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

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15 **ABSTRACT**

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

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

32 **1. Devonian Vegetation and Sedimentation**

33 Land plants are some of the most effective biogeomorphic agents on Earth today, modifying
34 physical processes and landforms by complex and diverse means that include: roots
35 increasing substrate shear strength and resistance to erosion; canopies and litter reducing the
36 efficacy of raindrop impact and surface runoff; plant- and fungal symbiont-induced
37 weathering and modification of the critical zone, soils and regolith; the provision of organic
38 matter that can change sediment properties such as cohesiveness; baffling and binding of
39 sediment to promote the accretion of landforms; or acting as obstacles to flowing air and
40 water, changing turbulence properties through friction and drag effects (e.g., Corenblit et al.,
41 2007, 2015, 2020; Phillips, 2016; Horton et al., 2017; Kleinhans et al., 2018; Larsen, 2019).
42 Trees in particular are effective ecosystem engineers, promoting landscape heterogeneity not
43 only through their physical presence, but also due to the hydrodynamic resistance of their
44 arborescent form and deeper rooting systems, their role in the hydraulic redistribution of
45 groundwater, their propensity for uprooting release of sediment and creation of microhabitats,
46 and the production of large woody debris that can modify landscapes through island
47 formation or log-jamming of streams (e.g., Harmon et al., 1986; Jones et al., 1994; Gurnell et

48 al., 2002; Gurnell, 2003; Wohl, 2013, 2017; Gurnell, 2014; Davidson et al., 2015; Kramer
49 and Wohl, 2015; Pawlik et al., 2016; Sullivan et al., 2016).

50 These contributions to the operation of continental landscapes were absent for most of the
51 planet's history, and establishing a timeline for their origin and radiation is essential for
52 understanding the mechanistic evolution of the Earth system. A consensus of hypotheses has
53 arisen that it was the Devonian Period (419-359 Ma) that was the critical interval for the
54 initiation, expansion and development of land plant controls on climate, landscape and
55 terrestrial biodiversity (e.g., Algeo and Scheckler, 1998; Davies and Gibling, 2010a,b;
56 Gibling and Davies, 2012; Corenblit et al., 2015; Morris et al., 2015; Pawlik et al., 2016,
57 2020; Boyce and Lee, 2017; Dahl and Arens, 2020). This mirrors the Devonian palaeobotanic
58 record, which shows a rapid transition from small leafless plants at the start of the period
59 (Kenrick and Strullu-Derrien, 2014), through the evolution of fully vascular plant roots, with
60 meristems, around 411 Ma (Matsunaga and Tomescu, 2016; Hetherington and Dolan, 2018),
61 the earliest wood at 407 Ma (Gerrienne et al., 2011; Strullu-Derrien et al., 2014), the earliest
62 trees at 390-388 Ma (Berry and Fairon-Demaret, 1997, 2002; Giesen and Berry, 2013), and
63 the earliest forests by 385 Ma (Stein et al., 2012, 2020).

64 The physiologies and life habits that originated at this time are all fundamental to the role of
65 plants as biogeomorphic agents in modern landscapes, yet there is little reported direct
66 evidence for Devonian plant-sediment interactions. In this paper we rectify this omission
67 with examples from the late Silurian- to Devonian-aged "Old Red Sandstone" strata that crop
68 out across northwest Spitsbergen, in the Svalbard archipelago of Arctic Norway (Figs. 1 and
69 2). Here we: 1) introduce the constituent stratigraphic units of the Spitsbergen ORS; 2)
70 describe and illustrate a catalogue of features that provide tangible geological evidence for
71 plant-sediment interactions; and 3) demonstrate how the local stratigraphic distribution of
72 these features reflects the global onset and development of plant-related biogeomorphic

73 processes. The Spitsbergen ORS is shown to be an archetypal case study that yields insights
74 into the ‘Devonian landscape factory’: a key interval of Earth history when plants first came
75 online as biogeomorphic agents, influenced terrestrial surface processes in ways analogous to
76 modern flora, and sculpted still-familiar landforms, landscapes and habitats.

77 **2. The ‘Old Red Sandstone’ of NW Spitsbergen**

78 The ‘Old Red Sandstone’ (ORS) is an informal term used for successions of dominantly
79 terrigenous strata that crop out around the north Atlantic region, and whose deposition was
80 contemporaneous with mid-late Palaeozoic orogenic events in Laurussia (e.g., Friend et al.,
81 2000; Kendall, 2017). The Spitsbergen ORS is one of a number of near-contemporaneous
82 Silurian-Devonian successions of non-marine-dominated sedimentary strata across
83 Scandinavia and Greenland (e.g., Marshall and Stephenson, 1997; Anderson and Cross, 2001;
84 Davies et al., 2005a,b; Astin et al., 2010), and has been the subject of intermittent but
85 significant geological investigations for over 120 years (e.g., Nordenskiöld, 1892; Høeg, 1914).
86 It was an instrumental case study in the development of non-marine sedimentary
87 facies models that later found global application (e.g., Friend, 1965; Moody Stuart, 1966),
88 and has proved to be particularly rich in fossil plant material. The earliest geological
89 expeditions to the region collected abundant and well-preserved megafossils (see summaries
90 in Høeg 1942; Schweitzer, 1999; Berry 2005), the palynological record of the succession has
91 been studied for over half a century (Vigran 1964; Allen 1965, 1967), and, more recently,
92 fossil forests of lycopsids and archaeopterids have been discovered in the youngest units of
93 the succession (Dallman et al., 2004; Berry and Marshall, 2015). The succession is
94 exceptionally well-suited for tracking the onset of plant-sediment interactions not only
95 because of its fossil content, but also because it provides a well-exposed and near continuous
96 record of non-marine and coastal sedimentation between the latest Silurian and early Frasnian
97 (early Late Devonian).

98 **2.1. Geological Setting**

99 Formally, the Spitsbergen ORS consists of three groups: the upper Silurian Siktefjellet
100 Group, the Lower Devonian Red Bay Group, and the Lower to Upper Devonian Andréland
101 Group (Wood Bay, Grey Hoek, Wijde Bay formations and Mimerdalen Subgroup) (Figure 2;
102 Friend, 1961; Murašov and Mokin, 1979; Harland, 1997; Piepjohn and Dallman, 2014). The
103 succession was deposited during the development of the Ellesmerian Orogeny to the west
104 (McCann 2000), and the groups are bounded by unconformities resulting from drainage
105 reorganization during intervals of renewed strike-slip faulting (Beranek et al., 2020). As a
106 result, there is some discordance between their tectonic dips, and the younger units can
107 contain reworked clasts from the older strata (Friend, 1961; McCann, 2000; Piepjohn, 2000).
108 Regional variations in syn- and post-depositional uplift have meant that the oldest preserved
109 deposits (Silurian and Lochkovian) are restricted to small extensional basins in the north, the
110 youngest deposits (Frasnian) are restricted to fragments of foreland basin fill in the south, and
111 there is also north-south palaeoenvironmental and age variation in Middle Devonian strata
112 (Figs. 1 and 2) (Friend, 1961; Manby and Lyberis, 1992; Piepjohn, 2000; McCann, 2000;
113 Piepjohn and Dallman, 2014; Beranek et al., 2020). The Old Red Sandstone across the region
114 is capped by a regional unconformity, associated with uplift during the Late Devonian
115 Svalbardian event (Manby and Lyberis, 1992; Piepjohn, 2000; McCann, 2000; Bergh et al.,
116 2011; Piepjohn and Dallman, 2014; Beranek et al., 2020).

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

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

125 **2.2. Constituent Units**

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

131 *2.2.1. Silurian (Siktefjellet Group)*

132 The Siktefjellet Group is the least well-understood unit of the Spitsbergen ORS: it crops out
133 only the far northwest of the region (Gjelsvik and Ilyes, 1991) and exposure is poor due to
134 internal faulting (with shales acting as shear planes), scree coverage and frost-weathering,
135 which renders confident architectural analysis of the strata impossible (Figure 3A). Further,
136 although the unit has previously been interpreted as recording braided fluvial, and possible
137 lacustrine, deposition (Friend et al., 1997), the strata contain few unambiguous indicators of
138 depositional environment and a marine influence cannot be ruled out (Gjelsvik and Ilyes,
139 1991). At Siktefjellet they consist of fine- to medium-grained light grey sandstones and dark
140 grey shales, and the only sedimentary structures observed in this investigation were climbing
141 ripple lamination and two indistinct horizontal burrow traces. The succession has been
142 reported to contain plant macrofossils (Murašov and Mokin, 1979), but only comminuted
143 carbonaceous debris was witnessed in this study. Analyses undertaken for this study reveal
144 the palynological assemblages are very poorly preserved and much more thermally mature
145 than elsewhere in the Spitsbergen ORS. The assemblages are dominated by phytodebris
146 (cuticles, tubes, etc.) and the few spores are present are mostly indeterminable, except for rare

147 cryptospore tetrads. In addition no marine chitinozoans or acritarchs are present, and the unit
148 yields no other reliable age indicators. Despite this a Silurian age is most likely based on the
149 general palynological motif, and because the Siktefjellet Group lies tilted and unconformable
150 below the base of the Red Bay Group (Friend et al., 1997).

151 2.2.2. Lower Devonian (Red Bay Group and Wood Bay Formation)

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

155 The Red Bay Group is an overall-fining upwards succession. The conglomerate-dominated
156 lower half of the group consists of the Wulffberget Formation, syn-tectonic alluvial fan
157 deposits that rest directly on basement marble (Fig. 3B), followed by a poorly exposed shale
158 unit (Rabotdalen Formation), and then further alluvial fan deposits (Prinsesse Alicefjellet
159 Formation) (Murašov and Mokin, 1979; Harland, 1997; Friend et al., 1997; McCann, 2000).

160 These coarse-grained facies lack plant macrofossils and are dominated by physical
161 sedimentary structures of high-energy debris-flow and stream-flow, rendering them
162 unsuitable for assessing early Lochkovian plant-sediment interactions. The upper Red Bay
163 Group comprises three finer-grained units. 1) The Andréebreen Formation comprises grey-
164 green fine- to medium-grained sandstones with subordinate interbedded dark grey shales and
165 pebble-lag conglomerates. The unit yielded newly discovered macrofossils of small shrubby
166 plants (cf. *Zosterophyllum*) during this study (Fig. 4). Observed downstream accretion
167 elements (Miall, 1985), allied with reworked calcretes and *in situ* plant material, supports
168 previous explanations of the strata as braided river alluvium (Friend et al., 1997). 2) The
169 Fränkelryggen Formation comprises archetypal ORS alluvial facies (Fig. 3C): predominant
170 red bed mudrocks (overbank deposits) with recurrent fine sandstone horizons (in-channel

171 deposits). It has previously yielded abundant small plant macrofossils, in addition to
172 enigmatic (*Pachythecca*) and possible fungal (*Prototaxites*) fossils (Høeg, 1942; Schweitzer,
173 1999). 3) The topmost unit of the Red Bay Group, the Ben Nevis Formation, marks a return
174 to grey-green strata, dominated by fine- to coarse-grained cross-bedded sandstones of
175 probable braided fluvial origin (Fig. 3D) (Friend et al., 1997). It is not known to contain any
176 plant fossils.

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

192 2.2.3. Middle Devonian (*Grey Hoek, Wijde Bay and Tordalen formations*)

193 Middle Devonian strata exhibit pronounced regional variability in northwest Spitsbergen.

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

211 In contrast to the north, Middle Devonian strata in the south of the region comprise only the
212 late Givetian-aged Tordalen Formation (lower Mimerdalen Subgroup), resting
213 unconformably on the Dicksonfjorden Member of the erosionally-truncated Wood Bay
214 Formation. Palynological samples from the Tordalen Formation are dominated by
215 *Geminospora* and *Cymbosporites*, showing that its deposition was not contemporaneous with
216 the Wijde Bay Formation, as has been previously reported (Piepjohn & Dallmann, 2014).
217 Additionally, it has a distinct lithological signature: 1) the lower Estheriahaugen Member:
218 thinly- (5 cm-thick) bedded grey-green sandstones and shales, with common siderite nodules,

219 occasional ostracod fossils, and thin coal (Vogt, 1941; Harland et al., 1976; Piepjohn &
220 Dallmann, 2014; Blumenberg et al., 2018); and 2) the slightly finer-grained upper Fiskekløfta
221 Member (Fig. 3J), named for its extremely abundant fossil fish fauna, and comprising darker
222 grey mudstones and sandstones that are capped with a distinct 50 metre-thick marker horizon
223 of white-coloured quartz-rich medium-grained sandstones (informally termed the “Lower
224 Svalbardia Sandstone”) (Piepjohn & Dallmann, 2014). The strata have been interpreted as
225 freshwater-brackish lagoonal facies, with sand input from marginal deltas and washovers
226 (e.g., Friend, 1961; Newman et al., 2020).

227 2.2.4. Upper Devonian (*Planteryggen* and *Plantekløfta* formations)

228 Two early Frasnian-aged units comprise the remainder of the Mimerdalen Subgroup – the
229 lower Planteryggen Formation and upper Plantekløfta Formation. The definition of the
230 Planteryggen Formation has recently been adjusted (the “Lower Svalbardia Sandstone”
231 having been moved into the upper Tordalen Formation: Piepjohn and Dallman, 2014), and
232 now comprises only poorly-exposed sandstones and conglomerates. The overlying
233 Plantekløfta Formation has better exposure, on ridges and along actively-eroding banks of the
234 Mimer River (Figs. 3K-L). The Plantekløfta Formation comprises heterolithic dark grey
235 overbank mudrocks and yellow-grey fluvial sandstones, with prominent and laterally
236 continuous horizons of poorly-sorted, clast- and matrix-supported debris flow conglomerates.
237 The unit also contains abundant standing lycopsid and archaeopterid tree fossils, in addition
238 to the remains of non-woody shrubs (Berry, 2005; Berry and Marshall, 2015). Notably, we
239 now recognise that the Plantekløfta Formation contains the distinctive sandy layer of
240 green/yellow sandstone which contains the rich ‘Planteryggen’ or ‘Upper Svalbardia
241 Sandstone’ flora (Høeg, 1942; Berry and Fairon-Demaret, 2000), previously thought to
242 belong to the Planteryggen Formation (e.g. Piepjohn and Dallmann, 2014). The overall
243 succession records deposition by small fluvial channels with forested floodplains, punctuated

244 by deposition from catastrophic debris flow events that were sourced from locally-uplifted
245 highlands to the east, at the onset of the Svalbardian Event (Piepjohn and Dallman, 2014;
246 Berry and Marshall, 2015).

247 **3. Plant-sediment interactions in the Old Red Sandstone**

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

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

265 **3.1. Fossilized Plant Debris**

266 The simplest evidence for direct interplay between vegetation and surface processes occurs
267 where plant debris is preserved within a sediment pile, either having been transported for a

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

287 Comminuted debris –

288

289

290

291

292 *3.1.1. Comminuted debris*

293 Comminuted debris includes dark grey or black flecks of carbonaceous material, >1 mm to
294 >5 mm across, that most often cannot be taxonomically identified. Such debris records
295 physical degradation of plant matter, either where plant tissues are not mechanically resistant,
296 or where the intensity and duration of physical attrition is high. Comminuted debris occurs in
297 patchy accumulations, indicating that the debris underwent sorting during transport and
298 deposition (e.g., Spicer and Wolfe, 1987). The earliest instances of comminuted debris in the
299 Spitsbergen ORS occur within the Silurian Siktefjellet Group and examples are present in
300 every subsequent unit.

301

302 3.1.2. *Fragmentary remains*

303 Recognisable stems, axes, branches, and appendages of non-woody plants of shrub-like and
304 herb-like habit occur throughout the Spitsbergen ORS in Lochkovian and younger strata
305 (earliest examples from the Andréebreen Formation of the Red Bay Group). Accumulations
306 of such delicate material imply reduced attrition, either due to less intense fluid energy,
307 limited transport distance (i.e., near *in situ* burial), and/or mechanically-resilient plant tissues.
308 Examples from Lower and Middle Devonian strata illustrate how small stature plants
309 interacted with their physical environments. Figure 4 illustrates the sedimentary architecture
310 and lithologies of the Andréebreen Formation (Lochkovian, Red Bay Group), which hosts the
311 oldest identifiable plant debris recognised in this study. The succession is dominated by
312 sandstones, packaged as downstream accretion sets up to 1.5 metres thick, and punctuated
313 with fissile grey shales (Fig. 4A-E). Shallow braided stream bars, capped with shale during
314 intervals of channel switching, provide a reasonable palaeoenvironmental explanation for
315 these sedimentary signatures (e.g., see also Friend et al., 1997). While the sandstones in these
316 successions are barren of fossil plant material, the shales host branching specimens of cf.

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

341 coastal waters at this time had a mixed sediment load of both siliciclastic and plant-derived
342 organic sediment.

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

349 3.1.3. *Woody Debris*

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

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

363 3.1.3.1. Individual woody debris clasts

364 The oldest instances of woody debris in the succession occur as patches or isolated clasts of
365 randomly oriented material, hosted within very fine-grained coastal channel sandstone facies
366 of the Eifelian Grey Hoek Formation (Fig. 7A) (Høeg, 1942) and Wijde Bay Formation (Fig.
367 7B) (Schweitzer, 1968). Taxonomic identification of the plant material is not possible (it is
368 associated with *Protocephalopteris* branches), but it has a sulcate ornamentation and appears
369 frayed at the margins. At the time of deposition, the debris likely comprised clusters of
370 individual xylem strands with a stringy structure, rather than robust wood particles. Larger
371 and more robust woody particles are known from the south of the outcrop area, and are
372 particularly prominent within the Givetian ‘Lower Svalbardia Sandstone’ (uppermost
373 Tordalen Formation). Here, individual clasts of woody debris occur up to 2 metres in length,
374 that are dominated by flattened trunks of probable archaeopterid trees (plus minor lycopsid
375 material) (Fig. 7C). These examples, dating in time from close to Earth’s earliest known tree
376 fossils (Berry and Fairon-Demaret, 1997, 2002; Giesen and Berry, 2013), provide evidence
377 for the origination of wood as a sedimentary particle. Woody debris has subsequently
378 persisted as a component of many sedimentary environments throughout the remainder of
379 Earth history (e.g., Davies and Gibling, 2013; Wohl, 2013, 2017; Gulbranson et al., 2020;
380 Trümper et al., 2020).

381 3.1.3.2. Accumulations of woody debris

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

387 In contrast, accumulations are conspicuous in a 5 metre-thick section of the upper Tordalen
388 Formation (Fig. 8D-F), where 11 successive dense woody debris horizons cap 20-80 cm-
389 thick fine-grained sandstone bodies. The Tordalen accumulations have superficial
390 resemblance to logjam deposits, the earliest known of which presently date from the
391 Carboniferous (Gastaldo and Degges, 2007; Gibling et al., 2010). However, detailed analysis
392 of the fabric of the Tordalen accumulations does not support a logjam origin, because: 1) they
393 are strongly oriented in one direction (c. 020-200°), with little variance (Fig. 8); 2) they occur
394 in medium-grained sandstone that lacks the intraformational or extraformational clasts that
395 would be caught in a logjam; 3) they occur in 11 successive sandstone layers over a vertical
396 distance of 5 metres, with no evidence for any avulsive impact of the wood accumulations;)
397 when seen in association with sandstone mounds, they are oriented parallel with the mound
398 crests (Fig. 8F); 5) they occur on bedding planes with evidence for post-depositional stasis
399 (*Diplichnites* arthropod trackways and aeolian adhesion marks between individual logs (Fig.
400 8F)), rather than instantaneous hydrodynamic re-organisation; and 6) they are thin
401 accumulations that mantle sands, rather than intermingle with them: the logs have a mean
402 width of 50 mm, approximating to original diameter (see Gibling et al., 2010), and a mean
403 individual thickness of 3 mm. As each woody debris mantle is approximately 3 cm thick, this
404 gives a compaction value for the wood of 16.6, and suggests that each original wood
405 accumulation was only c. 50 cm in thickness. Taken together, these characteristics of the
406 Tordalen accumulations suggest that, rather than active logjams, they likely record
407 driftcretions (Kramer and Wohl, 2015): persistent accumulations of driftwood that form
408 where fluvial driftwood export to a shoreline is high, and woody debris accumulates in stable
409 mats or berms . Explaining the Tordalen accumulations as early driftcretions fits with the
410 interpretation of the Lower Svalbardia Sandstone as delta-top sands, infilling the

411 lacustrine/lagoonal setting recorded by the finely-bedded sands of the Fiskekløfta Member
412 (Friend, 1961; Newman et al., 2020).

413 3.1.4. Plants preserved in growth position

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

421 3.2. Rooting Traces

422 The earliest root fossils worldwide are known from the Pragian (Matsunaga and Tomescu,
423 2016; Hetherington and Dolan, 2018), but structures that have been interpreted to record the
424 sediment-filling of plant root structures occur in slightly older, Lochkovian, strata (Hillier et
425 al., 2008). Such structures consist of traces of sediment that share morphological attributes
426 with plant roots, and dissimilarities with animal burrows; for example: decreases in diameter
427 after branching, irregular and sinuous forms, downwards-branching, horizontal and vertical
428 components and colloidal clay linings (Hillier et al., 2008). Preserved organic root material is
429 absent from the Spitsbergen ORS until the Frasnian Plantekløfta Formation. However,
430 sedimentary traces of putative root structures are known from the Lower Devonian onwards,
431 in the form of casts, moulds and elongate drab haloes that may branch downwards (Figure 9).

432 The Andréebreen Formation of the Red Bay Group yields what may be the oldest root
433 structure in the Spitsbergen ORS (Fig. 9A). A root interpretation for this particular structure
434 is not unequivocal, and it could also be explained as an instance of an invertebrate burrow

435 (such structures also appearing in alluvial settings for the first time in the early Lochkovian:
436 e.g., Minter et al., 2016; Shillito and Davies, 2017). However, favouring the former over the
437 latter is the slight irregularity to its form, coupled with its context: it descends from the base
438 of the same bar top shales that yield parautochthonous cf. *Zosterophyllum* (discussed above
439 and illustrated in Fig. 4).

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

455 Rooting structures are less common in Middle Devonian strata, possibly due to the
456 environmental bias imparted by the persistent marine influence. However, putative
457 sedimentological evidence for rooting structures is present: in both the Grey Hoek and Wijde
458 Bay formations, there occur downwards-tapering structures which exhibit diameter-decreases
459 after branching (to 10 cm in vertical length) (Fig. 9 C-D). The structures are clearly

460 differentiated from the regular form of invertebrate trace fossils in the same successions (e.g.,
461 U-shaped and dumbbell-shaped burrows) and were passively infilled with dark, organic-rich
462 mud. Significantly, they occur in strata that yield marine ostracod and bivalve faunas.

463 Other rooting sedimentary structures in the Spitsbergen ORS date from the Mid-Late
464 Devonian transition (Figure 9E). The stratigraphic position of these strata is uncertain, but
465 they post-date large woody-debris deposits (Fig. 8) and occur in either the uppermost
466 Tordalen Formation or lowermost Planteryggen Formation. The structures comprise
467 successive palaeosols, densely patterned with vertical drab reduction haloes that extend up to
468 2 metres in vertical length and imply dense and mature vegetation had developed within those
469 parts of the sedimentary environment that were experiencing stasis. The rooted beds are
470 punctuated by c. 1 metre-thick erosively-based sandstones, recording intermittent reworking
471 of the densely vegetated floodplains.

472 **3.3. Vegetation-Induced Sedimentary Structures**

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

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

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

493 3.3.1. *Lower and Middle Devonian VISS*

494 Figure 11 shows an instance of what are likely the earliest VISS in the Spitsbergen ORS,
495 occurring at the contact between the top of a red mudrock bed and the base of a crevasse
496 splay sandstone in the Emsian Dicksonfjorden Member of the Wood Bay Formation. The
497 contact may record a synoptic topography, i.e. a true representation of the geomorphic form
498 of the depositional substrate (see Paola et al., 2018; Davies et al., 2019), because 1) the
499 massive sandstone passively drapes the mudrock bed; 2) the upper 5 cm of the oxidized
500 mudrock shows a mantle of drab mottling, which may be suggestive of reduction by
501 shallowly-penetrating roots; and 3) individual elongated drab haloes extend and branch up to
502 a metre downward from the apices of the gentle mounds: although their discontinuity
503 hampers confident recognition, these resemble similar-aged root traces of deeply-anchored
504 small-stature plants (Xue et al., 2016). These characteristics imply that deeper rooted plants
505 were individually centred within gentle mounds on the ancient floodplain. On modern
506 floodplains, large-scale mounds can develop because of the preferential accumulation of plant
507 matter and sediment around standing plants (e.g., Scheihing and Pfefferkorn, 1984; Small,

508 1997; Sullivan et al., 2016). Similar sediment interactions should also be expected to have
509 been associated with small stature Early Devonian plants, whose primitive physiological
510 constructions were already adept at baffling fine sediment (Mitchell et al., 2016). In this
511 instance, the potentially original undulatory floodplain topography, induced by early
512 herbaceous plants, has been preserved because it was cast by overbank flooding splays,
513 which lose capacity to erode and rework synoptic topography as they wane away from their
514 source (e.g., see Davies and Shillito, 2018).

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

527 3.3.2. *Upper Devonian VISS*

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

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

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

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

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

566 3.3.3. *VISS in different lithologies*

567 Almost all of the VISS observed in this study occur within sandstones: a natural bias arising
568 from the greater readability of hydrodynamic bedforms in that lithology in the field (an
569 exception being the mound-shaped mudrock seat-earth topography seen in Figures 11 and
570 15A). However, Figure 14 shows how vegetation has also influenced the sedimentary
571 architecture and fabric of conglomerates in the Plantekløfta Formation. The figure shows a
572 stand of small archaeopterid trees, rooted into a poorly-drained dark mudrock seat-earth (Fig.
573 14E-F: note that the roots here are fossilized, rather than being sedimentary traces). The stand
574 occupied a topographic depression (channel margin?), that was entombed in fine-grained
575 sandstone during recurrent flow events that left a record of multiple instances of
576 hydrodynamic VISS (Fig. 14B). The sandstone was subsequently capped by at least two
577 metres of conglomerate, deposited instantaneously as a poorly-sorted and partially clast-
578 supported debris flow. The truncation of sandstone laminae (e.g., Fig. 14G-H) shows that the
579 emplacement of the debris flow deposit was associated with reworking of the underlying

580 substrate. However, whilst the archaeopterid trunks have also been truncated, their bases
581 nonetheless protrude upwards into the debris flow, where they are seen to have acted as
582 obstacle that forced the deposition of clusters of larger cobbles (e.g., Fig. 14B, D, H). This
583 shows that the presence of the trees acted to retard the erosive capacity of the debris flow
584 event: if they had not been present, scouring would have removed more sandstone than is
585 now preserved. This instance demonstrates how VISS may present as constructed boundaries
586 (*sensu* Paola et al., 2018), internal to a sediment pile, in addition to their more common
587 appearance as engineered synoptic topographies (e.g, hydrodynamic forms).

588 3.3.4. *VISS without preserved vegetation*

589 VISS are unequivocal when seen in direct association with standing trees, but may be
590 underdetermined when trigger fossils are not exposed at outcrop. Figure 16 shows an
591 example of how instances of scour-and-mound beds can reflect vegetation-sediment
592 interaction, even where fossil plants are missing. Figure 16A-B shows an exposure of
593 outcrop of the Plantekløfta Formation on the banks of the Mimer River, in photographs taken
594 six years apart. In both images, the scour-and-mound topography is apparent, but individual
595 standing trees have variably become exposed or eroded as the river has cut back into the cliff
596 face. In this instance, the preserved VISS can rarely be attributed to particular obstacles (Figs.
597 16C-H), but subsequent exposure indicates bed architecture to be related to buried vegetation.
598 Modern analogue confirms that it is appropriate to search for putative VISS beyond the area
599 immediately adjacent to a standing plant fossil: substrates can develop irregular topography
600 when flow structures are inherited from upstream conditions or cross-stream circulation
601 induced by tree or woody debris obstacles (Reesink et al., 2020).

602 Middle and Upper Devonian strata of the Spitsbergen ORS contain many examples where
603 VISS may be interpreted, but not proven by current exposure (Figure 17). In these instances,

604 features such as concave- and convex-upwards bedding, often at high angles, are seen in
605 association with circumstantial evidence for standing vegetation, such as rooting traces (Fig.
606 17A-C) or parautochthonous woody debris (Fig. 17D-F), or have a proximity to sites with
607 abundant evidence for trees (e.g., the site shown in Fig. 17G is the same horizon of the Lower
608 Svalbardia Sandstone that hosts the woody debris layers shown in Fig. 8D-F).

609 According to Rygel et al. (2004), the term “VISS” excludes sedimentary structures induced
610 by fallen or transported woody debris. However, driftwood can also act as an obstacle that
611 induces sediment deposition, erosion and mounding (Nakayama et al. 2002; Reesink et al.,
612 2020) and Trümper et al. (2020) have recently documented multiple ‘VISS-like’ forms
613 associated with flow deflection by accumulations of large woody debris in ancient strata
614 (“LWDISS”). In instances where there is no preservation of plant material, but strata contain
615 VISS-like structures (Figure 17), it may be impossible to tell whether they are VISS *sensu*
616 *stricto*, whilst being confident that bedform irregularities were induced by plants, either *in*
617 *situ* or transported: it is thus practical to expand the original definition of VISS to capture
618 such instances. It is here proposed that reasonable confidence in a VISS interpretation for any
619 bedforms may be achieved where they exhibit several of the following characteristics: 1) they
620 exhibit sediment structures that are not readily explainable by models of aggradation under
621 undisturbed hydrodynamic flows; 2) they are known to be a product of unequivocal VISS
622 elsewhere; 3) they occur in a succession known to host unequivocal VISS or standing fossil
623 trees; and 4) they host fossil debris, or rooting traces, that indicates the former presence of
624 standing vegetation. The forms in Figure 17 exhibit all of these characteristics, and provide
625 extra circumstantial evidence that arborescent land plants were obstructing flows, and
626 sculpting landforms by forcing erosion and deposition from at least the Givetian onwards.

627 There are numerically more instances of ‘likely VISS’ (lacking fossils) than ‘definitive VISS’
628 (with fossils) in the Spitsbergen ORS, but this is not unexpected, because VISS have fewer

629 taphonomic hurdles to overcome than organic plant remains. The majority of plant biomass
630 has always been fated to be reused by living biota through biogeochemical cycles (Gastaldo
631 and Demko 2011), whereas, although sediment piles accrued around vegetation may diminish
632 in thickness over decades as plants decay, VISS forms can persist (Small, 1997). Better
633 recognition of these forms may improve our understanding of the extent to which trees have
634 sculpted sedimentary landforms that are preserved in the rock record.

635 3.3.5. *Vegetation without preserved VISS*

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

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

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

663 3.3.6. *Characteristics of Devonian VISS*

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

670 The early examples of VISS observed here are generally less diverse than the forms
671 originally described by Rygel et al. (2004), but this may in part be explained by the larger
672 dimensions of many of the Carboniferous trees in the original description. In such instances,
673 wake flow is the most significant driver of VISS creation (e.g., Allen, 1982; Rygel et al.,
674 2004), arising where approaching flow is deflected downwards upon meeting a pillar-like
675 obstacle, inducing 1) an erosional horseshoe vortex; and 2) a reduced wake zone flow in the
676 lee of the obstacle. The smaller stature of the Devonian trees may explain why hydrodynamic
677 erosional forms (e.g., centroclinal cross-strata) are rarer than depositional forms (e.g.,

678 upturned laminae) in the Spitsbergen ORS, because large trees promote scour holes more so
679 than smaller vegetation (which may be more effective at promoting leewise deposition) (e.g.,
680 Nakayama et al. 2002; Schlömer et al., 2020). Height differences may also explain the
681 observed phenomenon whereby vegetation shadows are apparently smaller for archaeopterids
682 than they are for lycopsids (e.g., compare Figs. 13 and 15) as obstacle marks become larger
683 during shallower flows relative to the obstacle height (Schlömer et al., 2020).

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

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

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

705 **3.4. Cannel Coal**

706 Cannel coal is a prominent, but volumetrically-minor, lithology that occurs in four seams
707 (maximum 80 cm thickness) within the Estheriahaugen Member of the Tordalen Formation
708 (Figure 20). The cannel coals have previously been described in detail elsewhere (e.g., Vogt,
709 1941; Harland et al., 1976; Blumenberg et al., 2018; Marshall et al., 2019). They are
710 composed of lipid rich organic matter derived from *Archaeopteris* and lycopod spores
711 (Marshall et al., 2019), which accumulated in lacustrine settings (Blumenberg et al., 2018),
712 rather than in situ coal swamps. Although not considered further here, they are significant for
713 proving that vegetation-dependent lithologies (Davies et al., 2020) were being deposited by
714 the Givetian.

715 **3.5. Vegetation-Influenced Facies**

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

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

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

747 **4. Role of Climate and Tectonics**

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

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

759

760 **4.1. Climate**

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

774 The tropical setting also likely played a role in the delivery of woody debris in Middle and
775 Upper Devonian strata. In the modern tropics, most forest floor wood decays within < 10

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

785 **4.2. Tectonics**

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

796 The preservation of standing trees in sedimentary successions (e.g., as seen in the
797 Plantekløfta Formation: Figs. 13-18) has previously been interpreted as requiring exceptional
798 intervals of rapid subsidence or relative sea-level rise (e.g., Bailey, 2011). This is based upon
799 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

825 (Corenblit et al., 2007; 2015; 2020). This conceptual model was originally developed to
826 explain successional effects after modern flood disturbances in alluvial settings (Corenblit et
827 al., 2007), and has previously been discussed with respect to Carboniferous plant evolution.
828 The discoveries in this present study indicate that aspects of biogeomorphic succession had
829 developed by the Devonian, earlier than previously reported (e.g., Davies and Gibling, 2013;
830 Gibling et al., 2014; Corenblit et al., 2015). Present-day biogeomorphic succession begins
831 with pioneer seedlings on fresh post-flood substrates, incrementally inducing feedbacks (e.g.,
832 enhanced sedimentation) such that eventually biological geomorphic processes dominate
833 (e.g., years later there may be raised islands with successional forests) (Corenblit et al.,
834 2020). Such well-established modern biogeomorphic systems can experience feedback from
835 vegetation influence that extends over thousands of years. Here we summarise how such
836 feedback was instigated in some of the earliest vascular plant communities, as evolutionary
837 innovation increased the repertoire of plant-biogeomorphic processes and produced novel
838 landforms and habitats.

839 **5.1. Silurian and Early Devonian**

840 Silurian strata of the Siktefjellet Group contain only comminuted carbonaceous material,
841 showing that small stature land plants were in existence, but had limited direct geomorphic
842 influence. There is no evidence in the unit that land plants were influencing sedimentation to
843 an extent that readable signatures were preserved, except for an elevated mudrock content.
844 Mud could be produced and trapped by even primitive flora, and is common in post-
845 Ordovician alluvium (McMahon and Davies, 2018b; Mitchell et al., 2019; Zeichner et al.,
846 2021): globally, some of the earliest vegetation-influenced effects may have been enacted
847 vicariously through this cohesive sediment (Davies et al., 2020). However, as individuals, the
848 flora in the depositional environment apparently responded analogously to small stature
849 vegetation in modern ephemeral stream bed settings: suffering mortality and entrainment

850 when exposed to only minor hydrodynamic stress (Sandercock and Hooke, 2010; Edwards et
851 al., 2015). Analogous flora are seen in modern post-flood settings during the ‘geomorphic’
852 stage of biogeomorphic succession (Corenblit et al., 2007; 2015; 2020): small diaspores and
853 propagules that colonize fresh substrates, but which will be totally destroyed if the same
854 patch of substrate experiences further disturbance before the plants take hold. In modern
855 settings, the geomorphic phase persists for a few hours to a few months following a flood, but
856 it would have effectively persisted indefinitely during the Silurian, when the maximum
857 attainable plant stature offered negligible resistance to flow, and colonization of active
858 sedimentary environments would have been opportunistic and reliant on intervals or spatial
859 patches of hydrodynamic quiescence.

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

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

878 In modern settings, complexity of river form induces a complexity of hydromorphology and
879 thus of biodiversity (Garcia et al., 2012), so the incremental shift towards physical
880 stabilization and landform modification induced by even small stature Early Devonian plants
881 can be seen as a key component of the terrestrialization process. This heterogeneity continued
882 to develop throughout the remainder of the Early Devonian: for example, the Pragian-Emsian
883 Wood Bay Formation contains not only some of the oldest palaeosols in the Spitsbergen ORS
884 (e.g. Fig. 10), but also some of the oldest known palaeosol ichnofauna in the world
885 (Morrissey et al., 2012; Genise et al., 2016). The Wood Bay Formation also yields further
886 evidence that bar tops were now semi-stable vegetated patches within riparian environments,
887 and direct evidence for pioneer vegetation in overbank settings. Figure 10 shows rooting in
888 instantaneously-deposited climbing-ripple-laminated crevasse splay sands that could be
889 analogous to post-flood colonization in modern rivers: where plants either reproduce
890 asexually when propagules are snapped off and transported with flood sediment, or because
891 they preferentially release spores or seeds at the end of the annual flooding season (Gurnell,
892 2014). In any instance, the plants certainly promoted fine sediment, shown by clay-lined roots
893 (Fig. 10B), and the accrual of multi-year palaeosols in the floodplain fines that accrued in
894 between crevasse events (Fig. 10). The influence of rooted vegetation in overbank fines is
895 further emphasised by the earliest putative VISS, seen towards the end of the Early
896 Devonian: the development of incipient hummocks at the bases of herbaceous plants,
897 composed of baffled sediment and (presumably) organic matter (Fig. 11). Such landforms
898 appear negligible in size, but the increasing three-dimensionalization of terrestrial substrates
899 would have led to a cascade of ecological effects. Mounded topographies can alter patterns of

900 groundwater flow, bidirectional exchange with surface water, and evaporation; all of which
901 may redistribute and partition nutrients or amenable conditions for habitation (e.g.,
902 temperature or oxygen) (e.g., Poole et al., 2008; Sullivan et al., 2016). Similar impacts would
903 have been inevitable after the Early Devonian first appearance of vegetation mounds as they
904 would have had profound influences on evolution and terrestrial habitats, despite the fact that
905 tangible evidence of such processes may be lacking or unreadable.

906 **5.2. Mid and Late Devonian**

907 While the Middle Devonian interval witnessed major palaeobotanical innovations, the record
908 of biogeomorphic innovation in the Spitsbergen ORS is partly masked by an increased
909 marine influence and transgressive shift towards coastal environments. Despite this, there is
910 evidence that the sedimentary environments of all the Middle Devonian units were colonized
911 by plants. The Eifelian Grey Hoek and Wijde Bay formations contain circumstantial evidence
912 that habitats analogous to modern salt marshes may have developed in the Devonian, in the
913 form of root structures hosted within dark organic-rich sediments that yield a marine fauna
914 (Figure 9D-E). Salt marshes are some of the most biogeomorphologically-active
915 environments at the present day (e.g., Mudd et al., 2010), but there are very few
916 interpretations of such environments from the rock record. Putative Silurian instances have
917 been interpreted from waterlogged palaeosols with marine fossils (Retallack, 2008), but these
918 lack direct evidence for plants and remain speculative. The earliest unequivocal salt marshes
919 currently known from the rock record are Cretaceous in age, and are identified by dark
920 coloured mudrocks, with a high total organic carbon content, compacted halophyte leaf litter
921 fossils, rootlets and marine microfossils (Uličný and Špičáková, 1997). In this instance, the
922 key diagnostic criterion is the presence of fossil material from extant salt marsh halophytes.
923 However, as almost all extant salt marsh plants are angiosperms, such a criterion cannot be
924 employed in the search for potential Palaeozoic salt marshes, where a different flora must

925 have been involved if such systems existed. The Grey Hoek and Wijde Bay examples
926 provide evidence that small stature rooted vegetation was located in low gradient marginal
927 marine settings that were traversed by channels (e.g., Fig. 6), and they do post-date the
928 evolution of halophily (evidenced by the hot spring flora of the Early Devonian Rhynie
929 Chert; Channing and Edwards, 2009). However, whether the rooted horizons record true salt
930 marshes, inundated on a tidal rhythm by the sea, remains inconclusive from the available
931 sedimentological and palaeontological evidence.

932 Although lacking the diversity of landforms that might be expected in purely alluvial facies,
933 the coastal, lacustrine and deltaic facies of the Middle Devonian ORS do show that potential
934 stages of biogeomorphic succession had expanded by at least the late Eifelian (Figure 23).
935 Post-disturbance plant communities would develop through the geomorphic and pioneer
936 stages over the course of hours to months, but would then progress into the biogeomorphic
937 phase. The biogeomorphic phase is characterized by landforms that are colonized by
938 secondary successions of established vegetation, which can promote active accretion of those
939 landforms: in other words, there is a balanced feedback between abiotic and biotic controls
940 on local geomorphology. Evidence for this phase can be seen in the definitive (e.g., Fig. 12)
941 and putative (e.g. Fig. 17) VISS in the Wijde Bay and Tordalen Formations. The driftcretions
942 in the Lower Svalbardia Sandstone (Fig. 8) provide evidence for landforms that were wholly
943 constructed from woody debris. There is also evidence that parts of the depositional
944 environment progressed into the ecologic phase of the biogeomorphic succession model
945 (Corenblit et al., 2007). This phase is characterized by autogenic vegetation successions and
946 the stabilisation of landforms to the extent that they become disconnected from
947 hydrogeomorphic disturbance: it reflects patches of the landscape where biotic geomorphic
948 processes dominate over abiotic geomorphic processes for prolonged intervals of decades to
949 centuries, until reset by extreme low frequency disturbances. Direct evidence for autogenic

950 vegetation successions is provided by the thin cannel coals in the Estheriahaugen Member
951 (Fig. 20). Further, the multiple logs that comprise the driftcretions of the Lower Svalbardia
952 Sandstones imply that the parts of the sedimentary environment from which they were
953 sourced had had the opportunity to develop dense forested stands, detached from high
954 frequency hydrodynamic disturbance.

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

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

975 15A). In addition to true VISS, the Late Devonian also contains evidence for uprooting of
976 trees, in the form the fallen lycopsid crown shown in Figure 18. Uprooting is a significant
977 biogeomorphic phenomenon in modern settings, with implications for novel microhabitats as
978 well as instantaneous exposure of piles of sediment that can be entrained into a sedimentary
979 environment (Phillips et al., 2017).

980 **5.3. The Devonian sedimentary record as an archive of biogeomorphic complexity**

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

997 **6. Conclusions**

- 998 • The Old Red Sandstone of northwest Spitsbergen was deposited in tropical land plant-
999 colonized sedimentary environments that left a near-continuous record of Silurian
1000 through to Late Devonian strata. The succession thus provides an archetypal case
1001 study for tracking the sedimentary impacts of evolving vegetation through the
1002 Devonian.
- 1003 • The Spitsbergen ORS contains the earliest known vegetation-induced sedimentary
1004 structures in the global rock record, as well as very early examples of rooting
1005 structures, large woody debris, and cannel coal. It is also typical of similar-aged strata
1006 in terms of its vegetation-influenced signatures, being high in mudrock content, rich
1007 in palaeosols, and containing alluvial sandbodies with architectural complexity.
- 1008 • Signatures within the succession can be interpreted as first known occurrences of
1009 many biogeomorphic phenomena, including the earliest plant-colonized braided river
1010 in-channel bars (Lochkovian), possible salt marshes (Eifelian), driftcretions
1011 (Givetian), and coal-forming environments (Givetian).
- 1012 • The extensive botanic and biogeomorphic innovation during this interval meant that
1013 the ‘Devonian landscape factory’ was instrumental in shaping sedimentary
1014 environments that are familiar and analogous with present-day settings.

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1429 **FIGURE AND TABLE CAPTIONS**

1430 Figure 1 – Bedrock geology of NW Spitsbergen showing localities and constituent units of
1431 the Old Red Sandstone.

1432 Figure 2 – Lithostratigraphy of the Old Red Sandstone in NW Spitsbergen (after Piepjohn
1433 and Dallman (2014); revised dating after Berry and Marshall (2015) and from original
1434 palynological work in this study: see main text). Vertical scale proportional to time in Ma.
1435 Timing of earliest global macrofossil evidence for evolutionary innovations in vegetation
1436 shown on right hand side of figure, compiled from Gerrienne (2012), Stein et al., (2012,
1437 2020), Giesen and Berry (2013), Strullu-Derrien (2014), Matsunaga and Tomescu, (2016),
1438 and Hetherington and Dolan (2018).

1439 Figure 3 – Outcrop appearance of the constituent units of the Old Red Sandstone in NW
1440 Spitsbergen. A) Grey sandstones and recessive shales of the Siktefjellet Group, Siktefjellet.
1441 B) Basal debris flow conglomerate of the Red Bay Group, Wulffberget Formation,
1442 Rivieratoppen. C) Red mudrocks and subordinate sandstones of the upper Red Bay Group,
1443 Fränkelryggen Formation, Fränkelryggen. D) Thick fluvial sandbodies within drab
1444 mudrocks of the uppermost Red Bay Group, Ben Nevis Formation, Ben Nevis. E) Thick
1445 succession of red heterolithic strata within the Wood Bay Formation, Dicksonfjorden

1446 Member, Roosfjella. F) Frost-shattered, scree covered outcrops of the Wood Bay Formation,
1447 Dicksonfjorden Member, Scott Keltiefjellet. G) Red-drab transition between the Wood Bay
1448 Formation (Verdalen Member) (foreground) and Grey Hoek Formation (background),
1449 Woodfjorden. H) Gradational transition between red palaeosols of the Wood Bay Formation
1450 (Verdalen Member) (background) and grey ostracod-bearing shales of the Grey Hoek
1451 Formation (foreground), Sørlifjellet. I) Heterolithic succession of yellow sandstones and grey
1452 shales of the Wijde Bay Formation, Tage Nilssonfjellet. J) Finely laminated lacustrine
1453 sandstones of the lower Tordalen Formation, Fiskekløfta Member, Fiskekløfta. K)
1454 Sandstones of the Plantekløfta Formation, Planteryggen. L) Typical actively-eroding
1455 riverbank outcrop of heterolithic strata of the Plantekløfta Formation, Munindalen.

1456 Figure 4 – Lochkovian plant-sediment interactions in the Red Bay Group (Andréebeen
1457 Formation) at Buchananhalvøya. A-B) Laterally-continuous braided fluvial sandbodies
1458 (highlighted yellow) and minor shales (grey). Palaeoflow towards left of image. C-D) Detail
1459 of boxed area highlighted in A and B: Two braid bar deposits, separated by bar-top fines.
1460 Palaeoflow towards left of image. E) Detail of the base of the upper barform, showing basal
1461 lag of intraformational calcrete conglomerate (arrowed) resting on grey shale. F) Abundant
1462 zosterophyll fragments, preserved within the bar top shales. G-H) Biogenic signatures
1463 associated with bar top zosterophylls include casts of *Cruziana* arthropod furrows in base of
1464 overlying sandstone (G) and helical fish coprolites within the plant-bearing shales (H). Scale
1465 bar 1 cm in G, 1 mm in H.

1466 Figure 5 – Sedimentary context of plant fossil remains in the Pragian-Emsian Wood Bay
1467 Formation (Austfjorden Member) at Kapp Petermann. A-D) Plant remains restricted to
1468 inflection point of a downstream accreting sand barform (A-B), and consisting of relatively
1469 complete specimens of small ?psilophytes (C-D), that would have been growing at the bar top
1470 and margins. Palaeoflow towards left of image. E-H) Stratigraphically further up the same

1471 section, braided alluvial in-channel sandy bedforms form a discrete unit within palaeosols (E-
1472 F); within these, plant remains are restricted to reworked instances of comminuted
1473 carbonaceous matter along trough cross-bed foresets (G) or small fragmentary remains within
1474 planar-bedded sandstones (H). Scale bar 1 cm in C, D, G, H.

1475 Figure 6 - Sedimentary context of plant fossil remains in the Eifelian Grey Hoek Formation at
1476 Ranfjellet. A-B) Heterolithic succession bearing ostracod fauna and consisting of IHS-LA
1477 (inclined heterolithic stratification, exhibiting lateral accretion: see main text), recording
1478 deposition by small meandering coastal channels. Palaeoflow into image. Rifle is 1.1 m long.
1479 C) Plan view of preserved ridge-and-swale topography of scroll bar top of one such channel.
1480 D) Fragmentary transported plant debris preferentially accumulated in sheltered swales of the
1481 scroll bars.

1482 Figure 7 – Earliest woody debris in the Old Red Sandstone of NW Spitsbergen. A) Eifelian:
1483 Individual strands of xylem with frayed edges from unknown tree, up to 15 cm wide and 40
1484 cm long. Grey Hoek Formation, Ranfjellet. Scale bar is 10 cm. B) Eifelian: Individual clasts
1485 of woody debris up to 40 cm long and 17 cm wide within marine-influenced facies of the
1486 Wijde Bay Formation, Kronprins Haralds Fjell. Visible part of ruler is 20 cm. C) Givetian:
1487 Largest woody debris in the succession: 2 metre-long log of likely *Archaeopteris* within the
1488 deposits shown in Fig. 8, Tordalen Formation (Fiskekløfta Member), Fiskekløfta. Metre stick
1489 for scale.

1490 Figure 8 – Accumulations of woody debris within the Old Red Sandstone of NW
1491 Spitsbergen. A-C) Eifelian accumulation of smaller woody debris within flat-bedded (A)
1492 heterolithic strata of the Wijde Bay Formation at Kronprins Haralds Fjell, comprising
1493 unoriented compressed wood material up to 40 cm in length (B-C). Rifle in A is 1.1 m long,
1494 scale bar in B, C is 10 cm. D-F) Oldest known driftcretion deposit (Givetian) within the

1495 Tordalen Formation (Fiskekløfta Formation) at Fiskekløfta. Individual accumulation of
1496 dominantly archaeopterid wood, up to 2 metres length (D) persists within a series of eleven
1497 sandstone beds that form a 5 metre-thick amalgamated succession (E). Some of the drifted
1498 logs can be seen to have rested on subaerially-exposed bars, as shown by close association
1499 with true substrates of extensive aeolian adhesion marks (F). Inset rose diagram in (D) shows
1500 axial orientation of 151 individual pieces of woody debris measured throughout the 5 metre-
1501 succession. Metre stick for scale, inset scale bar in F is 1 cm.

1502 Figure 9 – Rooting structures throughout the Old Red Sandstone of NW Spitsbergen. A)
1503 Lochkovian: Putative 5 cm root structure at the top of a sandstone braid bar, immediately
1504 underlying the zosterophyll-bearing shales shown in Fig. 4. Red Bay Group (Andréebeen
1505 Formation), Buchananhalvøya. B) Pragian-Emsian: Dense assemblages of clay-lined root
1506 structures (up to 50 cm vertical length), common within vertic palaeosols and associated
1507 strata of the Wood Bay Formation (Austfjorden Member) at Kapp Petermann. C) Eifelian:
1508 Suspected root structures (bifurcating downwards), forming a 5 cm thick mantle within
1509 ostracod-bearing and carbon-rich marine influenced strata, possibly recording early salt
1510 marsh vegetation. Grey Hoek Formation, Ranfjellet. D) Eifelian: Similar forms in similar
1511 marine-influenced facies to C, but extending up to 10 cm vertical length. Wijde Bay
1512 Formation, Tage Nilssonfjellet. E) Givetian-Frasnian: Two horizons of densely root-mottled
1513 palaeosols separated by sandbodies, implying root penetration to at least one metre, tops of
1514 rooted horizons arrowed. Boundary between Tordalen Formation and Planteryggen
1515 Formation, Fiskekløfta. Scale bar in A-D is 1 cm, scale bar in E is 1 m.

1516 Figure 10 – Detail of rooting structures in the Pragian-Emsian Wood Bay Formation
1517 (Austfjorden Member) at Kapp Petermann. A) Succession consists of alternating blocky red
1518 palaeosols, punctuated with thin sandstones representing crevasse splay deposition. B-C)
1519 Details of crevasse splay sandstones showing penetration by clay-lined roots (B) and

1520 climbing ripple-laminated (C). Scale bar in A is 1 m, scale bar in B is 1 cm, ruler in C is 20
1521 cm.

1522 Figure 11 – Emsian primitive VISS in the form of gently mounded synoptic topography to a
1523 root-mottled palaeosol (A) in the Wood Bay Formation (Dicksonfjorden Member),
1524 Germaniabekken. Detail of mound above root mottle shown in B. Visible ruler is 50 cm in A,
1525 70 cm in B.

1526 Figure 12 – Eifelian decay-related VISS formed as hollow plant stem filled with mud and
1527 decayed, causing downturning of beds. Asymmetry of downturning and tilt of plant cast
1528 suggests that the plant toppled as it decayed. Wijde Bay Formation, Tage Nilssonfjellet. Ruler
1529 is 20 cm.

1530 Figure 13 – Frasnian VISS associated with standing archaeopterid flora: A-B) Narrow
1531 archaeopterid stem with steeply upturned laminae (hydrodynamic VISS). Plantekløfta
1532 Formation, Munindalen. C-D) Buckled and steeply upturned laminae on either side of small
1533 archaeopterid stem apparently with some flexibility and bent into flow. Plantekløfta
1534 Formation, Munindalen. E-F) Large archaeopterid encased in sandstone and flanked by
1535 upturned laminae (hydrodynamic VISS). Plantekløfta Formation, Munindalen. Ruler in A, B
1536 is 1 m, ruler in C, D is 20 cm, scale bar in E, F is 1 m.

1537 Figure 14 – Hydrodynamic VISS associated with standing archaeopterids, buried by a debris
1538 flow. Plantekløfta Formation, Munindalen. A-B) Three archaeopterid stems are seen within
1539 sandstones, containing VISS that indicated they interacted with the flows that deposited the
1540 sandstones. The fossil trees have been truncated by a debris flow depositing a thick
1541 conglomerate, with prominent clusters of cobbles preferentially deposited around the tops of
1542 the decapitated tree trunks. C-J) Details of the image shown in A, demonstrating how the
1543 archaeopterids were rooted in mudrock (E-F) and persisted as sand was deposited around

1544 them, before being truncated during the individual debris flow event. Metre stick/ 1 m scale
1545 bar in each image, except 20 cm scale bar in E, F.

1546 Figure 15 – Frasnian VISS associated with standing lycopsid flora: A-B) Small lycopods
1547 provide armoured mantle to muddy substrate, preserved as synoptic topography of small
1548 hummocks and swales. Plantekløfta Formation, Munindalen. Visible ruler is 80 cm. C-D)
1549 Hydrodynamic VISS showing upward transition from centroclinal fill of scour to upturned
1550 laminae. Plantekløfta Formation, Planteryggen. Visible ruler is 25 cm. E-F) Buckled and
1551 upturned laminae developed on the stoss side of a buried flexible stem. Plantekløfta
1552 Formation, Planteryggen. Visible ruler is 40 cm.

1553 Figure 16 – Hydrodynamic VISS associated with standing lycopsids in the Plantekløfta
1554 Formation at Munindalen, demonstrating how distorted bedding persists even where fossil
1555 plant material is lost. A-B) Images of the same cliff face taken 6 years apart, showing erosion
1556 of the lycopsid bearing sandstone bed by bank collapse into the Mimer River. White arrow
1557 provides reference point, yellow arrows point to standing lycopsids. White box in A shows
1558 view of standing lycopsids figured by Berry and Marshall (2015, their fig. 4L). C-H) Details
1559 of the fossil bearing bed taken in 2016 showing hydrodynamic VISS in direct association
1560 with *in situ* plants (C-F), as well as instances along the same horizon where structures are
1561 likely to be hydrodynamic VISS despite the absence of direct fossil evidence (G-H). Scale
1562 bar in A, B is 2 m, visible ruler in C is 30 cm, scale bar in E, G is 50 cm.

1563 Figure 17 – Frequently oversteepened concavo-convex bedding within amalgamated
1564 sandstone bodies that appear too irregular, localized and individually unique to be formed by
1565 undisturbed hydrodynamic flow. These are putative VISS as they contain abundant evidence
1566 for standing vegetation or woody debris, but lack direct association with unequivocal plant
1567 triggers. A-C) Putative VISS in the Eifelian Wijde Bay Formation, Tage Nilssonfjellet:

1568 convex-upwards mound in centre of A-B contains 10 cm carbonaceous root structures (C).
1569 Metre stick for scale. D-F) Putative VISS in the latest Givetian Tordalen Formation
1570 (Fisklekløfta Member) at Torelva, comprising thick convex-up mounds (arrowed) of steep-
1571 margined sandstone beds with frequent large plant debris (F) between beds. Mounds appear
1572 to be a result of flow diversion around woody debris, possibly in addition to decay- or
1573 compression-related deformation of the woody sediment pile. Metre stick and pen (20 cm) for
1574 scale. G-H) Putative VISS in the latest Givetian Tordalen Formation (Fisklekløfta Member)
1575 at Fiskekløfta (similar stratigraphic horizon to D-F). Continuous scour-and-mound
1576 topography persists across the same amalgamated sandbody that contains driftcretion
1577 accumulations of woody debris on the opposite side of the river (Figure 8). Scale bar is 1 m.

1578 Figure 18 – Evidence for tree uprooting in the earliest Frasnian, revealed by fallen lycopsid
1579 crown that had toppled onto a small meander point bar (IHS-LA in Fig. 21B). Plantekløfta
1580 Formation, Munindalen. A-D) Upwards deflected lycopsid branches, encased by both mud and
1581 sand. Metre stick for scale. E-F) Details of the above, showing minimal deflection of
1582 sedimentary laminae by the small flexible lycopod branches. Visible part of ruler is 60 cm in
1583 E, scale bar is 10 cm in F.

1584 Figure 19 – Potential variability in influence of standing vegetation physiology on fluid flow
1585 and bed shear stress, illustrated with (non-exclusive) examples of Devonian flora known from
1586 the Spitsbergen Old Red Sandstone.

1587 Figure 20 – Development of cannel coal in Givetian strata of the Tordalen Formation
1588 (Estheriahaugen Member) at Munindalen. A) Outcrop. B) Hand specimen.

1589 Figure 21 – Examples of IHS-LA sets throughout the Old Red Sandstone in NW Spitsbergen.
1590 A) Emsian: 5 metre-thick IHS-LA within the Wood Bay Formation. Dicksonfjorden Member,
1591 Scott Keltiefjellet. B) Frasnian: 2 metre-thick IHS-LA associated with both standing and

1592 fallen lycopsid and archeopterid vegetation (fallen lycopsid in Figure 18 occurs at same
1593 stratigraphic level highlighted). Plantekløfta Formation, Munindalen. Scale bar in each image
1594 is 1 m.

1595 Figure 22 – Early Devonian plant-sediment interactions in the Spitsbergen Old Red
1596 Sandstone. A) Reconstruction of the general alluvial palaeoenvironmental setting of the Red
1597 Bay Group and Wood Bay Formation. B) Detail of plant interactions in the Red Bay Group,
1598 showing colonization of braid bar tops and margins by small zosterophylls with little
1599 resistance to erosion during flood stages. C) Duration of re-establishment of geomorphic
1600 phases after flood disturbance for riparian vegetation in the Early Devonian (see Fig. 22D and
1601 Corenblit et al., 2007 for details). D) Key to Figures 22-24.

1602 Figure 23 – Middle Devonian plant-sediment interactions in the Spitsbergen Old Red
1603 Sandstone. A) Reconstruction of the general nearshore and alluvial palaeoenvironmental
1604 setting of the Grey Hoek and Wijde Bay formations, with nearshore lacustrine/lagoonal and
1605 deltaic setting of the Tordalen Formation. B) Detail of plant interactions in the Tordalen
1606 Formation, showing delta-top driftcretion of large woody debris. C) Duration of re-
1607 establishment of geomorphic phases after flood disturbance for riparian vegetation in the Mid
1608 Devonian (see Fig. 22D and Corenblit et al., 2007 for details).

1609 Figure 24 – Late Devonian plant-sediment interactions in the Spitsbergen Old Red Sandstone.
1610 A) Reconstruction of the general alluvial and debris flow palaeoenvironmental setting of the
1611 Plantekløfta Formation. B) Detail of plant interactions in the Plantekløfta Formation, showing
1612 trees rooted in floodplain fines, interacting with flood deposited crevasse splay sands, and
1613 uprooting of large trees on meander bends. C) Duration of re-establishment of geomorphic
1614 phases after flood disturbance for riparian vegetation in the Late Devonian (see Fig. 22D and
1615 Corenblit et al., 2007 for details).

1616 Table 1 – Characteristics of the formations of the Old Red Sandstone in NW Spitsbergen
1617 (compiled using information from Worsley (1970); Friend and Moody-Stuart (1972); Friend
1618 et al. (1997); Blomeier et al. (2003a,b)); Bergh et al. (2011); Piepjohn & Dallman (2014);
1619 Berry & Marshall (2015); Blumenberg et al., (2018)).

1620 Table 2 – Presently known fossil plant genera and forms from the Old Red Sandstone in NW
1621 Spitsbergen. Table compiled from Høeg (1942), Schweizer (1968, 1999) and Berry (2005),
1622 plus material identified here. Note that this table is based on provisional data: extensive
1623 collections made during this study are the subject of presently ongoing investigation at
1624 Cardiff University.

1625 Table 3 – Distribution of plant-influenced and plant-dependent phenomena in the formations
1626 of the Old Red Sandstone in NW Spitsbergen.