Wood Bay Formation (Fig. 3G-H). The basal strata of the Grey Hoek Formation yield abundant ostracod and bivalve fossils, burrows, and pisolitic limestones, which attest to transgression over the underlying Verdalen Member and the start of a pervasive marine influence. The unit also contains evidence for channelized unidirectional flow, suggestive of coastal or estuarine deposition (e.g., Friend, 1961; Worsley, 1972), and yields plant fossils of both small stature shrubs and larger potentially woody fragments of possible tree origin (Høeg, 1942). The Grey Hoek Formation passes vertically into the Wijde Bay Formation, a lithologically-similar unit except for its lighter grey-coloured mudrocks and yellow-grey sandstones (Fig. 3I). The Wijde Bay Formation also yields littoral palaeoecological signatures: a similar marine-influenced fauna and shrub-like and woody floral remains (Schweitzer, 1968). The unit has traditionally been considered to be Givetian in age, but original palynological work undertaken for this study reveals an assemblage of mostly simple spores, lacking an abundance of *Geminospora*: the diagnostic palynological signature of Givetian-aged strata in the region (McGregor and Camfield, 1982). As such, we here consider the unit to most likely be predominantly Eifelian in age.

In contrast to the north, Middle Devonian strata in the south of the region comprise only the late Givetian-aged Tordalen Formation (lower Mimerdalen Subgroup), resting unconformably on the Dicksonfjorden Member of the erosionally-truncated Wood Bay Formation. Palynological samples from the Tordalen Formation are dominated by *Geminospora* and *Cymbospores*, showing that its deposition was not contemporaneous with the Wijde Bay Formation, as has been previously reported (Piepjohn & Dallmann, 2014). Additionally, it has a distinct lithological signature: 1) the lower Estheriahaugen Member: thinly- (5 cm-thick) bedded grey-green sandstones and shales, with common siderite nodules, occasional ostracod fossils, and thin coal (Vogt, 1941; Harland et al., 1976; Piepjohn & Dallmann, 2014; Blumenberg et al., 2018); and 2) the slightly finer-grained upper Fiskekløfta Member (Fig. 3J), named for its extremely abundant fossil fish fauna, and comprising darker grey mudstones and sandstones that are capped with a distinct 50 metre-thick marker horizon of white-coloured quartz-rich medium-grained sandstones (informally termed the "Lower Svalbardia Sandstone") (Piepjohn & Dallmann, 2014). The strata have been interpreted as freshwater-brackish lagoonal facies, with sand input from marginal deltas and washovers (e.g., Friend, 1961; Newman et al., 2020).

2.2.4. Upper Devonian (Planteryggen and Plantekløfta formations)

Two early Frasnian-aged units comprise the remainder of the Mimerdalen Subgroup – the lower Planteryggen Formation and upper Plantekløfta Formation. The definition of the Planteryggen Formation has recently been adjusted (the "Lower Svalbardia Sandstone" having been moved into the upper Tordalen Formation: Piepjohn and Dallman, 2014), and now comprises only poorly-exposed sandstones and conglomerates. The overlying Plantekløfta Formation has better exposure, on ridges and along actively-eroding banks of the Mimer River (Figs. 3K-L). The Plantekløfta Formation comprises heterolithic dark grey overbank mudrocks and yellow-grey fluvial sandstones, with prominent and laterally continuous horizons of poorly-sorted, clast- and matrix-supported debris flow conglomerates. The unit also contains abundant standing lycopsid and archaeopterid tree fossils, in addition to the remains of non-woody shrubs (Berry, 2005; Berry and Marshall, 2015). Notably, we now recognise that the Plantekløfta Formation contains the distinctive sandy layer of green/yellow sandstone which contains the rich 'Planteryggen' or 'Upper Svalbardia Sandstone' flora (Høeg, 1942; Berry and Fairon-Demaret, 2000), previously thought to belong to the Planteryggen Formation (e.g. Piepjohn and Dallmann, 2014). The overall succession records deposition by small fluvial channels with forested floodplains, punctuated by deposition from catastrophic debris flow events that were sourced from locally-uplifted highlands to the east, at the onset of the Svalbardian Event (Piepjohn and Dallman, 2014; Berry and Marshall, 2015).

3. Plant-sediment interactions in the Old Red Sandstone

The ORS of northwest Spitsbergen fortuitously records continual deposition within land plant-colonized sedimentary environments from at least the Lochkovian to the Frasnian, rendering it the perfect natural laboratory to search for signatures of early plant-sediment interactions.

Here we describe and interpret multiple features that have been observed throughout the succession, and highlight their stratigraphic distribution and variability. Two overarching classes of signature are recognised (after Davies et al., 2020): 1) Vegetation-Dependent Signatures – novel materials (e.g., plant debris, woody debris), structures (e.g., rooting traces, vegetation-induced sedimentary structures) and lithologies (e.g., coal) which require direct input of plant detritus or sediment manipulation by vegetation. These were absent from the global sedimentary record before particular specific innovations or thresholds were passed in the timeline of botanic evolution. 2) Vegetation-Influenced Signatures – facies signatures whose creation would have been influenced by the presence of vegetation at the time of deposition (e.g., weathering products, sedimentary architecture). The extent of indirect vegetation influence is problematic to determine from any individual case study, so the particular characteristics of the Spitsbergen ORS are discussed with reference to contemporaneous strata from the global sedimentary-stratigraphic record.

3.1. Fossilized Plant Debris

The simplest evidence for direct interplay between vegetation and surface processes occurs where plant debris is preserved within a sediment pile, either having been transported for a distance, or interred at its growth site. In any such instances, fossilized plant debris is indicative either that fluids were transporting organic clasts, or that a preserved patch of substrate had a mantle of vegetation that would inevitably have influenced thresholds of erosion and deposition at that particular spot. Recognising the sedimentary context of sites where plant debris has been interred requires: 1) that fossil plant material can be observed at outcrop, and has not been over-collected; and 2) that any plant material has fortuitously overcome taphonomic hurdles of syn- and post-depositional decay and replacement (Gastaldo & Demko, 2011). In the Spitsbergen ORS, the first obstacle is less of an issue than it is in classic ORS sites elsewhere in Europe and America: the strata are comparably very rich in fossil material because there has been limited palaeontological collection across the region, and the outcrops are relatively dynamic (i.e., being prone to rejuvenation through frost-shattering, cliff collapse and riverbank retreat). Taphonomic filters undoubtedly mean that only a fraction of original plant matter has been preserved, particularly within well-drained red bed facies (i.e., the Wood Bay Formation and parts of the Red Bay Group). However, as fossil plant material is known from every stage of the Devonian that is preserved in Spitsbergen, it is possible to compare the nature of the preserved material between constituent units of the ORS. Such a comparison reveals that, in addition to being taxonomically-variable (Table 2), the physical nature of preserved fossil material also differs, and four types can be recognised:

Comminuted debris –

3.1.1. Comminuted debris

Comminuted debris includes dark grey or black flecks of carbonaceous material, >1 mm to >5 mm across, that most often cannot be taxonomically identified. Such debris records physical degradation of plant matter, either where plant tissues are not mechanically resistant, or where the intensity and duration of physical attrition is high. Comminuted debris occurs in patchy accumulations, indicating that the debris underwent sorting during transport and deposition (e.g., Spicer and Wolfe, 1987). The earliest instances of comminuted debris in the Spitsbergen ORS occur within the Silurian Siktefjellet Group and examples are present in every subsequent unit.

3.1.2. Fragmentary remains

Recognisable stems, axes, branches, and appendages of non-woody plants of shrub-like and herb-like habit occur throughout the Spitsbergen ORS in Lochkovian and younger strata (earliest examples from the Andréebreen Formation of the Red Bay Group). Accumulations of such delicate material imply reduced attrition, either due to less intense fluid energy, limited transport distance (i.e., near *in situ* burial), and/or mechanically-resilient plant tissues.

Examples from Lower and Middle Devonian strata illustrate how small stature plants interacted with their physical environments. Figure 4 illustrates the sedimentary architecture and lithologies of the Andréebreen Formation (Lochkovian, Red Bay Group), which hosts the oldest identifiable plant debris recognised in this study. The succession is dominated by sandstones, packaged as downstream accretion sets up to 1.5 metres thick, and punctuated with fissile grey shales (Fig. 4A-E). Shallow braided stream bars, capped with shale during intervals of channel switching, provide a reasonable palaeoenvironmental explanation for these sedimentary signatures (e.g., see also Friend et al., 1997). While the sandstones in these successions are barren of fossil plant material, the shales host branching specimens of cf.

Zosterophyllum (Figure 4F). The relatively undegraded nature of these plant remains suggests minimal transport, and implies they were interred parautochthonously on bar tops (they may also be associated with rooting structures, see Section 3.2.). There is no direct evidence for these Early Devonian plants inducing any hydrodynamic sedimentary structures so it cannot be ascertained whether they occupied submerged parts of the bars, but they are seen in association with trace fossil evidence that suggests geologically-early riverine habitats of co-existing plants, fish and invertebrates (Figure 4G,H). Similar signatures are present in slightly younger strata, within the Pragian-Emsian Wood Bay Formation (Austfjorden Member) at Kapp Petermann (Figure 5). Here, fragments of branching stems (some with spines) of small stature (*?Psilophyton*) are restricted in their distribution to inflection points at the topsets of barforms in very fine sandstones (Fig. 5A-D). The relative completeness of delicate fossil elements suggests the remains are also parautochthonous, and the restriction to topsets implies a further instance where Lower Devonian plants had colonized the tops and margins of exposed braid bars during low flow stage. The partial fragments preserved in this setting can be compared with more water-worn plant fragments further up section at the same locality (Figure 5E-H). Here in-channel sandy bedforms host only comminuted debris (throughout cross-bed sets), and parting-lineated sandstones contain sparse clusters of unornamented sticks, attesting to the entrainment and attrition of clasts and plant material within active river channels. Figure 6 shows a Middle Devonian example from marine fauna-bearing strata of the Grey Hoek Formation, demonstrating how phytoclasts have a hydrodynamic equivalence to very fine clastic sediment. Here, unidentified carbonaceous fragments are preferentially hosted in muddy sediment patches that occupy the swales of a scroll bar (Fig. 6C). This illustrates how the topographic lows on the margins of meandering shallow coastal channels acted as traps and sieves for phytoclasts, and demonstrates that coastal waters at this time had a mixed sediment load of both siliciclastic and plant-derived organic sediment.

The examples illustrated in Figures 4 to 6 show how debris from small stature herbs and shrubs were common sedimentary clasts in Early and Mid Devonian fluvial and coastal channels, and had preservation potential in both poorly-drained (grey-green Andréebreen and Grey Hoek formations) and well-drained (red bed Wood Bay Formation) settings. The most complete fragments occur in the sediments of quiescent, emergent fluvial bars, implying that these landforms, at least, were colonized by plants in the Early Devonian.

3.1.3. Woody Debris

True woody debris is predominantly composed of xylem tissues. However, as sedimentary particles (Harmon et al., 1986), a liberal definition of woody debris refers to any allochtonous accumulations of large (typically 0.1-2.0 metres) woody plant material. In the Spitsbergen ORS, the earliest instances of such debris occur within the Grey Hoek Formation and persist in units thereafter.

In modern forested streams, woody debris is an important sediment constituent, recruited both continuously and episodically, through mechanisms such as individual or mass mortality, hillslope failure, floodplain erosion, or bank collapse (Wohl, 2017). In the rock record, fossilized accumulations of such debris are common from the Carboniferous onwards but extremely rare in older strata, even after the Emsian evolution of wood (Davies and Gibling, 2011, 2013). The Spitsbergen ORS is significant in that it contains some of the earliest known instances of both individual clasts of woody debris (Figure 7), and dense accumulations of woody debris (Figure 8) worldwide.

3.1.3.1. Individual woody debris clasts

The oldest instances of woody debris in the succession occur as patches or isolated clasts of randomly oriented material, hosted within very fine-grained coastal channel sandstone facies of the Eifelian Grey Hoek Formation (Fig. 7A) (Høeg, 1942) and Wijde Bay Formation (Fig. 7B) (Schweitzer, 1968). Taxonomic identification of the plant material is not possible (it is associated with *Protocephalopteris* branches), but it has a sulcate ornamentation and appears frayed at the margins. At the time of deposition, the debris likely comprised clusters of individual xylem strands with a stringy structure, rather than robust wood particles. Larger and more robust woody particles are known from the south of the outcrop area, and are particularly prominent within the Givetian 'Lower Svalbardia Sandstone' (uppermost Tordalen Formation). Here, individual clasts of woody debris occur up to 2 metres in length, that are dominated by flattened trunks of probable archaeopterid trees (plus minor lycopsid material) (Fig. 7C). These examples, dating in time from close to Earth's earliest known tree fossils (Berry and Fairon-Demaret, 1997, 2002; Giesen and Berry, 2013), provide evidence for the origination of wood as a sedimentary particle. Woody debris has subsequently persisted as a component of many sedimentary environments throughout the remainder of Earth history (e.g., Davies and Gibling, 2013; Wohl, 2013, 2017; Gulbranson et al., 2020; Trümper et al., 2020).

3.1.3.2. Accumulations of woody debris

Figure 8 shows the sedimentary context of accumulations of woody debris. Accumulations in the Wijde Bay Formation (Fig. 8A-C) occur as randomly oriented patches of tens of pieces of woody debris, up to 40 cm in length, and surrounded by a sandstone matrix. Such debris appears to have had little effect on preserved sedimentary architecture, which comprises heterolithic coastal channel fills (Fig. 8A).

In contrast, accumulations are conspicuous in a 5 metre-thick section of the upper Tordalen Formation (Fig. 8D-F), where 11 successive dense woody debris horizons cap 20-80 cm-thick fine-grained sandstone bodies. The Tordalen accumulations have superficial resemblance to logjam deposits, the earliest known of which presently date from the Carboniferous (Gastaldo and Degges, 2007; Gibling et al., 2010). However, detailed analysis of the fabric of the Tordalen accumulations does not support a logjam origin, because: 1) they are strongly oriented in one direction (c. 020-200°), with little variance (Fig. 8); 2) they occur in medium-grained sandstone that lacks the intraformational or extraformational clasts that would be caught in a logjam; 3) they occur in 11 successive sandstone layers over a vertical distance of 5 metres, with no evidence for any avulsive impact of the wood accumulations;) when seen in association with sandstone mounds, they are oriented parallel with the mound crests (Fig. 8F); 5) they occur on bedding planes with evidence for post-depositional stasis (*Diplichnites* arthropod trackways and aeolian adhesion marks between individual logs (Fig. 8F)), rather than instantaneous hydrodynamic re-organisation; and 6) they are thin accumulations that mantle sands, rather than intermingle with them: the logs have a mean width of 50 mm, approximating to original diameter (see Gibling et al., 2010), and a mean individual thickness of 3 mm. As each woody debris mantle is approximately 3 cm thick, this gives a compaction value for the wood of 16.6, and suggests that each original wood accumulation was only c. 50 cm in thickness. Taken together, these characteristics of the Tordalen accumulations suggest that, rather than active logjams, they likely record driftcretions (Kramer and Wohl, 2015): persistent accumulations of driftwood that form where fluvial driftwood export to a shoreline is high, and woody debris accumulates in stable mats or berms . Explaining the Tordalen accumulations as early driftcretions fits with the interpretation of the Lower Svalbardia Sandstone as delta-top sands, infilling the lacustrine/lagoonal setting recorded by the finely-bedded sands of the Fiskekløfta Member (Friend, 1961; Newman et al., 2020).

3.1.4. Plants preserved in growth position

Instances of the lower trunks of isolated plants or clustered assemblages of plants, preserved in life position and extending vertically through sediment from a rooted base, occur only in the uppermost ORS (Frasnian Plantekløfta Formation; although transported fossils of the same plant genera occur in older strata of the Givetian Tordalen Formation). Their presence indicates plants with a mechanical strength that was sufficient to resist toppling by the fluids and sediment that interred them, and the impact that such remains have had on sedimentary structures are discussed in Section 3.3.

3.2. Rooting Traces

The earliest root fossils worldwide are known from the Pragian (Matsunaga and Tomescu, 2016; Hetherington and Dolan, 2018), but structures that have been interpreted to record the sediment-filling of plant root structures occur in slightly older, Lochkovian, strata (Hillier et al., 2008). Such structures consist of traces of sediment that share morphological attributes with plant roots, and dissimilarities with animal burrows; for example: decreases in diameter after branching, irregular and sinuous forms, downwards-branching, horizontal and vertical components and colloidal clay linings (Hillier et al., 2008). Preserved organic root material is absent from the Spitsbergen ORS until the Frasnian Plantekløfta Formation. However, sedimentary traces of putative root structures are known from the Lower Devonian onwards, in the form of casts, moulds and elongate drab haloes that may branch downwards (Figure 9).

The Andréebreen Formation of the Red Bay Group yields what may be the oldest root structure in the Spitsbergen ORS (Fig. 9A). A root interpretation for this particular structure is not unequivocal, and it could also be explained as an instance of an invertebrate burrow (such structures also appearing in alluvial settings for the first time in the early Lochkovian: e.g., Minter et al., 2016; Shillito and Davies, 2017). However, favouring the former over the latter is the slight irregularity to its form, coupled with its context: it descends from the base of the same bar top shales that yield parautochtonous cf. *Zosterophyllum* (discussed above and illustrated in Fig. 4).

Unequivocal clay-lined root structures are present in likely Pragian-aged strata of the lower Wood Bay Formation (Fig. 9B), the sedimentary context of which is illustrated in Figure 10. The roots are hosted within heterolithic overbank deposits (Fig. 10A) at the same locality as illustrated in Fig. 5. The succession comprises decimetre-scale sandstones that are composed entirely of continuous climbing ripple laminae (Fig. 10B-C), attesting to near-instantaneous out-of-channel deposition as thin crevasse splays, separated by decimetre-scale mudrocks with pedogenic slickensides, indicative of multi-year floodplain stability. The roots can be seen anchored into the top of the crevasse splay sands, indicating plants colonized sandy event beds prior to the accrual of overbank fines. This instance indicates that the colonization of freshly-created post-flood sandy substrates, by small herbaceous plants, was occurring on alluvial floodplains in the Early Devonian. Younger strata of the Wood Bay Formation yield further indirect evidence for rooting, potentially up to one metre in vertical length, in the form of drab haloes and calcic rhizoliths within red palaeosols (see Section 3.5.). However, helical 'rhizoliths' previously reported from the Verdalen Member (Volohonsky et al., 2008) are actually specimens of the invertebrate burrow trace fossil *Gyrolithes* (Laing et al., 2018).

Rooting structures are less common in Middle Devonian strata, possibly due to the environmental bias imparted by the persistent marine influence. However, putative sedimentological evidence for rooting structures is present: in both the Grey Hoek and Wijde Bay formations, there occur downwards-tapering structures which exhibit diameter-decreases after branching (to 10 cm in vertical length) (Fig. 9 C-D). The structures are clearly differentiated from the regular form of invertebrate trace fossils in the same successions (e.g., U-shaped and dumbbell-shaped burrows) and were passively infilled with dark, organic-rich mud. Significantly, they occur in strata that yield marine ostracod and bivalve faunas.

Other rooting sedimentary structures in the Spitsbergen ORS date from the Mid-Late Devonian transition (Figure 9E). The stratigraphic position of these strata is uncertain, but they post-date large woody-debris deposits (Fig. 8) and occur in either the uppermost Tordalen Formation or lowermost Planteryggen Formation. The structures comprise successive palaeosols, densely patterned with vertical drab reduction haloes that extend up to 2 metres in vertical lengthand imply dense and mature vegetation had developed within those parts of the sedimentary environment that were experiencing stasis. The rooted beds are punctuated by c. 1 metre-thick erosively-based sandstones, recording intermittent reworking of the densely vegetated floodplains.

3.3. Vegetation-Induced Sedimentary Structures

Vegetation-induced sedimentary structures (VISS) provide physical evidence for plants having mediated sediment accumulation and erosion in clastic deposystems. The umbrella term “VISS” was coined by Rygel et al. (2004) to refer to sedimentary structures formed by the interaction of sediment with *in situ* plants. They defined seven types of VISS in two categories: A) *VISS formed due to hydrodynamic processes interacting with standing vegetation:* 1) upturned beds around a plant, recording deposition in its shadow; 2) centroclinal cross-strata centred on a plant, recording the infill of a scour hollow formed at its base; 3) scour-and-mound beds, formed by a coalescence of upturned beds and centroclinal cross-strata along a common horizon; 4) complex internal stratification of sand bodies, arising from multiple coalesced scour fills associated with multiple individual plants arranged in a stand; and 5) scratch circles on bedding planes, formed by rotation of flexible plant parts;

B) *VISS formed due to the decay of in situ plants within a sediment pile:* 6) downturned beds arising from the decay of an in situ buried trunk, and the collapse of sediment into the mould after decay; and 7) mudstone-filled hollows formed by casting of internal voids within decayed trunks.

Although not all types of VISS have been recognized in the Spitsbergen ORS, instances of upturned beds, centroclinal cross-strata and scour-and-mound beds occur frequently in the Frasnian-aged strata, and analogous forms may also be present in Lower and Middle Devonian parts of the succession. These features are the earliest examples of VISS presently reported worldwide.

3.3.1. Lower and Middle Devonian VISS

Figure 11 shows an instance of what are likely the earliest VISS in the Spitsbergen ORS, occurring at the contact between the top of a red mudrock bed and the base of a crevasse splay sandstone in the Emsian Dicksonfjorden Member of the Wood Bay Formation. The contact may record a synoptic topography, i.e. a true representation of the geomorphic form of the depositional substrate (see Paola et al., 2018; Davies et al., 2019), because 1) the massive sandstone passively drapes the mudrock bed; 2) the upper 5 cm of the oxidized mudrock shows a mantle of drab mottling, which may be suggestive of reduction by shallowly-penetrating roots; and 3) individual elongated drab haloes extend and branch up to a metre downward from the apices of the gentle mounds: although their discontinuity hampers confident recognition, these resemble similar-aged root traces of deeply-anchored small-stature plants (Xue et al., 2016). These characteristics imply that deeper rooted plants were individually centred within gentle mounds on the ancient floodplain. On modern floodplains, large-scale mounds can develop because of the preferential accumulation of plant matter and sediment around standing plants (e.g., Scheihing and Pfefferkorn, 1984; Small, 1997; Sullivan et al., 2016). Similar sediment interactions should also be expected to have been associated with small stature Early Devonian plants, whose primitive physiological constructions were already adept at baffling fine sediment (Mitchell et al., 2016). In this instance, the potentially original undulatory floodplain topography, induced by early herbaceous plants, has been preserved because it was cast by overbank flooding splays, which lose capacity to erode and rework synoptic topography as they wane away from their source (e.g., see Davies and Shillito, 2018).

One Mid Devonian instance of VISS associated with *in situ* plant remains was recognised within the Wijde Bay Formation (Figure 12). Here an inclined sub-vertical mud-filled tube is hosted within thin beds of very fine-grained sandstone that deflect downwards where they make contact with the structure. Although the structure lacks ornamentation and cannot be identified as a specific plant fossil, it is unlikely to be an animal burrow because the deflection of the beds is asymmetric (more symmetrical deflection would be expected if the structure was emplaced through directed penetration of the sediment). Instead it is likely the structure records the internal casting of the hollow interior of a standing, decaying plant stem at the time of deposition, with the deflection of the adjacent beds recording localized subsidence as buried parts of the plant decayed away. The structure is the earliest instance in the Spitsbergen ORS that can be ascribed to one of the types of VISS originally outlined by Rygel et al., (2004).

3.3.2. Upper Devonian VISS

Abundant instances of VISS are recorded within Frasnian strata, in association with both standing archaeopterids (Figs. 13, 14) and lycopsids (Figs.15, 16). Some of the Frasnian VISS are analogous to older strata in the Spitsbergen ORS: for example, mound-shaped substrates below lycopsids (Fig. 15A) that resemble the putative Early Devonian VISS (Fig.

11). In addition the Plantekløfta Formation hosts the earliest instances of hydrodynamic VISS (*sensu* Rygel et al., 2004) currently known worldwide: marking the evolutionary onset of arborescent vegetation as a resistant obstacle to flow. Four types of hydrodynamic VISS are recognised in the Plantekløfta Formation: upturned laminae, centroclinal cross-strata, scour-and-mound beds, and buckled laminae.

Upturned laminae (Figs. 13, 14, 15C) are the cross-sectional record of current shadows: elongate accretionary sediment mounds that develop in the lee of an obstruction to flow (Allen, 1982; Rygel et al., 2004). They are readily diagnosed when witnessed immediately adjacent to standing vegetation, but other instances of convex-up laminae are also seen, and likely record downstream cross-sections of the vegetation shadows in the lee of plants (e.g., Figure 15E-F). Upturned laminae have a tendency to be steeper where they are seen adjacent to archaeopterids (e.g., Fig. 13C-D) and gentler where they are seen adjacent to lycopsids (e.g., Fig. 14C-D): implying that archaeopterids were associated with smaller scale shadows (see later discussion).

Centroclinal cross-strata (Figs. 14B, 15D, 16) occur as sandstone bodies with concave-up bases, flat tops, and form-concordant laminae. The structures formed by the infilling of antecedent scours that had developed when water flowed around a tree obstacle, with an erosive component of the flow being forced down the upstream side of the trunk. Instances where there is an upwards transition from centroclinal cross-strata into upturned laminae (e.g, Fig. 15C-D) record a change from erosive to aggradational conditions, likely during waning flow. Where multiple instances of both centroclinal cross-strata and upturned laminae coalesce along the same horizon, compound scour-and-mound beds are seen (e.g., Fig 16) with alternating convex- and concave-up components.

Upturned laminae, centroclinal cross-strata and scour-and-mound beds are all within the canon of VISS described by Rygel et al. (2004). A fourth type of previously undescribed VISS is seen recurrently in the Plantekløfta Formation, and here referred to as buckled laminae (Figs. 13C, 15F, 16D). Buckled laminae are always seen on the upstream side of *in situ* plants that are often curved, and inclined towards the palaeoflow direction: implying flexibility of their woody stems in life. The buckled laminae comprise disharmonic crests and troughs that lack the regularity and continuity of current ripples. They are here interpreted as irregular surfaces that developed on the upstream side of standing plants under highly erratic flow conditions: the flexibility of the plants meaning that they would have oscillated irregularly in the flow, with complex and discontinuous upstream feedback of downflow and vortices sculpting the substrate.

3.3.3. VISS in different lithologies

Almost all of the VISS observed in this study occur within sandstones: a natural bias arising from the greater readability of hydrodynamic bedforms in that lithology in the field (an exception being the mound-shaped mudrock seat-earth topography seen in Figures 11 and 15A). However, Figure 14 shows how vegetation has also influenced the sedimentary architecture and fabric of conglomerates in the Plantekløfta Formation. The figure shows a stand of small archaeopterid trees, rooted into a poorly-drained dark mudrock seat-earth (Fig. 14E-F: note that the roots here are fossilized, rather than being sedimentary traces). The stand occupied a topographic depression (channel margin?), that was entombed in fine-grained sandstone during recurrent flow events that left a record of multiple instances of hydrodynamic VISS (Fig. 14B). The sandstone was subsequently capped by at least two metres of conglomerate, deposited instantaneously as a poorly-sorted and partially clast-supported debris flow. The truncation of sandstone laminae (e.g., Fig. 14G-H) shows that the emplacement of the debris flow deposit was associated with reworking of the underlying substrate. However, whilst the archaeopterid trunks have also been truncated, their bases nonetheless protrude upwards into the debris flow, where they are seen to have acted as obstacle that forced the deposition of clusters of larger cobbles (e.g., Fig. 14B, D, H). This shows that the presence of the trees acted to retard the erosive capacity of the debris flow event: if they had not been present, scouring would have removed more sandstone than is now preserved. This instance demonstrates how VISS may present as constructed boundaries (*sensu* Paola et al., 2018), internal to a sediment pile, in addition to their more common appearance as engineered synoptic topographies (e.g, hydrodynamic forms).

3.3.4. VISS without preserved vegetation

VISS are unequivocal when seen in direct association with standing trees, but may be underdetermined when trigger fossils are not exposed at outcrop. Figure 16 shows an example of how instances of scour-and-mound beds can reflect vegetation-sediment interaction, even where fossil plants are missing. Figure 16A-B shows an exposure of outcrop of the Plantekløfta Formation on the banks of the Mimer River, in photographs taken six years apart. In both images, the scour-and-mound topography is apparent, but individual standing trees have variably become exposed or eroded as the river has cut back into the cliff face. In this instance, the preserved VISS can rarely be attributed to particular obstacles (Figs. 16C-H), but subsequent exposure indicates bed architecture to be related to buried vegetation. Modern analogue confirms that it is appropriate to search for putative VISS beyond the area immediately adjacent to a standing plant fossil: substrates can develop irregular topography when flow structures are inherited from upstream conditions or cross-stream circulation induced by tree or woody debris obstacles (Reesink et al., 2020).

Middle and Upper Devonian strata of the Spitsbergen ORS contain many examples where VISS may be interpreted, but not proven by current exposure (Figure 17). In these instances, features such as concave- and convex-upwards bedding, often at high angles, are seen in association with circumstantial evidence for standing vegetation, such as rooting traces (Fig. 17A-C) or parautochthonous woody debris (Fig. 17D-F), or have a proximity to sites with abundant evidence for trees (e.g., the site shown in Fig. 17G is the same horizon of the Lower Svalbardia Sandstone that hosts the woody debris layers shown in Fig. 8D-F).

According to Rygel et al. (2004), the term "VISS" excludes sedimentary structures induced by fallen or transported woody debris. However, driftwood can also act as an obstacle that induces sediment deposition, erosion and mounding (Nakayama et al. 2002; Reesink et al., 2020) and Trümper et al. (2020) have recently documented multiple 'VISS-like' forms associated with flow deflection by accumulations of large woody debris in ancient strata ("LWDISS"). In instances where there is no preservation of plant material, but strata contain VISS-like structures (Figure 17), it may be impossible to tell whether they are VISS *sensu stricto*, whilst being confident that bedform irregularities were induced by plants, either *in situ* or transported: it is thus practical to expand the original definition of VISS to capture such instances. It is here proposed that reasonable confidence in a VISS interpretation for any bedforms may be achieved where they exhibit several of the following characteristics: 1) they exhibit sediment structures that are not readily explainable by models of aggradation under undisturbed hydrodynamic flows; 2) they are known to be a product of unequivocal VISS elsewhere; 3) they occur in a succession known to host unequivocal VISS or standing fossil trees; and 4) they host fossil debris, or rooting traces, that indicates the former presence of standing vegetation. The forms in Figure 17 exhibit all of these characteristics, and provide extra circumstantial evidence that arborescent land plants were obstructing flows, and sculpting landforms by forcing erosion and deposition from at least the Givetian onwards.

There are numerically more instances of 'likely VISS' (lacking fossils) than 'definitive VISS' (with fossils) in the Spitsbergen ORS, but this is not unexpected, because VISS have fewer taphonomic hurdles to overcome than organic plant remains. The majority of plant biomass has always been fated to be reused by living biota through biogeochemical cycles (Gastaldo and Demko 2011), whereas, although sediment piles accrued around vegetation may diminish in thickness over decades as plants decay, VISS forms can persist (Small, 1997). Better recognition of these forms may improve our understanding of the extent to which trees have sculpted sedimentary landforms that are preserved in the rock record.

3.3.5. Vegetation without preserved VISS

In instances where plants were shallowly rooted, non-woody, or small stature, *in situ* fossils are unknown. Such organisms have negligible preservation potential in growth position, and because of their limited mechanical resistance, they are likely to have been torn up or flattened during the deposition of siliciclastic sediment (their former presence evident only from parautochthonous or allochthonous remains, or sub-surface rooting structures). However, one instance is known in the Plantekløfta Formation where seemingly *in situ* vertical stems of diminutive size appear: apparently standing, but also having had little apparent influence on the architecture of the sediments that entombed it. Figure 18 illustrates this, and shows tens of vertically-oriented and occasionally bifurcating lycopsid branches that extend through a heterolithic package of shale and very fine sandstone. These are interpreted as multiple branches of the same recumbent lycopsid crown, which would have been attached to the main trunk at an unexposed, lower stratigraphic horizon. The crown appears to have been interred with minimal effect on the internal structure of the host sediment, despite the apparent shift in depositional energy attested to by the shift from mud to sand deposition. In this instance it seems likely that the attachment to a fallen trunk has acted as a disproportionately effective anchor (i.e., relative to roots of similar-sized individual plants), such that the branches have remained vertical when buffeted by flow and aggrading sediment. The most apparent plant-sediment interaction is of sediment upon vegetation (i.e., opposite to

VISS), as the weight of the interring mass appears to have caused the branches to bend (e.g., Figure 18D).

The recumbent crown is hosted within facies that record deposition on the point bars of small meandering streams (Section 3.5.) and likely records the uprooting of a large lycopsid: a significant biogeomorphic process in its own right (e.g., Phillips et al., 2017). An alternative explanation would be that the tree had adopted a prostrate, downstream growth habit (a stabilizing mechanism adopted by some modern trees that grow within seasonally-flooded river channels; Fielding et al. (1997)). However, no definitive conclusion can be reached because of the singular nature of the occurrence.

3.3.6. Characteristics of Devonian VISS

VISS were first catalogued from Carboniferous-aged strata (Rygel et al., 2004), and have since been reported from almost every subsequent geological period (e.g., Durand, 2008; Neff et al., 2011; Bashforth et al., 2014; Trümper et al., 2020). However, prior to this study, no true VISS have been described from the Devonian (although microscopic structures attesting to the sub-mm-scale movement and deposition of silt particles around comminuted debris have been described as such (Allen and Gastaldo, 2006)).

The early examples of VISS observed here are generally less diverse than the forms originally described by Rygel et al. (2004), but this may in part be explained by the larger dimensions of many of the Carboniferous trees in the original description. In such instances, wake flow is the most significant driver of VISS creation (e.g., Allen, 1982; Rygel et al., 2004), arising where approaching flow is deflected downwards upon meeting a pillar-like obstacle, inducing 1) an erosional horseshoe vortex; and 2) a reduced wake zone flow in the lee of the obstacle. The smaller stature of the Devonian trees may explain why hydrodynamic erosional forms (e.g., centroclinal cross-strata) are rarer than depositional forms (e.g., upturned laminae) in the Spitsbergen ORS, because large trees promote scour holes more so than smaller vegetation (which may be more effective at promoting leewise deposition) (e.g., Nakayama et al. 2002; Schlömer et al., 2020). Height differences may also explain the observed phenomenon whereby vegetation shadows are apparently smaller for archaeopterids than they are for lycopsids (e.g., compare Figs. 13 and 15) as obstacle marks become larger during shallower flows relative to the obstacle height (Schlömer et al., 2020).

Recent advances in the understanding of flow around plant obstacles (e.g., Schnauder and Moggridge, 2009; Larsen, 2019; Reesink et al., 2020; Schlömer et al., 2020) suggest that the diversity of Devonian plants observed in the Spitsbergen ORS would also have caused other fluid responses, in addition to wake flow (summarized in Figure 19). For example, elevated dense canopy can divert flow downwards, resulting in a sub-canopy downwards directed jet of water with accelerated velocity and propensity to erode. Such a scenario might be expected in association with archeopterids (e.g., see the relatively large centroclinal scour fill association with such plants in Fig. 14B). Likewise, porous canopies or emergent stands can induce bleed-flow, baffling flow by reducing velocity gradients and turbulence (Schnauder and Moggridge, 2009), and sparse stands of vegetation may induce a different response (increased turbulence) (e.g., Fig. 16) to dense stands (reduced turbulence) (Larsen, 2019). An example of the latter may be seen in Figure 18, where the small branches of the fallen lycopsid crown were passively entombed by sand, demonstrated by the lack of shadow or scour structures in the sandstone laminae even where they are directly in contact with branches. The unusual instance of a multitude of small but well-anchored obstacles would have been highly likely to induce bleed-flow.

It has also been recognised that flexible vegetation tends to have a higher rooting strength, bending towards the bed during high flow to avoid uprooting (Larsen, 2019), but also inducing drag especially where branches terminate in leaves or other constructions

(Schnauder and Moggridge, 2009). Such complex hydrodynamic interactions can explain the buckled laminae seen in Figures 13D and 15F.

3.4. Cannel Coal

Cannel coal is a prominent, but volumetrically-minor, lithology that occurs in four seams (maximum 80 cm thickness) within the Estheriahaugen Member of the Tordalen Formation (Figure 20). The cannel coals have previously been described in detail elsewhere (e.g., Vogt, 1941; Harland et al., 1976; Blumenberg et al., 2018; Marshall et al., 2019). They are composed of lipid rich organic matter derived from *Archaeopteris* and lycopod spores (Marshall et al., 2019), which accumulated in lacustrine settings (Blumenberg et al., 2018), rather than in situ coal swamps. Although not considered further here, they are significant for proving that vegetation-dependent lithologies (Davies et al., 2020) were being deposited by the Givetian.

3.5. Vegetation-Influenced Facies

Several common facies characteristics of the Spitsbergen ORS have previously been identified as being promoted by the presence of vegetation. In isolation, they cannot be recognised as causal effects of vegetation but, in the context of the global sedimentary-stratigraphic record, they are signatures that can both be explained by, and observed to exhibit a worldwide increase in frequency and distribution following, particular events in land plant evolution. These include:

Elevated mudrock content: In common with other Siluro-Devonian ORS localities, the succession has a high proportion of mudrock within its alluvial facies. At the localities visited in this study, mudrock strata comprise approximately 20% of the vertical succession of the Silurian Siktefjellet Group, 50% of the Lochkovian Red Bay Group, 60% of the Pragian-Emsian Wood Bay Formation, and 45% of the Frasnian

Plankeløfta Formation. Such elevated alluvial mudrock content is rare before the advent of land plants, and the observed global stratigraphic shift towards muddier alluvium (from the Ordovician onwards) can be credited to both production (enhanced weathering) and retention (through baffling, binding, and enhanced flocculation) of fines by vegetation (McMahon and Davies, 2018b; Davies and McMahon, 2021; Zeichner et al., 2021). The mudrock motif seen in the Spitsbergen ORS is typical of alluvial settings operating within early vegetated landscapes, accentuated by their proximity to an active orogeny and equatorial palaeolatitude (Davies et al., 2017).2) Complex alluvial architecture: a prominent feature of the Spitsbergen ORS is the abundance of inclined heterolithic stratification that can be recognised as recording lateral accretion of bank-attached fluvial bars (IHS-LA sets) (Figure 21). IHS-LA sets are a common, though non-exclusive, signature of meandering streams that exhibit a worldwide increase in abundance in the rock record from the Devonian onwards, as land plants and mud increased resistance to flow and corralled rivers into single-thread channels (Davies and Gibling, 2010a,b; McMahon and Davies, 2018a). All the Devonian stages in the Spitsbergen ORS contain at least isolated instances of IHS-LA, often in association with fossil plant debris. The largest occur within the Emsian Wood Bay Formation (Moody Stuart, 1966), where they can reach thicknesses in excess of 5 metres, attesting to river channels of a similar bankfull water depth (e.g., Bridges and Leeder, 1976).

4. Role of Climate and Tectonics

In addition to vegetation-mediated controls on deposition, the Spitsbergen ORS also yields direct and indirect evidence for cyclic allogenic variables of tectonics and climate that interacted with the evolving vegetation in the region and will have impacted the plant-sediment interactions that were active, and the sedimentary products that were preserved..

Abiotic allogenic influences can be read in many of the successions signatures: for example, 1) the stratigraphic interval of increased marine signatures in the Grey Hoek and Wijde Bay formations, attesting to higher relative sea-level during the Mid Devonian; 2) the stratigraphic partitioning of red bed and grey-green strata attesting to long-term fluctuations in drainage and oxidizing conditions (Table 1); or 3) the alluvial fan and debris flow conglomerates, associated with intervals of renewed local uplift (e.g., Beranek et al., 2020), that are more common in early Lochkovian (Red Bay Group) and Frasnian (Plantekløfta Formation) strata.

4.1. Climate

The tropical setting for the Spitsbergen ORS would have influenced climate, and it has previously been proposed that scarcity of thick calcretes (common in comparable ORS successions) indicates that the precipitation regime was monsoonal in nature (Reed, 1991). Monsoonal climates are associated with large annual ranges of rainfall (relative to the mean), with pronounced precipitation peaks (Plink-Björklund, 2015). Sedimentological evidence for the highly-variant seasonal discharge associated with such regimes can include the preferential preservation of bedforms associated with supercritical flow conditions, high-deposition-rate sedimentary structure, in-channel muds, abrupt lateral and vertical facies shifts and an abundance of in-channel VISS in alluvial strata (e.g., Plink-Björklund, 2015; Fielding et al., 2018). With the exception of supercritical flow bedforms, these features are all typical of much of the succession; particularly within Upper Devonian strata, deposited by which time Spitsbergen had migrated northwards to a palaeolatitiude of around 5°S (Torsvik and Cocks, 2017).

The tropical setting also likely played a role in the delivery of woody debris in Middle and Upper Devonian strata. In the modern tropics, most forest floor wood decays within < 10 years (Clark et al., 2002), but while decay is high, so is input. In particular, tropical storms and monsoons can induce mass recruitment from hinterlands, and rapidly transport huge volumes of wood from source to sink (Hilton et al., 2008; Wohl, 2017). The recurring driftcretions in the Tordalen Formation (Fig. 8) could attest to such events on, for example, annual to centennial scales. However, woody debris supply would also have been moderated through other distinctly-Devonian evolutionary influences that presently remain speculative (e.g., in terms of plant physiology, forest density, or interactions with any other Devonian organisms that may have played a role in inducing mass mortality or decay; compare with Wohl, 2017; her Fig. 2).

4.2. Tectonics

Sedimentary signatures attributable to tectonic influences recur in the Spitsbergen ORS at a lower frequency cyclicity to those attributable to climate cycles (Table 1): for example, the alluvial fan and debris flow intervals, or the unconformities that bound different units of the Spitsbergen ORS. These signatures, coupled with persistent non-marine dominance of the depositional environments, are explained with reference to local strike-slip tectonics related to the ongoing Ellesmerian Orogeny to the west of the region during the Devonian (e.g., McCann, 2000; Beranek et al., 2020). The proximity to this orogeny would have accentuated some signatures that are vegetation-influenced over longer timescales, such as mudrock abundance, but generally there are few intensive sedimentary signatures that can be directly ascribed to tectonic controls.

The preservation of standing trees in sedimentary successions (e.g., as seen in the Plantekløfta Formation: Figs. 13-18) has previously been interpreted as requiring exceptional intervals of rapid subsidence or relative sea-level rise (e.g., Bailey, 2011). This is based upon the recognition that burial of the trees must have happened faster than decay (Gastaldo et al., 1995; DiMichele and Falcon-Lang, 2011). However, recent conceptual advances in the understanding of how time is preserved in the rock record have shown that it is unnecessary to invoke rapid subsidence as an explanation. Specifically, this is because outcrop-scale exposures can record thick localized sediment piles that accumulated by effectively instantaneous aggradation, within underfilled accommodation space (e.g., Miall, 2015; Reesink et al., 2015; Paola et al., 2018; Davies et al., 2019; Holbrook and Miall, 2020). Such localized rapid deposition recurs frequently in active alluvial settings (especially within systems with highly-seasonal discharge: Allen et al., 2013; Plink-Björklund, 2015; Fielding et al., 2018), sometimes buries trees, and sometimes the resulting sediment entombment maintains or enhances the dysoxia or anoxia that is necessary for their longer term preservation (Gastaldo and Demko, 2011). In the context of the specific trees that can be seen at outcrop today this chain of events may seem unlikely (Bailey, 2011), but would in reality be unexceptional over the time-length scales that the Plantekløfta Formation depositional environment persisted (Miall, 2015; Holbrook and Miall, 2020). The preserved trees are a miniscule sample of the multiple successive generations of trees that existed during this interval, but there is no need to invoke exceptional tectonic or taphonomic conditions for their preservation.

5. Timeline of Devonian Biogeomorphic Innovations

The accrual of the Spitsbergen ORS was contemporaneous with major events in vegetation evolution. This unidirectional development of increasingly complex and diverse plant life imparted novel allogenic controls on Earth surface processes and landforms, sedimentary evidence for which is transposed upon the cyclic signals of tectonic and climate influence. Figures 22 to 24 show reconstructions of the plant-sediment interactions that resulted in the sedimentary phenomena described previously. These are discussed below with reference to ongoing changes to biogeomorphology, as described by the biogeomorphic succession model

(Corenblit et al., 2007; 2015; 2020). This conceptual model was originally developed to explain successional effects after modern flood disturbances in alluvial settings (Corenblit et al., 2007), and has previously been discussed with respect to Carboniferous plant evolution. The discoveries in this present study indicate that aspects of biogeomorphic succession had developed by the Devonian, earlier than previously reported (e.g., Davies and Gibling, 2013; Gibling et al., 2014; Corenblit et al., 2015). Present-day biogeomorphic succession begins with pioneer seedlings on fresh post-flood substrates, incrementally inducing feedbacks (e.g., enhanced sedimentation) such that eventually biological geomorphic processes dominate (e.g., years later there may be raised islands with successional forests) (Corenblit et al., 2020). Such well-established modern biogeomorphic systems can experience feedback from vegetation influence that extends over thousands of years. Here we summarise how such feedback was instigated in some of the earliest vascular plant communities, as evolutionary innovation increased the repertoire of plant-biogeomorphic processes and produced novel landforms and habitats.

5.1. Silurian and Early Devonian

Silurian strata of the Siktefjellet Group contain only comminuted carbonaceous material, showing that small stature land plants were in existence, but had limited direct geomorphic influence. There is no evidence in the unit that land plants were influencing sedimentation to an extent that readable signatures were preserved, except for an elevated mudrock content. Mud could be produced and trapped by even primitive flora, and is common in post-Ordovician alluvium (McMahon and Davies, 2018b; Mitchell et al., 2019; Zeichner et al., 2021): globally, some of the earliest vegetation-influenced effects may have been enacted vicariously through this cohesive sediment (Davies et al., 2020). However, as individuals, the flora in the depositional environment apparently responded analogously to small stature vegetation in modern ephemeral stream bed settings: suffering mortality and entrainment when exposed to only minor hydrodynamic stress (Sandercock and Hooke, 2010; Edwards et al., 2015). Analogous flora are seen in modern post-flood settings during the ‘geomorphic’ stage of biogeomorphic succession (Corenblit et al., 2007; 2015; 2020): small diaspores and propagules that colonize fresh substrates, but which will be totally destroyed if the same patch of substrate experiences further disturbance before the plants take hold. In modern settings, the geomorphic phase persists for a few hours to a few months following a flood, but it would have effectively persisted indefinitely during the Silurian, when the maximum attainable plant stature offered negligible resistance to flow, and colonization of active sedimentary environments would have been opportunistic and reliant on intervals or spatial patches of hydrodynamic quiescence.

Signatures in the Red Bay Group show that, by the Lochkovian, plants were able to resist flow and influence sedimentary processes (Figure 22). This was in part mediated by the cumulative and attendant accrual of weathered and retained mud, which increasingly formed thick accumulations in the less frequently-active parts of alluvial systems such as floodplains and emergent bar tops (e.g., Fig. 4). The stability afforded by these cohesive sediment accumulations, coupled with evolutionary innovations in plant habit (e.g., rooting), meant that post-disturbance landscapes could begin to operate within the pioneer stage of biogeomorphic succession (Corenblit et al., 2007; 2015; 2020). This stage could now take over from the geomorphic stage after a few hours to months, and marked the recruitment of established vegetation on substrates, and the instigation of some resistance to purely abiotic forcing of landform development. Evidence for this stage is seen in the muddy braid bar-tops likely colonized by cf. *Zosterophyllum* that has only been reworked parautochthonously (Fig. 4). In addition to physical feedbacks, the development of temporally-persistent vegetation patches within fluvial settings would have promoted habitat heterogeneity: such patches in modern rivers are associated with nutrient enrichment from allochthonous fecal material

(Larsen 2019), and the co-occurrence of cf. *Zosterophyllum*, coprolites and trace fossils (Fig. 4) demonstrates that multiple organisms occupied the ecosystems that were likely engineered by bar-top flora.

In modern settings, complexity of river form induces a complexity of hydromorphology and thus of biodiversity (Garcia et al., 2012), so the incremental shift towards physical stabilization and landform modification induced by even small stature Early Devonian plants can be seen as a key component of the terrestrialization process. This heterogeneity continued to develop throughout the remainder of the Early Devonian: for example, the Pragian-Emsian Wood Bay Formation contains not only some of the oldest palaeosols in the Spitsbergen ORS (e.g. Fig. 10), but also some of the oldest known palaeosol ichnofauna in the world (Morrissey et al., 2012; Genise et al., 2016). The Wood Bay Formation also yields further evidence that bar tops were now semi-stable vegetated patches within riparian environments, and direct evidence for pioneer vegetation in overbank settings. Figure 10 shows rooting in instantaneously-deposited climbing-ripple-laminated crevasse splay sands that could be analogous to post-flood colonization in modern rivers: where plants either reproduce asexually when propagules are snapped off and transported with flood sediment, or because they preferentially release spores or seeds at the end of the annual flooding season (Gurnell, 2014). In any instance, the plants certainly promoted fine sediment, shown by clay-lined roots (Fig. 10B), and the accrual of multi-year palaeosols in the floodplain fines that accrued in between crevasse events (Fig. 10). The influence of rooted vegetation in overbank fines is further emphasised by the earliest putative VISS, seen towards the end of the Early Devonian: the development of incipient hummocks at the bases of herbaceous plants, composed of baffled sediment and (presumably) organic matter (Fig. 11). Such landforms appear negligible in size, but the increasing three-dimensionalization of terrestrial substrates would have led to a cascade of ecological effects. Mounded topographies can alter patterns of groundwater flow, bidirectional exchange with surface water, and evaporation; all of which may redistribute and partition nutrients or amenable conditions for habitation (e.g., temperature or oxygen) (e.g., Poole et al., 2008; Sullivan et al., 2016). Similar impacts would have been inevitable after the Early Devonian first appearance of vegetation mounds as they would have had profound influences on evolution and terrestrial habitats, despite the fact that tangible evidence of such processes may be lacking or unreadable.

5.2. Mid and Late Devonian

While the Middle Devonian interval witnessed major palaeobotanical innovations, the record of biogeomorphic innovation in the Spitsbergen ORS is partly masked by an increased marine influence and transgressive shift towards coastal environments. Despite this, there is evidence that the sedimentary environments of all the Middle Devonian units were colonized by plants. The Eifelian Grey Hoek and Wijde Bay formations contain circumstantial evidence that habitats analogous to modern salt marshes may have developed in the Devonian, in the form of root structures hosted within dark organic-rich sediments that yield a marine fauna (Figure 9D-E). Salt marshes are some of the most biogeomorphologically-active environments at the present day (e.g., Mudd et al., 2010), but there are very few interpretations of such environments from the rock record. Putative Silurian instances have been interpreted from waterlogged palaeosols with marine fossils (Retallack, 2008), but these lack direct evidence for plants and remain speculative. The earliest unequivocal salt marshes currently known from the rock record are Cretaceous in age, and are identified by dark coloured mudrocks, with a high total organic carbon content, compacted halophyte leaf litter fossils, rootlets and marine microfossils (Uličny and Špičáková, 1997). In this instance, the key diagnostic criterion is the presence of fossil material from extant salt marsh halophytes. However, as almost all extant salt marsh plants are angiosperms, such a criterion cannot be employed in the search for potential Palaeozoic salt marshes, where a different flora must have been involved if such systems existed. The Grey Hoek and Wijde Bay examples provide evidence that small stature rooted vegetation was located in low gradient marginal marine settings that were traversed by channels (e.g., Fig. 6), and they do post-date the evolution of halophily (evidenced by the hot spring flora of the Early Devonian Rhynie Chert; Channing and Edwards, 2009). However, whether the rooted horizons record true salt marshes, inundated on a tidal rhythm by the sea, remains inconclusive from the available sedimentological and palaeontological evidence.

Although lacking the diversity of landforms that might be expected in purely alluvial facies, the coastal, lacustrine and deltaic facies of the Middle Devonian ORS do show that potential stages of biogeomorphic succession had expanded by at least the late Eifelian (Figure 23). Post-disturbance plant communities would develop through the geomorphic and pioneer stages over the course of hours to months, but would then progress into the biogeomorphic phase. The biogeomorphic phase is characterized by landforms that are colonized by secondary successions of established vegetation, which can promote active accretion of those landforms: in other words, there is a balanced feedback between abiotic and biotic controls on local geomorphology. Evidence for this phase can be seen in the definitive (e.g., Fig. 12) and putative (e.g. Fig. 17) VISS in the Wijde Bay and Tordalen Formations. The driftcretions in the Lower Svalbardia Sandstone (Fig. 8) provide evidence for landforms that were wholly constructed from woody debris. There is also evidence that parts of the depositional environment progressed into the ecologic phase of the biogeomorphic succession model (Corenblit et al., 2007). This phase is characterized by autogenic vegetation successions and the stabilisation of landforms to the extent that they become disconnected from hydrogeomorphic disturbance: it reflects patches of the landscape where biotic geomorphic processes dominate over abiotic geomorphic processes for prolonged intervals of decades to centuries, until reset by extreme low frequency disturbances. Direct evidence for autogenic vegetation successions is provided by the thin cannel coals in the Estheriahaugen Member (Fig. 20). Further, the multiple logs that comprise the driftcretions of the Lower Svalbardia Sandstones imply that the parts of the sedimentary environment from which they were sourced had had the opportunity to develop dense forested stands, detached from high frequency hydrodynamic disturbance.

Evidence shows that the Mid Devonian was a revolutionary interval in the evolution of Earth surface processes, with many biogeomorphic processes coming online for the first time. All stages of biogeomorphic succession had become available, and, within the Spitsbergen ORS, the stratigraphic interval hosts a number of both regional and global biogeomorphic 'firsts': for example, the first driftcretions, the first cannel coal accumulations, and possibly the first salt marshes. These are apparent despite the fact that the Spitsbergen ORS preferentially records littoral strata from this time: sedimentary environments further inland would have seen a comparative explosion in biogeomorphic forms – for example, the existence of large woody debris accumulations proves that logjam processes and forms must have been in existence in fully alluvial settings (and evidence for such should be expected to be discovered with concerted searches in Middle Devonian alluvium elsewhere in the world).

Late Devonian plant-sediment interactions recorded in the Spitsbergen ORS (Figure 24) are apparent continuations of Mid Devonian innovations, but preserved within inland settings. The abundance of hydrodynamic VISS from the Plantekløfta Formation (Figs. 13-16) provide undisputable evidence that arborescent plants were acting as obstructions, inducing scour or deposition depending on factors such as stand density, flexibility and depth of flowing water (Figure 19). The impact of these interactions would not have been restricted to landforms, flow conditions and sediment distribution, but would have further accentuated the three-dimensional complexity of non-marine substrates: the ecological and evolutionary consequences of which were instigated in the Early Devonian (e.g., compare Figs. 10 and

15A). In addition to true VISS, the Late Devonian also contains evidence for uprooting of trees, in the form the fallen lycopsid crown shown in Figure 18. Uprooting is a significant biogeomorphic phenomenon in modern settings, with implications for novel microhabitats as well as instantaneous exposure of piles of sediment that can be entrained into a sedimentary environment (Phillips et al., 2017).

5.3. The Devonian sedimentary record as an archive of biogeomorphic complexity

Many of the signatures in the Spitsbergen ORS can be used to confirm that biogeomorphic processes and products, still active in analogous settings today, appeared on Earth for the first time in the Devonian. Modern observations attest to linkages between these phenomena, and show how the development of one biogeomorphic feature can have cascade effects on habitat heterogeneity and organisms, which in turn feedback further local innovation in biogeomorphic process and form. The sedimentary record imperfectly captures such nuanced chains of events in the form of vegetation-dependent and vegetation-influenced signatures, which provide limited evidence for how Devonian land plants began to impose themselves as essential components in the mechanistic operation of the Earth surface. However, whilst coarsely resolved, these sedimentary signatures provide tangible evidence for the timeline of the onset of plant influences on the intensive properties of the sedimentary-stratigraphic record. The tectonic and climatic setting of Spitsbergen during the Devonian has fortuitously meant that it provides a natural archive of many biogeomorphic firsts. The succession illustrates how the crucial c. 40 myr interval between the Lochkovian and Frasnian witnessed the rapid and incremental onset of the plant-engineered non-marine landscapes that have persisted and evolved ever since, and retain recognisable analogues at the present day.

6. Conclusions

- The Old Red Sandstone of northwest Spitsbergen was deposited in tropical land plant-colonized sedimentary environments that left a near-continuous record of Silurian through to Late Devonian strata. The succession thus provides an archetypal case study for tracking the sedimentary impacts of evolving vegetation through the Devonian.
- The Spitsbergen ORS contains the earliest known vegetation-induced sedimentary structures in the global rock record, as well as very early examples of rooting structures, large woody debris, and cannel coal. It is also typical of similar-aged strata in terms of its vegetation-influenced signatures, being high in mudrock content, rich in palaeosols, and containing alluvial sandbodies with architectural complexity.
- Signatures within the succession can be interpreted as first known occurrences of many biogeomorphic phenomena, including the earliest plant-colonized braided river in-channel bars (Lochkovian), possible salt marshes (Eifelian), driftcretions (Givetian), and coal-forming environments (Givetian).
- The extensive botanic and biogeomorphic innovation during this interval meant that the ‘Devonian landscape factory’ was instrumental in shaping sedimentary environments that are familiar and analogous with present-day settings.

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FIGURE AND TABLE CAPTIONS

Figure 1 – Bedrock geology of NW Spitsbergen showing localities and constituent units of the Old Red Sandstone.

Figure 2 – Lithostratigraphy of the Old Red Sandstone in NW Spitsbergen (after Piepjohn and Dallman (2014); revised dating after Berry and Marshall (2015) and from original palynological work in this study: see main text). Vertical scale proportional to time in Ma. Timing of earliest global macrofossil evidence for evolutionary innovations in vegetation shown on right hand side of figure, compiled from Gerrienne (2012), Stein et al., (2012, 2020), Giesen and Berry (2013), Strullu-Derrien (2014), Matsunaga and Tomescu, (2016), and Hetherington and Dolan (2018).

Figure 3 – Outcrop appearance of the constituent units of the Old Red Sandstone in NW Spitsbergen. A) Grey sandstones and recessive shales of the Siktefjellet Group, Siktefjellet. B) Basal debris flow conglomerate of the Red Bay Group, Wulffberget Formation, Rivieratoppen. C) Red mudrocks and subordinate sandstones of the upper Red Bay Group, Frænkelryggen Formation, Frænkelryggen. D) Thick fluvial sandbodies within drab mudrocks of the uppermost Red Bay Group, Ben Nevis Formation, Ben Nevis. E) Thick succession of red heterolithic strata within the Wood Bay Formation, Dicksonfjorden

Member, Roosfjella. F) Frost-shattered, scree covered outcrops of the Wood Bay Formation, Dicksonfjorden Member, Scott Keltiefjellet. G) Red-drab transition between the Wood Bay Formation (Verdalen Member) (foreground) and Grey Hoek Formation (background), Woodfjorden. H) Gradational transition between red palaeosols of the Wood Bay Formation (Verdalen Member) (background) and grey ostracod-bearing shales of the Grey Hoek Formation (foreground), Sørlifjellet. I) Heterolithic succession of yellow sandstones and grey shales of the Wijde Bay Formation, Tage Nilssonfjellet. J) Finely laminated lacustrine sandstones of the lower Tordalen Formation, Fiskekløfta Member, Fiskekløfta. K) Sandstones of the Plantekløfta Formation, Planteryggen. L) Typical actively-eroding riverbank outcrop of heterolithic strata of the Plantekløfta Formation, Munindalen.

Figure 4 – Lochkovian plant-sediment interactions in the Red Bay Group (Andréebreen Formation) at Buchananhalvøya. A-B) Laterally-continuous braided fluvial sandbodies (highlighted yellow) and minor shales (grey). Palaeoflow towards left of image. C-D) Detail of boxed area highlighted in A and B: Two braid bar deposits, separated by bar-top fines. Palaeoflow towards left of image. E) Detail of the base of the upper barform, showing basal lag of intraformational calcrete conglomerate (arrowed) resting on grey shale. F) Abundant zosterophyll fragments, preserved within the bar top shales. G-H) Biogenic signatures associated with bar top zosterophylls include casts of *Cruziana* arthropod furrows in base of overlying sandstone (G) and helical fish coprolites within the plant-bearing shales (H). Scale bar 1 cm in G, 1 mm in H.

Figure 5 – Sedimentary context of plant fossil remains in the Pragian-Emsian Wood Bay Formation (Austfjorden Member) at Kapp Petermann. A-D) Plant remains restricted to inflection point of a downstream accreting sand barform (A-B), and consisting of relatively complete specimens of small ?psilophytes (C-D), that would have been growing at the bar top and margins. Palaeoflow towards left of image. E-H) Stratigraphically further up the same

section, braided alluvial in-channel sandy bedforms form a discrete unit within palaeosols (E-F); within these, plant remains are restricted to reworked instances of comminuted carbonaceous matter along trough cross-bed foresets (G) or small fragmentary remains within planar-bedded sandstones (H). Scale bar 1 cm in C, D, G, H.

Figure 6 - Sedimentary context of plant fossil remains in the Eifelian Grey Hoek Formation at Ranfjellet. A-B) Heterolithic succession bearing ostracod fauna and consisting of IHS-LA (inclined heterolithic stratification, exhibiting lateral accretion: see main text), recording deposition by small meandering coastal channels. Palaeoflow into image. Rifle is 1.1 m long. C) Plan view of preserved ridge-and-swale topography of scroll bar top of one such channel. D) Fragmentary transported plant debris preferentially accumulated in sheltered swales of the scroll bars.

Figure 7 – Earliest woody debris in the Old Red Sandstone of NW Spitsbergen. A) Eifelian: Individual strands of xylem with frayed edges from unknown tree, up to 15 cm wide and 40 cm long. Grey Hoek Formation, Ranfjellet. Scale bar is 10 cm. B) Eifelian: Individual clasts of woody debris up to 40 cm long and 17 cm wide within marine-influenced facies of the Wijde Bay Formation, Kronprins Haralds Fjell. Visible part of ruler is 20 cm. C) Givetian: Largest woody debris in the succession: 2 metre-long log of likely *Archaeopteris* within the deposits shown in Fig. 8, Tordalen Formation (Fiskekløfta Member), Fiskekløfta. Metre stick for scale.

Figure 8 – Accumulations of woody debris within the Old Red Sandstone of NW Spitsbergen. A-C) Eifelian accumulation of smaller woody debris within flat-bedded (A) heterolithic strata of the Wijde Bay Formation at Kronprins Haralds Fjell, comprising unoriented compressed wood material up to 40 cm in length (B-C). Rifle in A is 1.1 m long, scale bar in B, C is 10 cm. D-F) Oldest known driftcretion deposit (Givetian) within the

Tordalen Formation (Fiskekløfta Formation) at Fiskekløfta. Individual accumulation of dominantly archaeopterid wood, up to 2 metres length (D) persists within a series of eleven sandstone beds that form a 5 metre-thick amalgamated succession (E). Some of the drifted logs can be seen to have rested on subaerially-exposed bars, as shown by close association with true substrates of extensive aeolian adhesion marks (F). Inset rose diagram in (D) shows axial orientation of 151 individual pieces of woody debris measured throughout the 5 metre-succession. Metre stick for scale, inset scale bar in F is 1 cm.

Figure 9 – Rooting structures throughout the Old Red Sandstone of NW Spitsbergen. A) Lochkovian: Putative 5 cm root structure at the top of a sandstone braid bar, immediately underlying the zosterophyll-bearing shales shown in Fig. 4. Red Bay Group (Andréebreen Formation), Buchananhalvøya. B) Pragian-Emsian: Dense assemblages of clay-lined root structures (up to 50 cm vertical length), common within vertic palaeosols and associated strata of the Wood Bay Formation (Austfjorden Member) at Kapp Petermann. C) Eifelian: Suspected root structures (bifurcating downwards), forming a 5 cm thick mantle within ostracod-bearing and carbon-rich marine influenced strata, possibly recording early salt marsh vegetation. Grey Hoek Formation, Ranfjellet. D) Eifelian: Similar forms in similar marine-influenced facies to C, but extending up to 10 cm vertical length. Wijde Bay Formation, Tage Nilssonfjellet. E) Givetian-Frasnian: Two horizons of densely root-mottled palaeosols separated by sandbodies, implying root penetration to at least one metre, tops of rooted horizons arrowed. Boundary between Tordalen Formation and Planteryggen Formation, Fiskekløfta. Scale bar in A-D is 1 cm, scale bar in E is 1 m.

Figure 10 – Detail of rooting structures in the Pragian-Emsian Wood Bay Formation (Austfjorden Member) at Kapp Petermann. A) Succession consists of alternating blocky red palaeosols, punctuated with thin sandstones representing crevasse splay deposition. B-C) Details of crevasse splay sandstones showing penetration by clay-lined roots (B) and

climbing ripple-laminated (C). Scale bar in A is 1 m, scale bar in B is 1 cm, ruler in C is 20 cm.

Figure 11 – Emsian primitive VISS in the form of gently mounded synoptic topography to a root-mottled palaeosol (A) in the Wood Bay Formation (Dicksonfjorden Member), Germaniabekken. Detail of mound above root mottle shown in B. Visible ruler is 50 cm in A, 70 cm in B.

Figure 12 – Eifelian decay-related VISS formed as hollow plant stem filled with mud and decayed, causing downturning of beds. Asymmetry of downturning and tilt of plant cast suggests that the plant toppled as it decayed. Wijde Bay Formation, Tage Nilssonfjellet. Ruler is 20 cm.

Figure 13 – Frasnian VISS associated with standing archaeopterid flora: A-B) Narrow archaeopterid stem with steeply upturned laminae (hydrodynamic VISS). Plantekløfta Formation, Munindalen. C-D) Buckled and steeply upturned laminae on either side of small archaeopterid stem apparently with some flexibility and bent into flow. Plantekløfta Formation, Munindalen. E-F) Large archaeopterid encased in sandstone and flanked by upturned laminae (hydrodynamic VISS). Plantekløfta Formation, Munindalen. Ruler in A, B is 1 m, ruler in C, D is 20 cm, scale bar in E, F is 1 m.

Figure 14 – Hydrodynamic VISS associated with standing archaeopterids, buried by a debris flow. Plantekløfta Formation, Munindalen. A-B) Three archaeopterid stems are seen within sandstones, containing VISS that indicated they interacted with the flows that deposited the sandstones. The fossil trees have been truncated by a debris flow depositing a thick conglomerate, with prominent clusters of cobbles preferentially deposited around the tops of the decapitated tree trunks. C-J) Details of the image shown in A, demonstrating how the archaeopterids were rooted in mudrock (E-F) and persisted as sand was deposited around

them, before being truncated during the individual debris flow event. Metre stick/ 1 m scale bar in each image, except 20 cm scale bar in E, F.

Figure 15 – Frasnian VISS associated with standing lycopsid flora: A-B) Small lycopods provide armoured mantle to muddy substrate, preserved as synoptic topography of small hummocks and swales. Plantekløfta Formation, Munindalen. Visible ruler is 80 cm. C-D) Hydrodynamic VISS showing upward transition from centroclinal fill of scour to upturned laminae. Plantekløfta Formation, Planteryggen. Visible ruler is 25 cm. E-F) Buckled and upturned laminae developed on the stoss side of a buried flexible stem. Plantekløfta Formation, Planteryggen. Visible ruler is 40 cm.

Figure 16 – Hydrodynamic VISS associated with standing lycopsids in the Plantekløfta Formation at Munindalen, demonstrating how distorted bedding persists even where fossil plant material is lost. A-B) Images of the same cliff face taken 6 years apart, showing erosion of the lycopsid bearing sandstone bed by bank collapse into the Mimer River. White arrow provides reference point, yellow arrows point to standing lycopsids. White box in A shows view of standing lycopsids figured by Berry and Marshall (2015, their fig. 4L). C-H) Details of the fossil bearing bed taken in 2016 showing hydrodynamic VISS in direct association with *in situ* plants (C-F), as well as instances along the same horizon where structures are likely to be hydrodynamic VISS despite the absence of direct fossil evidence (G-H). Scale bar in A, B is 2 m, visible ruler in C is 30 cm, scale bar in E, G is 50 cm.

Figure 17 – Frequently oversteepened concavo-convex bedding within amalgamated sandstone bodies that appear too irregular, localized and individually unique to be formed by undisturbed hydrodynamic flow. These are putative VISS as they contain abundant evidence for standing vegetation or woody debris, but lack direct association with unequivocal plant triggers. A-C) Putative VISS in the Eifelian Wijde Bay Formation, Tage Nilssonfjellet:

convex-upwards mound in centre of A-B contains 10 cm carbonaceous root structures (C). Metre stick for scale. D-F) Putative VISS in the latest Givetian Tordalen Formation (Fisklekløfta Member) at Torelva, comprising thick convex-up mounds (arrowed) of steep-margined sandstone beds with frequent large plant debris (F) between beds. Mounds appear to be a result of flow diversion around woody debris, possibly in addition to decay- or compression-related deformation of the woody sediment pile. Metre stick and pen (20 cm) for scale. G-H) Putative VISS in the latest Givetian Tordalen Formation (Fisklekløfta Member) at Fiskekløfta (similar stratigraphic horizon to D-F). Continuous scour-and-mound topography persists across the same amalgamated sandbody that contains driftcretion accumulations of woody debris on the opposite side of the river (Figure 8). Scale bar is 1 m.

Figure 18 – Evidence for tree uprooting in the earliest Frasnian, revealed by fallen lycopsid crown that had toppled onto a small meander point bar (IHS-LA in Fig. 21B). Plantekløfta Formation, Munindalen. A-D) Upwards deflected lycopsid branches, encase by both mud and sand. Metre stick for scale. E-F) Details of the above, showing minimal deflection of sedimentary laminae by the small flexible lycopod branches. Visible part of ruler is 60 cm in E, scale bar is 10 cm in F.

Figure 19 – Potential variability in influence of standing vegetation physiology on fluid flow and bed shear stress, illustrated with (non-exclusive) examples of Devonian flora known from the Spitsbergen Old Red Sandstone.

Figure 20 – Development of cannel coal in Givetian strata of the Tordalen Formation (Estheriahaugen Member) at Munindalen. A) Outcrop. B) Hand specimen.

Figure 21 – Examples of IHS-LA sets throughout the Old Red Sandstone in NW Spitsbergen. A) Emsian: 5 metre-thick IHS-LA within the Wood Bay Formation. Dicksonfjorden Member, Scott Keltiefjellet. B) Frasnian: 2 metre-thick IHS-LA associated with both standing and

fallen lycopsid and archeopterid vegetation (fallen lycopsid in Figure 18 occurs at same stratigraphic level highlighted). Plantekløfta Formation, Munindalen. Scale bar in each image is 1 m.

Figure 22 – Early Devonian plant-sediment interactions in the Spitsbergen Old Red Sandstone. A) Reconstruction of the general alluvial palaeoenvironmental setting of the Red Bay Group and Wood Bay Formation. B) Detail of plant interactions in the Red Bay Group, showing colonization of braid bar tops and margins by small zosterophylls with little resistance to erosion during flood stages. C) Duration of re-establishment of geomorphic phases after flood disturbance for riparian vegetation in the Early Devonian (see Fig. 22D and Corenblit et al., 2007 for details). D) Key to Figures 22-24.

Figure 23 – Middle Devonian plant-sediment interactions in the Spitsbergen Old Red Sandstone. A) Reconstruction of the general nearshore and alluvial palaeoenvironmental setting of the Grey Hoek and Wijde Bay formations, with nearshore lacustrine/lagoonal and deltaic setting of the Tordalen Formation. B) Detail of plant interactions in the Tordalen Formation, showing delta-top driftcretion of large woody debris. C) Duration of re-establishment of geomorphic phases after flood disturbance for riparian vegetation in the Mid Devonian (see Fig. 22D and Corenblit et al., 2007 for details).

Figure 24 – Late Devonian plant-sediment interactions in the Spitsbergen Old Red Sandstone. A) Reconstruction of the general alluvial and debris flow palaeoenvironmental setting of the Plantekløfta Formation. B) Detail of plant interactions in the Plantekløfta Formation, showing trees rooted in floodplain fines, interacting with flood deposited crevasse splay sands, and uprooting of large trees on meander bends. C) Duration of re-establishment of geomorphic phases after flood disturbance for riparian vegetation in the Late Devonian (see Fig. 22D and Corenblit et al., 2007 for details).

Table 1 – Characteristics of the formations of the Old Red Sandstone in NW Spitsbergen (compiled using information from Worsley (1970); Friend and Moody-Stuart (1972); Friend et al. (1997); Blomeier et al. (2003a,b)); Bergh et al. (2011); Piepjohn & Dallman (2014); Berry & Marshall (2015); Blumenberg et al., (2018)).

Table 2 – Presently known fossil plant genera and forms from the Old Red Sandstone in NW Spitsbergen. Table compiled from Høeg (1942), Schweizer (1968, 1999) and Berry (2005), plus material identified here. Note that this table is based on provisional data: extensive collections made during this study are the subject of presently ongoing investigation at Cardiff University.

Table 3 – Distribution of plant-influenced and plant-dependent phenomena in the formations of the Old Red Sandstone in NW Spitsbergen.