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

Neil S. Davies[1]*, Christopher M. Berry[2], John E. A. Marshall[3], Charles H. Wellman[4], Franz-Josef Lindemann[5]

[1]*Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, United Kingdom.*

[2]*School of Earth and Environmental Sciences, Cardiff University, Main Building, Park Place, Cardiff CF10 3AT, Wales, United Kingdom.*

[3]*School of Ocean and Earth Science, University of Southampton, European Way, Southampton SO14 3ZH, United Kingdom.*

[4]*Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, United Kingdom.*

5Natural History Museum, University of Oslo, Postboks 1172 Blindern, 0318 Oslo, Norway.

**Corresponding Author: nsd27@cam.ac.uk*

ABSTRACT

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

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

1. Devonian Vegetation and Sedimentation

Land plants are some of the most effective biogeomorphic agents on Earth today, modifying physical processes and landforms by complex and diverse means that include: roots increasing substrate shear strength and resistance to erosion; canopies and litter reducing the efficacy of raindrop impact and surface runoff; plant- and fungal symbiont-induced weathering and modification of the critical zone; the provision of organic matter that can change sediment properties such as cohesiveness; baffling and binding of sediment to promote the accretion of landforms; or acting as obstacles to flowing air and water and changing turbulence properties through friction and drag effects (e.g., Corenblit et al., 2007, 2015, 2020; Phillips, 2016; Horton et al., 2017; Kleinhans et al., 2018; Larsen, 2019). Trees in particular are effective ecosystem engineers, promoting landscape heterogeneity not only through their physical presence, but also due to the hydrodynamic resistance of their arborescent form and deeper rooting systems, their role in the hydraulic redistribution of groundwater, their propensity for uprooting release of sediment and creation of microhabitats, and the production of large woody debris that can modify landscapes through island formation or log-jamming of streams (e.g., Harmon et al., 1986; Jones et al., 1994; Gurnell et al., 2002; Gurnell, 2003; Wohl, 2013, 2017; Gurnell, 2014; Davidson et al., 2015; Kramer and Wohl, 2015; Pawlik et al., 2016; Sullivan et al., 2016; Wohl and Iroumé, 2021).

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

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

The Spitsbergen ORS is shown to be an archetypal case study that yields insights into the 'Devonian landscape factory': i.e., the earliest continental environments where plants could shape sedimentary landscapes on a scale analogous to present-day floras.

2. The 'Old Red Sandstone' of NW Spitsbergen

The 'Old Red Sandstone' is an informal term used for successions of dominantly terrigenous strata that crop out around the north Atlantic region, and whose deposition was contemporaneous with mid-late Palaeozoic orogenic events in Laurussia (e.g., Friend et al., 2000; Kendall, 2017). The Spitsbergen ORS is one of a number of near-contemporaneously deposited Silurian-Devonian successions of non-marine-dominated sedimentary strata across Scandinavia and Greenland (e.g., Marshall and Stephenson, 1997; Anderson and Cross, 2001; Davies et al., 2005a,b; Astin et al., 2010), and has been the subject of intermittent but significant geological investigations for over 120 years (e.g., Nordenskiöld, 1892; Holtedahl, 1914). It was an instrumental case study in the development of fluvial sedimentary facies models (e.g., Friend, 1965; Moody Stuart, 1966) and has proved to be particularly rich in fossil plant material. The earliest geological expeditions to the region collected abundant and well-preserved megafossils (see summaries in Høeg 1942; Schweitzer, 1999; Berry 2005), the palynological record of the succession has been studied for over half a century (Vigran 1964; Allen 1965, 1967), and, more recently, fossil forests of lycopsids and archaeopterids have been discovered in the youngest units of the succession (Dallman et al., 2004; Berry and Marshall, 2015). Additionally, one of the first ever observations that there could be a sedimentological signature of the evolution of land plants was made from the Spitsbergen ORS by Vogt (1941). He noted that the preservation of feldspar was greater in Lower Devonian sandstones than in Middle Devonian sandstones, reasoning that "a more continuous cover of vegetation… involved a slower transportation of the debris and an intensified chemical action on the mineral grains… (as well as) some change of the climate" (Vogt, 1941, p. 10).

2.1. Geological Setting

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

Palaeogeographically, Spitsbergen formed part of western Laurussia and occupied an equatorial location for the entire duration of ORS deposition, migrating only 5° of latitude during the Devonian (from c. 10° S to c. 5° S) (Torsvik and Cocks, 2017). Despite the stable tropical location, long-term climatic variability is recorded through the succession by evidence of either seasonal semi-arid (calcretes, vertisols: Friend and Moody-Stuart, 1970; Blomeier et al., 2003a) or humid conditions (coals: Vogt, 1941; Harland et al., 1976; Blumenberg et al., 2018). Red bed strata are also partitioned within the succession, attesting to long-term variability in levels of drainage (Sheldon, 2005).

2.2. Lithostratigraphic Units

Each of the lithostratigraphic units of the Spitsbergen ORS (Fig. 2, Table 1) was visited in this study.

2.2.1. Silurian (Siktefjellet Group)

The Siktefjellet Group crops out only in the far northwest of the region (Gjelsvik and Ilyes, 1991) and exposure is poor due to internal faulting and scree coverage, which renders confident architectural analysis of the strata impossible (Figure 3A). The unit has previously been interpreted as recording braided fluvial, and possible lacustrine, deposition (Friend et al., 1997) but contains few unambiguous indicators of depositional environment (Gjelsvik and Ilyes, 1991). The succession has been reported to contain plant macrofossils (Murašov and Mokin, 1979), but only comminuted carbonaceous phytodebris was witnessed in this study. Palynological assemblages are dominated by phytodebris (cuticles, tubes, etc.) and a few spores that are mostly indeterminable, except for rare cryptospore tetrads; all of which are very poorly preserved and much more thermally mature than elsewhere in the Spitsbergen ORS. No marine chitinozoans or acritarchs are present, and the unit yields no reliable age indicators. Despite this, a Silurian age is most likely based on the general palynological motif, and because the Siktefjellet Group lies tilted and unconformable below the base of the Red Bay Group (Friend et al., 1997).

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

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

The Red Bay Group is an overall-fining upwards succession. The conglomerate-dominated lower half of the group consists of syn-tectonic alluvial fan deposits of the Wulffberget (Fig. 3B) and Prinsesse Alicefjellet formations, which sandwich a poorly exposed shale unit (the Rabotdalen Formation) (Murašov and Mokin, 1979; Harland, 1997; Friend et al., 1997; McCann, 2000). These lower units lack plant macrofossils. The upper Red Bay Group comprises. 1) The Andréebreen Formation: grey-green fine- to medium-grained sandstones with subordinate interbedded dark grey shales and pebble-lag conglomerates, which have yielded newly discovered macrofossils of small shrubby plants (cf. *Zosterophyllum*) during this study (Fig. 4). 2) The Frænkelryggen Formation (Fig. 3C): red bed overbank mudrocks with recurrent fine sandstone horizons, yielding abundant small plant macrofossils, in addition to enigmatic (*Pachytheca*) and possible fungal (*Prototaxites)* fossils (Høeg, 1942; Schweitzer, 1999). 3) The Ben Nevis Formation: grey-green coloured, fine- to coarse-grained cross-bedded sandstones of probable braided fluvial origin (Fig. 3D) (Friend et al., 1997), lacking plant fossils.

The Wood Bay Formation rests unconformably on the Red Bay Group, and is the most widely distributed and well-studied unit of the Spitsbergen ORS (Friend, 1961, 1965; Moody-Stuart, 1966; Friend and Moody-Stuart, 1970, 1972; Blomeier et al., 2003a,b; Wisshak et al., 2004a,b). It is divided into the Austfjorden (basal), Dicksonfjorden (middle), and Verdalen (upper) members, on the basis of fossil fauna (Murašov and Mokin, 1979) but with little lithological variability. The Wood Bay Formation is a heterolithic red bed succession, dominated by calcrete-bearing fluvial overbank, palaeosol and lacustrine mudrocks (Blomeier et al., 2003a,b). Outcrop of the unit is superficially excellent, with large-scale architecture apparent in extensive mountainside exposures (Fig. 3E): however, these can comprise frost-shattered and scree-covered recessive mudrocks on the ground (Fig. 3F). The succession contains fossils of a small shrubby flora (e.g., *Psilophyton, Bucheria*) (Høeg, 1942) (Table 2).

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

Middle Devonian strata exhibit pronounced regional variability in northwest Spitsbergen.

In the north of the region, transgressive dark grey and grey-green heterolithic strata of the Eifelian Grey Hoek Formation conformably overlie red beds of the Verdalen Member (Fig. 3G-H), and yield abundant ostracod and bivalve fossils, burrows, and pisolitic limestones, in addition to evidence for channelized unidirectional flow; together suggestive of coastal or estuarine deposition (e.g., Friend, 1961; Worsley, 1972). The Grey Hoek Formation yields plant fossils of both small stature shrubs and larger potentially woody fragments of possible tree origin (Høeg, 1942). Conformably overlying the Grey Hoek Formation, the Wijde Bay Formation is a similar unit, with lighter grey-coloured mudrocks and yellow-grey sandstones (Fig. 3I), a marine-influenced fauna, and shrub-like and woody floral remains (Schweitzer, 1968). There is little direct evidence for the age of the Wijde Bay Formation and the unit has often been placed within the Givetian to overlap in age with the base of the Tordalen Formation (e.g., Piepjohn & Dallmann, 2014). However, the spore assemblages listed and illustrated by Riegel (in Schweitzer, 1999) are Eifelian in age, and notably different from those documented from the Tordalen Formation (Allen, 1965, 1967; Berry & Marshall, 2015). As such, we here consider the unit to most likely be predominantly Eifelian.

In the south of the region, Middle Devonian strata comprise the late Givetian-aged Tordalen Formation (lower Mimerdalen Subgroup), resting unconformably on the erosionally truncated Dicksonfjorden Member. Palynological samples from the Tordalen Formation are dominated by *Geminospora* and *Cymbosporites* (showing that its deposition was not contemporaneous with the Wijde Bay Formation). It comprises: 1) the Estheriahaugen Member: thinly (5 cm-thick) bedded grey-green sandstones and shales, with siderite nodules, ostracod fossils, and thin coal (Vogt, 1941; Harland et al., 1976; Piepjohn & Dallmann, 2014; Blumenberg et al., 2018); and 2) the Fiskekløfta Member (Fig. 3J): darker grey mudstones and sandstones, capped with a distinct 50 metre-thick marker horizon of white-coloured quartz-rich medium-grained sandstones (the "Lower Svalbardia Sandstone") (Piepjohn & Dallmann, 2014). The strata of the Tordalen Formation have been interpreted as freshwater-brackish lagoonal facies, with sand input from marginal deltas and washovers (e.g., Friend, 1961; Newman et al., 2020).

2.2.4. Upper Devonian (Planteryggen and Plantekløfta formations)

The remainder of the Mimerdalen Subgroup comprises the early Frasnian Planteryggen and Plantekløfta formations. The Planteryggen Formation comprises only poorly exposed sandstones and conglomerates. The overlying Plantekløfta Formation is well-exposed on ridges and river cuttings (Figs. 3K-L) and comprises heterolithic dark grey overbank mudrocks and yellow-grey fluvial sandstones, as well as prominent horizons of poorly sorted, clast- and matrix-supported debris-flow conglomerates. It also contains abundant standing lycopsid and archaeopterid tree fossils, in addition to the remains of non-woody plants of shrub-like habit (Berry, 2005; Berry and Marshall, 2015). The Frasnian succession has been interpreted to record deposition by small fluvial channels with forested floodplains, punctuated by deposition from debris flow events that were sourced from locally uplifted highlands to the east, at the onset of the Svalbardian Event (Piepjohn and Dallman, 2014; Berry and Marshall, 2015).

3. Plant-sediment interactions in the Old Red Sandstone

The Lochkovian–Frasnian stratigraphic record of the ORS of northwest Spitsbergen is a perfect natural laboratory to search for signatures of early plant-sediment interactions, and we here describe and interpret multiple features that have been observed throughout the succession. Two overarching classes of signature are recognised (after Davies et al., 2020): 1) Vegetation-Dependent Signatures – materials (e.g., plant debris, woody debris), structures (e.g., rooting traces, vegetation-induced sedimentary structures) and lithologies (e.g., coal) novel to the Devonian because they required direct input of plant detritus or sediment manipulation by vegetation. 2) Vegetation-Influenced Signatures – facies signatures whose creation would have been influenced by the presence of vegetation at the time of deposition (e.g., weathering products, sedimentary architecture). The extent of indirect vegetation influence is problematic to determine from any individual case study, so the characteristics of the Spitsbergen ORS are discussed with reference to contemporaneous strata from the global sedimentary-stratigraphic record.

3.1. Fossil Plant Material

The simplest evidence for direct interplay between vegetation and surface processes occurs where plant material is preserved within a sediment pile, either having been transported for a distance, or buried at its growth site. In any such instances, fossilized plant material is indicative either that fluids were transporting organic clasts, or that plant remains locally modified erosion and deposition thresholds. Recognising the outcrop sedimentary context of sites where plant material has been interred requires: 1) that fossil plant material has not been over-collected; and 2) that plant material is preserved. In the Spitsbergen ORS, the first obstacle is less of an issue than it is in other classic ORS sites: the strata are comparably very rich in fossil material because there has been limited palaeontological collection across the region, and outcrops are frequently rejuvenated through frost-shattering, cliff collapse and riverbank retreat. Taphonomic filters undoubtedly mean that only a fraction of original plant matter has been preserved, particularly within well-drained red bed facies. However, fossil plant material is known from all Devonian stages in Spitsbergen, occurring as four taphonomic types that have stepwise first appearances in the Spitsbergen ORS: 1) Comminuted debris; 2) Fragmentary remains of delicate plant parts; 3) Woody debris; and 4) Plants preserved in growth position.

3.1.1. Comminuted debris

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

3.1.2. Fragmentary remains

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

Examples from Lower and Middle Devonian strata illustrate how small stature plants interacted with their physical environments. Figure 4 illustrates the sedimentary architecture and lithologies of the Andréebreen Formation (Lochkovian, Red Bay Group), which hosts the oldest identifiable plant debris recognised in this study. The succession is dominated by sandstones, packaged as downstream accretion sets up to 1.5 metres thick, and punctuated with fissile grey shales (Fig. 4A-E). Shallow braided stream bars, capped with shale during intervals of channel switching, provide a reasonable palaeoenvironmental explanation for these sedimentary signatures (e.g., see also Friend et al., 1997). While the sandstones in these successions are barren of fossil plant material, the shales host branching specimens of cf. *Zosterophyllum* (Figure 4F). The relatively undegraded nature of these plant remains suggests minimal transport, and implies they were interred parautochthonously on bar tops (they may be associated with rooting structures, see Section 3.2.). There is no direct evidence for these Early Devonian plants inducing any hydrodynamic sedimentary structures so it cannot be ascertained whether they occupied submerged parts of the bars, but they are seen in association with trace fossil evidence that suggests geologically early riverine habitats of co-existing plants, fish and invertebrates (Figure 4G-H). Similar signatures are present in slightly younger strata, within the Pragian-Emsian Wood Bay Formation (Austfjorden Member) at Kapp Petermann (Figure 5). Here, fragments of branching spiny stems of small stature plants (*?Psilophyton*) are restricted in their distribution to inflection points at the topsets of barforms in very fine sandstones (Fig. 5A-D). The relative completeness of delicate fossil elements suggests the remains are parautochthonous, and the restriction to topsets implies a further instance where Lower Devonian plants had colonized the tops and margins of exposed braid bars during low flow stage. The partial fragments preserved in this setting can be compared with more water-worn plant fragments further up section at the same locality (Figure 5E-H). Here in-channel sandy bedforms host only comminuted debris (throughout cross-bed sets), and parting-lineated sandstones contain sparse clusters of unornamented sticks, attesting to the entrainment and attrition of clasts and plant material within active river channels.

Figure 6 shows a Middle Devonian example from marine fauna-bearing strata of the Grey Hoek Formation, demonstrating how phytoclasts have a hydrodynamic equivalence to very fine clastic sediment. Here, unidentified carbonaceous fragments are preferentially hosted in muddy sediment patches that occupy the swales of a scroll bar (Fig. 6C). This illustrates how the topographic lows on the margins of meandering shallow coastal channels acted as traps and sieves for phytoclasts, demonstrating that coastal waters at this time had a mixed sediment load of both siliciclastic and plant-derived organic sediment.

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

3.1.3. Woody Debris

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

In modern forested streams, woody debris is an important sediment constituent, recruited both continuously and episodically, through mechanisms such as individual or mass mortality, hillslope failure, floodplain erosion, or bank collapse (Wohl, 2017). In the rock record, fossilized accumulations of such debris are common from the Carboniferous onwards but extremely rare in older strata, even after the Emsian evolution of wood (Davies and

Gibling, 2011, 2013). The Spitsbergen ORS is significant in that it contains some of the earliest known instances of both individual allochthonous clasts of woody debris (Figure 7), and dense accumulations of woody debris (Figure 8) worldwide.

3.1.3.1. Individual woody debris clasts

The oldest instances of woody debris in the succession occur as isolated clasts of randomly oriented material, hosted within very fine-grained coastal channel sandstone facies of the Eifelian Grey Hoek (Fig. 7A) (Høeg, 1942) and Wijde Bay formations (Fig. 7B) (Schweitzer, 1968). Taxonomic identification of the plant material is not possible, but it is associated with *Protocephalopteris* branches, has a sulcate ornamentation, and appears frayed at the margins. At the time of deposition, the debris likely comprised clusters of individual xylem strands with a stringy structure, rather than robust wood particles.

Larger and more robust woody particles are known from the south of the outcrop area and are particularly prominent within the Givetian ‘Lower Svalbardia Sandstone’ of the uppermost Tordalen Formation. Here, individual clasts of woody debris occur up to 2 metres in length, that are dominated by flattened trunks of probable archaeopterid trees (plus minor lycopsid material) (Fig. 7C). These examples, dating in time from close to Earth’s earliest known tree fossils (Berry and Fairon-Demaret, 1997, 2002; Giesen and Berry, 2013), provide evidence for the origination of wood as a novel sedimentary particle. Woody debris has subsequently persisted as a component of many sedimentary environments throughout the remainder of Earth history (e.g., Davies and Gibling, 2013; Wohl, 2013, 2017; Gulbranson et al., 2020; Trümper et al., 2020).

3.1.3.2. Accumulations of woody debris

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

In contrast, true woody debris accumulations are conspicuous in a 5 metre-thick section of the upper Tordalen Formation (Fig. 8D-F), where 11 successive dense accumulations cap 20-80 cm-thick fine-grained sandstone bodies. The Tordalen accumulations have superficial resemblance to logjam deposits, the earliest known of which date from the Carboniferous (Gastaldo and Degges, 2007; Gibling et al., 2010). However, detailed analysis of the sedimentary fabric of the Tordalen accumulations does not support a logjam origin, because: 1) they are strongly oriented in one direction (c. 020-200°), with little variance (Fig. 8); 2) they occur in medium-grained sandstone that lacks the intraformational or extraformational clasts that would be caught in a logjam; 3) they occur in 11 successive sandstone layers over a vertical distance of 5 metres, with no evidence for any avulsive impact of the wood accumulations; 4) when seen in association with sandstone mounds, they are oriented parallel with the mound crests (Fig. 8F); 5) they occur on bedding planes with evidence for post-depositional stasis (*Diplichnites* arthropod trackways and aeolian adhesion marks between individual logs (Fig. 8F)), rather than instantaneous hydrodynamic re-organisation; and 6) they are thin accumulations that mantle sands, rather than intermingle with them: the logs have a mean width of 50 mm, approximating to original diameter (see Gibling et al., 2010), and a mean individual thickness of 3 mm. As each woody debris mantle is approximately 3 cm thick, this gives a compaction value for the wood of 16.6, and suggests that each original wood accumulation was only c. 50 cm in thickness. Taken together, these characteristics of the Tordalen accumulations suggest that, rather than logjams, they likely record driftcretions (Kramer and Wohl, 2015): persistent woody debris accumulations that form where fluvial driftwood export to a shoreline is high, and accumulates in stable mats or berms. Explaining the Tordalen accumulations as early driftcretions fits with the interpretation of the Lower Svalbardia Sandstone as delta-top sands, infilling the lacustrine/lagoonal setting recorded by the finely bedded sands of the Fiskekløfta Member (Friend, 1961; Newman et al., 2020).

3.1.4. Plants preserved in growth position

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

3.2. Rooting Traces

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

The Andréebreen Formation of the Red Bay Group yields what may be the oldest root structure in the Spitsbergen ORS (Fig. 9A). This particular structure is not unequivocal, and it could also be explained as an instance of an invertebrate burrow (such structures also appearing in alluvial settings for the first time in the early Lochkovian: e.g., Minter et al., 2016; Shillito and Davies, 2017). However, favouring the former over the latter is the slight irregularity to its form, coupled with its context, descending from the base of the same bar-top shales that yield parautochthonous cf. *Zosterophyllum* (see Section 3.1.2.; Fig. 4).

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

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

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

3.3. Vegetation-Induced Sedimentary Structures

Vegetation-induced sedimentary structures (VISS) are sedimentary structures formed by the interaction of sediment with in situ plants (Rygel et al., 2004), and provide physical evidence for plants having mediated sediment accumulation and erosion in clastic deposystems. Rygel et al. (2004) defined seven types of VISS in two categories: A) *VISS formed due to hydrodynamic processes interacting with standing vegetation:* 1) upturned beds around a plant, recording deposition in its shadow; 2) centroclinal cross-strata centred on a plant, recording the infill of a scour hollow formed at its base; 3) scour-and-mound beds, formed by a coalescence of upturned beds and centroclinal cross-strata along a common horizon; 4) complex internal stratification of sand bodies, arising from multiple coalesced scour fills associated with multiple individual plants arranged in a stand; and 5) scratch circles on bedding planes, formed by rotation of flexible plant parts; B) *VISS formed due to the decay of* in situin situ *plants within a sediment pile:* 6) downturned beds arising from the decay of aly n in situ buried trunk, and the collapse of sediment into the mould after decay; and 7) mudstone-filled hollows formed by casting of internal voids within decayed trunks.

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

3.3.1. Lower and Middle Devonian VISS

Figure 11A-B shows an instance of what are likely the earliest VISS in the Spitsbergen ORS, occurring at the contact between the top of a red mudrock bed and the base of a crevasse splay sandstone in the Emsian Dicksonfjorden Member of the Wood Bay Formation. The contact may record a synoptic topography, i.e. a true representation of the geomorphic form of the depositional substrate (see Paola et al., 2018; Davies et al., 2019), because 1) the massive sandstone passively drapes the mudrock bed with no evidence for erosion; 2) the upper 5 cm of the oxidized mudrock shows a mantle of drab mottling, which may be suggestive of reduction by shallowly penetrating roots; and 3) individual elongated drab haloes extend and branch up to a metre downward from the apices of the gentle mounds: although their discontinuity hampers confident recognition, these resemble similar-aged root traces of deeply anchored small-stature plants (Xue et al., 2016). These characteristics imply that deeper rooted plants were individually centred within gentle mounds on the ancient floodplain. On modern floodplains, large-scale mounds can develop because of the preferential accumulation of plant matter and sediment around standing plants (e.g., Scheihing and Pfefferkorn, 1984; Small, 1997; Sullivan et al., 2016). Similar sediment interactions should also be expected to have been associated with small stature Early Devonian plants, whose primitive physiological constructions were already adept at baffling fine sediment (Mitchell et al., 2016). In this instance, a potentially original undulatory floodplain topography, induced by early herbaceous plants, has been preserved because it was cast by overbank flooding splays, which can lose capacity to erode and rework synoptic topography as they wane away from their source (e.g., see Davies and Shillito, 2018).

One Mid Devonian instance of VISS associated with in situ plant remains was recognised within the Wijde Bay Formation (Figure 11C-D). Here an inclined sub-vertical mud-filled tube is hosted within thin beds of very fine-grained sandstone that deflect downwards where they contact with the structure. Although the structure lacks ornamentation and cannot be identified as a specific plant fossil, it is unlikely to be an animal burrow because the deflection of the beds is asymmetric (more symmetrical deflection would be expected if the structure was emplaced through directed penetration of the sediment). Instead it is likely the structure records the internal casting of the hollow interior of a standing, decaying plant stem at the time of deposition, with the deflection of the adjacent beds recording localized subsidence as buried parts of the plant decayed away. The structure is the earliest instance in the Spitsbergen ORS that can be ascribed to one of the types of VISS originally defined by Rygel et al., (2004).

3.3.2. Upper Devonian VISS

Abundant instances of VISS are recorded within Frasnian strata, in association with both standing archaeopterids (Figs. 12, 13) and lycopsids (Figs.14, 15). Some of the Frasnian VISS are analogous to older strata in the Spitsbergen ORS: for example, mound-shaped substrates below lycopsids (Fig. 14A) that resemble the putative Early Devonian VISS (Fig. 11A-B). In addition, the Plantekløfta Formation hosts the earliest instances of hydrodynamic

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

Upturned laminae (Figs. 12, 13, 14C) are the cross-sectional record of current shadows: elongate accretionary sediment mounds that develop in the lee of an obstruction to flow (Allen, 1982; Rygel et al., 2004). They are readily diagnosed when witnessed immediately adjacent to standing vegetation, but other instances of convex-up laminae are also seen, and likely record downstream cross-sections of the vegetation shadows in the lee of plants (e.g., Figure 14E-F). Upturned laminae tend to be steeper where they are seen adjacent to archaeopterids (e.g., Fig. 12C-D) and gentler where they are seen adjacent to lycopsids (e.g., Fig. 13C-D): implying that archaeopterids were associated with smaller scale shadows (see Section 3.3.6.).

Centroclinal cross-strata (Figs. 13B, 14D, 15) occur as sandstone bodies with concave-up bases, flat tops, and form-concordant laminae. The structures formed by the infilling of antecedent scours that had developed when water flowed around a tree obstacle, with an erosive component of the flow being forced down the upstream side of the trunk. Instances where there is an upwards transition from centroclinal cross-strata into upturned laminae (e.g, Fig. 14C-D) record a change from erosive to aggradational conditions, likely during waning flow. Where multiple instances of both centroclinal cross-strata and upturned laminae coalesce along the same horizon, compound scour-and-mound beds are seen (e.g., Fig 15) with alternating convex- and concave-up components.

Upturned laminae, centroclinal cross-strata and scour-and-mound beds are all within the canon of VISS described by Rygel et al. (2004). A fourth type of previously undescribed

VISS is seen recurrently in the Plantekløfta Formation, and here referred to as buckled laminae (Figs. 12C, 14F, 15D). Buckled laminae are always seen on the upstream side of in situ plants that are curved and inclined towards the palaeoflow direction: implying flexibility of their woody stems in life. The buckled laminae comprise disharmonic crests and troughs that lack the regularity and continuity of current ripples. They are here interpreted as irregular surfaces that developed on the upstream side of standing plants under highly erratic flow conditions: the flexibility of the plants meaning that they would have oscillated irregularly in the flow, with complex and discontinuous upstream feedback of downflow and vortices sculpting the substrate.

3.3.3. VISS in conglomerate facies

Figure 13 shows how in situ vegetation has influenced the sedimentary architecture and fabric of conglomerates in the Plantekløfta Formation. The figure shows a stand of small archaeopterid trees, rooted into a poorly drained dark mudrock (Fig. 13E-F: note that the organic material of the roots here is fossilized, rather than being sedimentary traces). The stand occupied a topographic depression that was entombed in fine-grained sandstone (Fig. 13B). The sandstone was subsequently capped by at least two metres of conglomerate, deposited instantaneously as a poorly sorted and partially clast-supported debris flow. The truncation of sandstone laminae (e.g., Fig. 13G-H) shows that the emplacement of the debris flow deposit was associated with reworking of the underlying substrate. However, while the archaeopterid trunks have been truncated, their bases nonetheless protrude upwards into the debris flow and are seen to have acted as obstacles that forced the deposition of clusters of larger cobbles (e.g., Fig. 13B, D, H). This shows that the presence of the trees limited the erosive capacity of the debris flow event by armouring the underlying sands. This instance demonstrates how VISS may present as constructed boundaries (*sensu* Paola et al., 2018), internal to a sediment pile, in addition to their more common appearance as engineered synoptic topographies (e.g, hydrodynamic forms).

3.3.4. VISS without preserved vegetation

VISS are unequivocal when seen in direct association with standing trees but may be underdetermined when trigger fossils are not exposed at outcrop. Figure 15 shows an example of how instances of scour-and-mound beds can reflect vegetation-sediment interaction, even where fossil plants are missing. Figure 15A-B shows an exposure of outcrop of the Plantekløfta Formation on the banks of the Mimer River, in photographs taken six years apart. In both images, the scour-and-mound topography is apparent, but individual standing trees have variably become exposed or eroded as the river has cut back into the cliff face. In this instance, the preserved VISS can rarely be attributed to specific obstacles (Figs. 15C-H), but subsequent exposure indicates bed architecture to be related to buried vegetation. Modern analogue confirms that it is appropriate to search for putative VISS beyond the area immediately adjacent to a standing plant fossil because substrates can develop irregular topography inherited from upstream or cross-stream tree or woody debris obstacles (Reesink et al., 2020).

Middle and Upper Devonian strata of the Spitsbergen ORS contain many examples where VISS may be interpreted, but not proven by current exposure (Figure 16). In these instances, features such as concave- and convex-upwards bedding, often at high angles, are seen in association with circumstantial evidence for standing vegetation, such as rooting traces (Fig. 16A-C) or parautochthonous woody debris (Fig. 16D-F), or have a proximity to sites with abundant evidence for trees (e.g., Fig. 16G is a separate outcrop of the same ‘Lower Svalbardia Sandstone’ that hosts the woody debris layers shown in Fig. 8D-F).

According to Rygel et al. (2004), the term “VISS” excludes sedimentary structures induced by fallen or transported woody debris. However, driftwood can also act as an obstacle that induces sediment deposition, erosion and mounding (Nakayama et al. 2002; Reesink et al., 2020), and Trümper et al. (2020) have recently documented multiple ‘VISS-like’ forms associated with flow deflection by accumulations of large woody debris in ancient strata (“LWDISS”). In instances where there is no preservation of plant material, but strata contain VISS-like structures (Figure 16), it may be impossible to tell whether they are VISS *sensu stricto*, whilst being confident that bedform irregularities were induced by plants, either in situ or transported. To capture such uncertainty, it is thus practical to expand the original definition of VISS. It is here proposed that reasonable confidence in a VISS interpretation for bedforms may be achieved where they exhibit several of the following characteristics: 1) their form is not readily explainable by models of aggradation under undisturbed hydrodynamic flows; 2) they are known to be a product of unequivocal VISS elsewhere; 3) they occur in a succession known to host unequivocal VISS or standing fossil trees; and 4) they host fossil debris, or rooting traces, that indicates the former presence of standing vegetation. The forms in Figure 16 exhibit all of these characteristics and provide additional circumstantial evidence that arborescent land plants were obstructing flows, and sculpting landforms by forcing erosion and deposition from at least the Givetian onwards.

There are numerically more instances of ‘likely VISS’ (lacking fossils) than ‘definitive VISS’ (with fossils) in the Spitsbergen ORS, partly because VISS have fewer taphonomic hurdles to overcome than organic plant remains. The majority of plant biomass has always been fated to be reused by living biota through biogeochemical cycles (Gastaldo and Demko 2011), but while sediment piles accrued around vegetation may diminish in thickness as plants decay, VISS forms can persist (Small, 1997). Better recognition of these forms may improve our understanding of the extent to which trees have sculpted sedimentary landforms that are preserved in the rock record.

3.3.5. Vegetation without preserved VISS

In instances where plants were shallowly rooted, non-woody, or small stature, fossils in growth position are unknown: due to their limited mechanical resistance, they are likely to have been torn up or flattened during the deposition of siliciclastic sediment. However, one example is known in the Plantekløfta Formation where seemingly in situ diminutive vertical stems appear (Figure 17). Here, approximately ten subparallel axes (18-25 mm in diameter) extend through an undisturbed heterolithic package of shale and very fine sandstone, and fan out from an unpreserved point of convergence over an area a metre wide. These are interpreted as multiple branches of a recumbent lycopsid crown because axes have mature leaf cushions suggestive of *Protolepidodendropsis* (e.g., see 4 in Fig. 17F), but are only about quarter to a third of the diameter of the upright trunks nearby (one 75 mm *Protolepidodendropsis* fragment was found loose at the bottom of the outcrop, and lycopsids do not grow by getting significantly wider).

The crown appears to have been interred with minimal effect on the internal structure of the heterolithic host sediment. In this instance it seems likely that the attachment to a fallen trunk has acted as a disproportionately effective anchor (i.e., relative to roots of similar-sized individual plants), such that the branches have remained vertical when buffeted by flow and aggrading sediment (although the weight of the interring mass appears to have caused the branches to bend: Figure 17D).

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

3.3.6. Characteristics of Devonian VISS

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

The early examples of VISS observed here are less diverse than the forms originally described by Rygel et al. (2004), but this may in part be explained by the larger dimensions of the Carboniferous trees. In such instances, wake flow is the most significant driver of VISS creation (e.g., Allen, 1982; Rygel et al., 2004), arising where approaching flow is deflected downwards upon meeting a pillar-like obstacle, inducing an erosional horseshoe vortex and a reduced wake zone flow in the lee of the obstacle. The stature of the Devonian trees may explain why hydrodynamic erosional forms (e.g., centroclinal cross-strata) are rarer than depositional forms (e.g., upturned laminae), because smaller vegetation is effective at promoting leewise deposition but less so at promoting scour holes (e.g., Nakayama et al. 2002; Schlömer et al., 2020). Height differences may also explain the observed phenomenon whereby vegetation shadows are apparently smaller for archaeopterids than they are for lycopsids (e.g., compare Figs. 12 and 14) as obstacle marks become larger during shallower flows relative to the obstacle height (Schlömer et al., 2020).

Recent advances in the understanding of flow around plant obstacles (e.g., Schnauder and Moggridge, 2009; Larsen, 2019; Reesink et al., 2020; Schlömer et al., 2020) suggest that the diversity of Devonian plants observed in the Spitsbergen ORS would have induced other fluid responses in addition to wake flow (summarized in Figure 18). For example, elevated dense canopy can divert flow downwards, resulting in a sub-canopy downwards directed jet of water with accelerated velocity and propensity to erode. Such a scenario might be expected in association with archaeopterids (e.g., see the relatively large centroclinal scour fill association with such plants in Fig. 13B). Likewise, porous canopies or emergent stands can induce bleed-flow, baffling flow by reducing velocity gradients (Schnauder and Moggridge, 2009), and either increasing turbulence (where stands are sparse; e.g., see Fig. 15) or decreasing turbulence (where stands are dense) (Larsen, 2019). Figure 17 potentially shows the sedimentary signature of bleed-flow through a dense stand, where the branches of the lycopsid crown have been passively entombed without shadow or scour structures in the sandstone laminae.

It has also been recognised that flexible vegetation tends to have a higher rooting strength, bending towards the bed during high flow to avoid uprooting (Larsen, 2019), but also inducing drag especially where branches terminate in leaves or other constructions (Schnauder and Moggridge, 2009). Such complex hydrodynamic interactions can explain the buckled laminae seen in Figures 12D and 14F.

3.4. Cannel Coal

Cannel coal is a prominent, but volumetrically minor, lithology that occurs in four seams (maximum 80 cm thickness) within the Estheriahaugen Member of the Tordalen Formation (Figure 19). The cannel coals have previously been described in detail elsewhere (e.g., Vogt, 1941; Harland et al., 1976; Blumenberg et al., 2018; Marshall et al., 2019). They are composed of lipid rich organic matter derived from *Archaeopteris* and lycopod spores (Marshall et al., 2019), which accumulated in lacustrine settings (Blumenberg et al., 2018), rather than in situ coal swamps. Although not considered further here, they are significant for proving that vegetation-dependent lithologies (Davies et al., 2020) were being deposited by the Givetian.

3.5. Vegetation-Influenced Facies

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

1) Elevated mudrock content: In common with other Siluro-Devonian ORS localities, the succession has a high proportion of mudrock within its alluvial facies. At the localities visited in this study, mudrock strata comprise approximately 20% of the vertical succession of the Silurian Siktefjellet Group, 50% of the Lochkovian Red Bay Group, 60% of the Pragian-Emsian Wood Bay Formation, and 45% of the Frasnian Plantekløfta Formation. Such elevated alluvial mudrock content is rare before the advent of land plants (Davies and Gibling, 2010a; McMahon and Davies, 2018b), and a global post-Ordovician stratigraphic shift towards muddier alluvium can be credited to both production (enhanced weathering) and retention (through baffling, binding, and enhanced flocculation) of fines by vegetation (McMahon and Davies, 2018b; Davies and McMahon, 2021; Zeichner et al., 2021). The mudrock motif seen in the Spitsbergen ORS is typical of alluvial settings operating within early vegetated

landscapes, accentuated by the proximity to an active orogeny and equatorial palaeolatitude (Davies et al., 2017).

2) Complex alluvial architecture: a prominent feature of the Spitsbergen ORS is the abundance of inclined heterolithic stratification, recognised as recording lateral accretion of bank-attached fluvial bars (IHS-LA sets) (Figure 20). IHS-LA sets are a common, though non-exclusive, signature of meandering streams that exhibit a worldwide increase in abundance in the rock record from the Devonian onwards, as land plants and mud increased resistance to flow and corralled rivers into single-thread channels (Davies and Gibling, 2010a,b; McMahon and Davies, 2018a). All the Devonian stages in the Spitsbergen ORS contain at least isolated instances of IHS-LA, often in association with fossil plant debris. The largest occur within the Emsian Wood Bay Formation (Moody Stuart, 1966; Figure 20A), where they can reach thicknesses of more than 5 metres, attesting to river channels of a similar bankfull water depth (e.g., Bridges and Leeder, 1976).

4. Role of Climate and Tectonics

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

4.1. Climate

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

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

4.2. Tectonics

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

The preservation of standing trees in sedimentary successions (e.g., as seen in the Plantekløfta Formation: Figs. 12-17) has previously been interpreted as requiring exceptional intervals of rapid subsidence or relative sea-level rise (e.g., Bailey, 2011). This is based upon the recognition that burial of the trees must have happened faster than decay (Gastaldo et al., 1995; DiMichele and Falcon-Lang, 2011). However, recent conceptual advances in the understanding of how time is preserved in the rock record have shown that it is unnecessary to invoke exceptionally 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 where discharge is seasonally variable (Allen et al., 2013; Plink-Björklund, 2015; Fielding et al., 2018), and sometimes the sediment that buries trees in such situations maintains or enhances the dysoxia/ anoxia necessary for their preservation (Gastaldo and Demko, 2011).

5. Timeline of Devonian Biogeomorphic Innovations

The accrual of the Spitsbergen ORS was contemporaneous with major events in vegetation evolution which imparted novel allogenic controls on Earth surface processes and landforms. In Figure 21, these are summarized with reference to ongoing changes to biogeomorphology, as described by the biogeomorphic succession model of Corenblit et al. (2007, 2015, 2020). This conceptual model was developed to explain successional effects after modern flood disturbances in alluvial settings (Corenblit et al., 2007), and has previously been applied on an evolutionary timescale with respect to Carboniferous plant evolution (Davies and Gibling, 2013; Gibling et al., 2014; Corenblit et al., 2015). The discoveries in this present study indicate that aspects of biogeomorphic succession had developed by the Devonian, earlier than previously reported.

Present-day biogeomorphic succession begins with pioneer seedlings on fresh post-flood substrates, incrementally inducing feedbacks (e.g., enhanced sedimentation) such that eventually biological geomorphic processes dominate (e.g., years later there may be raised islands with successional forests) (Corenblit et al., 2020). Such well-established biogeomorphic systems can experience feedback from vegetation influence that extends over thousands of years. Here we summarise how such feedback was instigated in some of the earliest vascular plant communities, as evolutionary innovation increased the repertoire of plant-biogeomorphic processes and produced novel landforms and habitats.

5.1. Silurian and Early Devonian

Silurian strata of the Siktefjellet Group contain only comminuted debris, showing that small stature land plants were in existence, but had limited direct geomorphic influence. The only putative vegetation influence can be seen in the elevated mudrock content, relative to pre-vegetation alluvium. Mud could be produced and trapped by even primitive flora and is common in post-Ordovician alluvium (McMahon and Davies, 2018b; Mitchell et al., 2019; Zeichner et al., 2021): globally, some of the earliest vegetation-influenced biogeomorphology may have been enacted vicariously through this cohesive sediment (Davies et al., 2020). However, as individuals, the flora in the depositional environment of the Siktefjellet Formation likely responded analogously to small stature vegetation in modern ephemeral stream bed settings: suffering mortality and entrainment when exposed to only minor hydrodynamic stress (Sandercock and Hooke, 2010; Edwards et al., 2015). Comparable flora are seen in modern post-flood settings during the ‘geomorphic’ stage of biogeomorphic succession (Corenblit et al., 2007; 2015; 2020). In such settings, small diaspores and propagules begin to colonize fresh substrates, but get destroyed if the colonized patch experiences further disturbance before the plants take hold. In modern settings, the geomorphic phase persists for a few hours to a few months following a flood, but would have persisted indefinitely during the Silurian, when the maximum attainable plant stature offered negligible resistance to flow, and colonization would have been opportunistic and reliant on intervals or spatial patches of hydrodynamic quiescence.

Signatures in the Red Bay Group show that, by the Lochkovian, plants were able to resist flow and influence sedimentary processes (Figure 21). This was in part mediated by the attendant accumulation of weathered and retained mud, which increasingly formed thick deposits in the less frequently active parts of alluvial systems (e.g., floodplains and emergent bar tops; Fig. 4). The stability afforded by this cohesive sediment, coupled with evolutionary innovations in plant habit (e.g., rooting), meant that post-disturbance landscapes could begin to operate within the pioneer stage of biogeomorphic succession (Corenblit et al., 2007; 2015; 2020). This stage could now take over from the geomorphic stage after a few hours to months, permitting the recruitment of established vegetation on substrates and resistance to purely abiotic forcing of landforms. Evidence for this stage is seen in the muddy braid bar-tops likely colonized by cf. *Zosterophyllum* (Figs. 4 and 5). In addition to physical feedbacks, the development of established vegetation patches in rivers would have promoted habitat heterogeneity: comparable modern settings are associated with nutrient enrichment from allochthonous fecal material (Larsen 2019), and the co-occurrence of cf. *Zosterophyllum*, coprolites and trace fossils (Fig. 4) demonstrates that multiple organisms occupied the ecosystems that were likely engineered by bar-top flora.

In modern settings, complex fluvial geomorphology induces complex hydromorphology and biodiversity (Garcia et al., 2012), and so the diversification of novel and stable fluvial forms, induced by small stature Early Devonian plants, can be seen as a key driver of floral and faunal terrestrialization. Heterogeneity continued to develop throughout the Early Devonian. The Pragian-Emsian Wood Bay Formation contains not only some of the oldest palaeosols in the Spitsbergen ORS (e.g. Fig. 10), but also some of the oldest known palaeosol ichnofauna in the world (Morrissey et al., 2012; Genise et al., 2016), as well as further evidence that bar tops had become semi-stable vegetated patches within riparian environments. The Wood Bay Formation additionally yields direct evidence for pioneer vegetation in overbank settings: Figure 10 shows rooting in flood-deposited climbing ripple-laminated crevasse splay sands. This evidence for post-flood colonization has modern analogue where riparian plants reproduce asexually when propagules are snapped off and transported with flood sediment, or preferentially release spores or seeds at the end of the annual flooding season (Gurnell, 2014). The Wood Bay Formation plants certainly promoted fine sediment, shown by clay-lined roots (Fig. 10B), and the accrual of multi-year palaeosols in the floodplain fines that accrued in between crevasse events (Fig. 10). The influence of rooted vegetation in overbank fines is further emphasised by the earliest putative VISS: incipient hummocks at the bases of herbaceous plants, composed of baffled sediment and (presumably) organic matter (Fig. 11). Such forms are negligible in size but represent a marked increase in topographic complexity of terrestrial substrates that would have led to a cascade of ecological effects. Mounded topographies can alter patterns of groundwater flow, bidirectional exchange with surface water, and evaporation; all of which redistribute and partition nutrients or amenable conditions for habitation (e.g., temperature or oxygen) (e.g., Poole et al., 2008; Sullivan et al., 2016).

5.2. Mid and Late Devonian

While the Middle Devonian interval witnessed major palaeobotanical innovations, the biogeomorphic record in the Spitsbergen ORS is partly masked by an increased marine influence and transgressive shift towards coastal environments. Despite this, there is evidence that the sedimentary environments of all the Middle Devonian units were colonized by plants. The Eifelian Grey Hoek and Wijde Bay formations contain circumstantial evidence that habitats analogous to modern salt marshes may have developed in the Devonian, in the form of root structures hosted within dark organic-rich sediments that yield a marine fauna (Figure 9D-E). Salt marshes are some of the most biogeomorphologically active environments at the present day (e.g., Mudd et al., 2010), but there are few interpretations of such environments from the rock record. Putative Silurian instances have been interpreted from waterlogged palaeosols with marine fossils (Retallack, 2008), but lack direct evidence for plants and remain speculative. The earliest unequivocal salt marshes currently reported are Cretaceous in age, and are identified by dark coloured mudrocks, with a high total organic carbon content, compacted leaf litter fossils of extant halophytes, rootlets and marine microfossils (Uličny and Špičáková, 1997). The Grey Hoek and Wijde Bay examples provide evidence that small stature rooted vegetation colonized low gradient marginal marine settings that were traversed by channels (e.g., Fig. 6), and post-date the evolution of halophily (Channing and

Edwards, 2009). However, whether the rooted horizons record true salt marshes, inundated on a tidal rhythm by the sea, remains inconclusive from the available sedimentological and palaeontological evidence.

Although lacking the diversity of signatures expected in alluvial facies, the coastal, lacustrine and deltaic facies of the Middle Devonian ORS do show that potential stages of biogeomorphic succession had expanded by at least the late Eifelian (Figure 21). Post-disturbance plant communities would develop through the geomorphic and pioneer stages over the course of hours to months, but could now progress into the biogeomorphic phase. The biogeomorphic phase is characterized by landforms that are colonized by secondary successions of established vegetation, which can promote a balanced feedback between abiotic and biotic controls on local geomorphology. Evidence for this phase can be seen in the definitive and likely VISS in the Wijde Bay and Tordalen Formations (e.g., Figs. 11 and 16). The likely driftcretions in the Lower Svalbardia Sandstone (Fig. 8) provide evidence for landform elements that were wholly constructed from woody debris. There is also evidence that parts of the depositional environment progressed into the ecologic phase of the biogeomorphic succession model (Corenblit et al., 2007). This phase is characterized by autogenic vegetation successions and the stabilization of landforms to the extent that they become disconnected from hydrogeomorphic disturbance (creating landscape patches where biotic geomorphic processes dominate over abiotic geomorphic processes for prolonged intervals of decades to centuries, until reset by extreme low frequency disturbances). Direct evidence for autogenic vegetation successions is provided by the thin cannel coals in the Estheriahaugen Member (Fig. 19), and the abundant large woody debris that demonstrates that parts of the sedimentary environment must have hosted dense forested stands, detached from high frequency hydrodynamic disturbance. Combined, this evidence shows that the Mid Devonian was a revolutionary interval in the evolution of Earth surface processes, when all stages of biogeomorphic succession had become possible, and the Spitsbergen ORS hosts the earliest known instances of several biogeomorphic phenomena: e.g., the earliest driftcretions, the earliest cannel coal accumulations, and possibly the earliest salt marshes.

Late Devonian plant-sediment interactions recorded in the Spitsbergen ORS (Figure 21) are apparent continuations of Mid Devonian innovations, preserved within inland settings. Uprooting of trees may have become more common (Figure 17), leading to potential shifts in microhabitat diversity and sediment supply (Phillips et al., 2017). The abundance of hydrodynamic VISS from the Plantekløfta Formation (Figs. 12-15) additionally provide evidence that arborescent plants were acting as obstructions, inducing scour or deposition depending on factors such as stand density, flexibility and depth of flowing water (Figure 18). These interactions would have further accentuated the ecological and evolutionary consequences of topographic complexity in non-marine substrates, first instigated in the Early Devonian (e.g., compare Figs. 10 and 14A).

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

Many of the signatures in the Spitsbergen ORS indicate that many biogeomorphic processes and products, still active in modern analogous settings, appeared on Earth for the first time in the Devonian. Modern observations attest to linkages between these phenomena, and show how the development of one biogeomorphic feature can have cascade effects on habitat heterogeneity and organisms, which in turn feedback further local innovation in biogeomorphic process and form. The sedimentary record imperfectly captures such nuanced chains of events in the form of vegetation-dependent and vegetation-influenced signatures, which provide limited evidence for how Devonian land plants began to impose themselves as essential components in the mechanistic operation of the Earth surface. However, whilst coarsely resolved, these sedimentary signatures provide a timeline for the onset of plant influences on the character of the sedimentary-stratigraphic record. The Spitsbergen ORS provides a fortuitous natural archive of many biogeomorphic firsts, and illustrates that a crucial c. 40 myr interval between the Lochkovian and Frasnian saw the rapid and incremental onset of many familiar plant-engineered non-marine landscapes.

6. Conclusions

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

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FIGURE AND TABLE CAPTIONS

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

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

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

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

Figure 4 – Lochkovian plant-sediment interactions in the Red Bay Group (Andréebreen Formation) at Buchananhalvøya. Downstream accretion elements (Miall, 1985), allied with reworked calcretes and in situ plant material, support previous explanations of these strata as braided river alluvium (Friend et al., 1997). A-B) Laterally continuous braided fluvial sandbodies (highlighted yellow) and minor shales (grey). Palaeoflow towards left of image. C-D) Detail of boxed area highlighted in A and B: Two braid bar deposits, separated by bar-top fines. Palaeoflow towards left of image. E) Detail of the base of the upper barform, showing basal lag of intraformational calcrete conglomerate (arrowed) resting on grey shale. F) Abundant zosterophyll fragments, preserved within the bar top shales. G-H) Biogenic signatures associated with bar top zosterophylls include casts of *Cruziana* arthropod furrows in base of overlying sandstone (G) and helical fish coprolites within the plant-bearing shales (H). Scale bar 1 cm in G, 1 mm in H.

Figure 5 – Sedimentary context of plant fossil remains in the Pragian-Emsian Wood Bay Formation (Austfjorden Member) at Kapp Petermann. A-D) Plant remains restricted to non-eroded inflection point of a downstream accreting sand barform (A-B), and consisting of relatively complete specimens of small ?psilophytes (C-D), that would have been growing at the bar top and margins. Palaeoflow towards left of image. E-H) Stratigraphically further up the same section, braided alluvial in-channel sandy bedforms form a discrete unit within palaeosols (E-F); within these, plant remains are restricted to reworked instances of comminuted carbonaceous matter along trough cross-bed foresets (G) or small fragmentary remains within planar-bedded sandstones (H). Scale bar 1 cm in C, D, G, H.

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

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

Figure 8 – Accumulations of woody debris within the Old Red Sandstone of NW Spitsbergen. A-C) Eifelian accumulation of smaller woody debris within flat-bedded (A) heterolithic strata of the Wijde Bay Formation at Kronprins Haralds Fjell, comprising unoriented compressed wood material up to 40 cm in length (B-C). Rifle in A is 1.1 m long, scale bar in B, C is 10 cm. D-F) Oldest known driftcretion deposit (Givetian) within the Tordalen Formation (Fiskekløfta Formation) at Fiskekløfta. Individual accumulation of dominantly archaeopterid wood, up to 2 metres length (D) persists within a series of eleven sandstone beds that form a 5 metre-thick amalgamated succession (E). Some of the drifted logs can be seen to have rested on subaerially exposed bars, as shown by close association with true substrates of extensive aeolian adhesion marks (F). Inset rose diagram in (D) shows axial orientation of 151 individual pieces of woody debris measured throughout the 5 metre-succession. Metre stick for scale, inset scale bar in F is 1 cm.

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

rooted horizons arrowed. Boundary between Tordalen Formation and Planteryggen Formation, Fiskekløfta. Scale bar in A-D is 1 cm, scale bar in E is 1 m.

Figure 10 – Detail of rooting structures in the Pragian-Emsian Wood Bay Formation (Austfjorden Member) at Kapp Petermann (same locality as Figure 5). A) Succession consists of alternating blocky red palaeosols, punctuated with thin sandstones representing crevasse splay deposition. B-C) Details of crevasse splay sandstones showing penetration by clay-lined roots (B) and climbing ripple-laminated (C). Scale bar in A is 1 m, scale bar in B is 1 cm, ruler in C is 20 cm.

Figure 11 – Earliest (Emsian-Eifelian) VISS in the Spitsbergen ORS. A-B) Emsian primitive VISS in the form of gently mounded synoptic topography to a root-mottled (arrowed) palaeosol (A) in the Wood Bay Formation (Dicksonfjorden Member), Germaniabekken. Detail of mound above root mottle shown in B. Visible ruler is 50 cm in A, 70 cm in B. C-D) Eifelian decay-related VISS formed as hollow plant stem filled with mud and decayed, causing downturning of beds. Asymmetry of downturning and tilt of plant cast suggests that the plant toppled as it decayed. Wijde Bay Formation, Tage Nilssonfjellet. Ruler is 20 cm.

Figure 12 – Frasnian VISS associated with standing archaeopterid flora: A-B) Narrow archaeopterid stem with steeply upturned laminae (hydrodynamic VISS). Plantekløfta Formation, Munindalen. C-D) Buckled and steeply upturned laminae on either side of small archaeopterid stem apparently with some flexibility and bent into flow. Plantekløfta Formation, Munindalen. E-F) Large archaeopterid encased in sandstone and flanked by upturned laminae (hydrodynamic VISS). Plantekløfta Formation, Munindalen. Ruler in A, B is 1 m, ruler in C, D is 20 cm, scale bar in E, F is 1 m.

Figure 13 – Hydrodynamic VISS associated with standing archaeopterids, buried by a debris flow. Plantekløfta Formation, Munindalen. A-B) Three archaeopterid stems are seen within

sandstones, containing VISS that indicated they interacted with the flows that deposited the sandstones. The fossil trees have been truncated by a debris flow depositing a thick conglomerate, with prominent clusters of cobbles preferentially deposited around the tops of the decapitated tree trunks. C-J) Details of the image shown in A, demonstrating how the archaeopterids were rooted in mudrock (E-F) and persisted as sand was deposited around them, before being truncated during the individual debris flow event. Metre stick/ 1 m scale bar in each image, except 20 cm scale bar in E, F.

Figure 14 – Frasnian VISS associated with standing lycopsid flora: A-B) Small lycopods provide armoured mantle to muddy substrate, preserved as synoptic topography of small hummocks and swales. Plantekløfta Formation, Munindalen. Visible ruler is 80 cm. C-D) Hydrodynamic VISS showing upward transition from centroclinal fill of scour to upturned laminae. Plantekløfta Formation, Planteryggen. Visible ruler is 25 cm. E-F) Buckled and upturned laminae developed on the stoss side of a buried flexible stem. Plantekløfta Formation, Planteryggen. Visible ruler is 40 cm.

Figure 15 – Hydrodynamic VISS associated with standing lycopsids in the Plantekløfta Formation at Munindalen, demonstrating how distorted bedding persists even where fossil plant material is lost. A-B) Images of the same cliff face taken 6 years apart, showing erosion of the lycopsid bearing sandstone bed by bank collapse into the Mimer River. White arrow provides reference point, yellow arrows point to standing lycopsids. White box in A shows view of standing lycopsids figured by Berry and Marshall (2015, their fig. 4L). C-H) Details of the fossil bearing bed taken in 2016 showing hydrodynamic VISS in direct association with in situ plants (C-F), as well as instances along the same horizon where structures are likely to be hydrodynamic VISS despite the absence of direct fossil evidence (G-H). Scale bar in A, B is 2 m, visible ruler in C is 30 cm, scale bar in E, G is 50 cm.

Figure 16 – Frequently oversteepened concavo-convex bedding within amalgamated sandstone bodies that appear too irregular, localized and individually unique to be formed by undisturbed hydrodynamic flow. These are putative VISS as they contain abundant evidence for standing vegetation or woody debris, but lack direct association with unequivocal plant triggers. A-C) Putative VISS in the Eifelian Wijde Bay Formation, Tage Nilssonfjellet: convex-upwards mound in centre of A-B contains 10 cm carbonaceous root structures (C). Metre stick for scale. D-F) Putative VISS in the latest Givetian Tordalen Formation (Fisklekløfta Member) at Torelva, comprising thick convex-up mounds (arrowed) of steep-margined sandstone beds with frequent large plant debris (F) between beds. Mounds appear to be a result of flow diversion around woody debris, possibly in addition to decay- or compression-related deformation of the woody sediment pile. Metre stick and pen (20 cm) for scale. G-H) Putative VISS in the latest Givetian Tordalen Formation (Fisklekløfta Member) at Fiskekløfta (similar stratigraphic horizon to D-F). Continuous scour-and-mound topography persists across the same amalgamated sandbody that contains driftcretion accumulations of woody debris on the opposite side of the river (Figure 8). Scale bar is 1 m.

Figure 17 – Evidence for tree uprooting in the earliest Frasnian, revealed by fallen lycopsid crown that had toppled onto a small meander point bar (IHS-LA in Fig. 20B). Plantekløfta Formation, Munindalen. A-D) Upwards deflected lycopsid branches, encase by both mud and sand. Metre stick for scale. E-F) Details of the above, showing minimal deflection of sedimentary laminae by the small flexible lycopod branches. Visible part of ruler is 60 cm in E, scale bar is 10 cm in F.

Figure 18 – Potential variability in influence of standing vegetation physiology on fluid flow and bed shear stress, illustrated with (non-exclusive) examples of Devonian flora known from the Spitsbergen Old Red Sandstone.

Figure 19 – Development of cannel coal in Givetian strata of the Tordalen Formation (Estheriahaugen Member) at Munindalen. A) Outcrop. B) Hand specimen.

Figure 20 – Examples of IHS-LA sets throughout the Old Red Sandstone in NW Spitsbergen. A) Emsian: 5 metre-thick IHS-LA within the Wood Bay Formation. Dicksonfjorden Member, Scott Keltiefjellet. B) Frasnian: 2 metre-thick IHS-LA associated with both standing and fallen lycopsid and archeopterid vegetation (fallen lycopsid in Figure 17 occurs at same stratigraphic level highlighted). Plantekløfta Formation, Munindalen. Scale bar in each image is 1 m.

Figure 21 – Summary of Devonian plant-sediment interactions in the Spitsbergen Old Red Sandstone, showing reconstructions of palaeoenvironmental settings and plant-sediment interactions for the Early, Mid and Late Devonian. Also shown are hypothesised duration of re-establishment of (bio)geomorphic phases after flood disturbance for each interval (see text and Corenblit et al., 2007 for further details).

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

Table 2 – Presently known fossil plant genera and forms from the Old Red Sandstone in NW Spitsbergen. Table compiled from Høeg (1942), Schweizer (1968, 1999) and Berry (2005), plus material identified here. Note that we now recognise that the Plantekløfta Formation contains the distinctive sandy layer of green/yellow sandstone which contains the rich 'Planteryggen' or 'Upper Svalbardia Sandstone' flora (Høeg, 1942; Berry and Fairon-Demaret, 2001). This was previously thought to either belong to the Fiskekløfta Member of the Tordalen Formation (Schweitzer, 1999) or the Planteryggen Formation (Piepjohn and

Dallmann, 2014): an uncertainty arising from an inaccurate locality description in Høeg (1942). Using archive sources of notebooks and original field collection labels from Høeg's expedition, we were able to conclusively locate the type locality of *Svalbardia* and *Enigmophyton* in 2016. The horizon of the 'Upper Svalbardia Sandstone' flora is definitively intercalated with conglomerates, well above the mapped base of the Plantekløfta Formation (extensive collections made during this study are the subject of presently ongoing investigation at Cardiff University, and this table is based on provisional data).

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

Age	Unit	Thickness	Lithology
Frasnian	Plantekløfta Formation	> 300 m	Dark mudrocks (c. 55%), sandstones, conglomerates.
Frasnian	Planteryggen Formation	335 m	Drab to red mudrocks (c. 45%), grey-green arkose sandstones.
Givetian	Tordalen Formation	c. 640 m	Drab to red mudrocks (c. 40%), grey-green arkose sandstones. Some coal.
Eifelian	Wijde Bay Formation	600 m	Grey to yellow sandstones and dark mudrocks (c. 45%)
Eifelian	Grey Hoek Formation	1000 m	Grey sandstones and dark mudrocks (c. 50%)
Pragian-Emsian	Wood Bay Formation	3000 m	Predominantly red mudrocks (c. 50%) and sandstones. Some calcrete.
Lochkovian	Red Bay Group	3250 m	Basal conglomerate units, red and drab mudrocks (c. 40%) and sandstones. Reworked calcrete.
Silurian	Siktefjellet Group	1825 m	Grey sandstones, conglomerates and mudrocks (c. 20%).

Depositional Setting
Meandering rivers, forested floodplains, debris flows

Poorly exposed and delineated, but likely fluvial

Brackish to freshwater lacustrine strata with fluviodeltaic deposits and coal mires
Coastal, estuarine setting

Fluvial deposition in brackish coastal swamp

Multiple different fluvial (braided and meandering) and floodplain settings
Alluvial fans, dominantly seasonal braided rivers, minor sporadic marine influence

Poor and localized exposure, limited palaeoenvironmental evidence: reported as braided fluvial deposition.

Unit	Flora	Plant form
Mimerdalen Subgroup (Frasnian)	Archaeopteridalean trunk bases in situ (i.e. *Svalbardia*)	Medium size leafy and woody progymnosperm tree (trunk)
	Svalbardia polymorpha	Medium size leafy and woody archaeopteridalean tree (branches), progymnosperm
	Caulopteris sp.	Trunk (up to 10 cm), with branch scars, likely of *Svalbardia* or *Enigmophyton*
	Enigmophyton superbum	Large leafed ?non-woody plant of shrub-like habit or small tree, unknown affinity
	Ibyka vogtii	Non-woody plant of shrub-like habit, iridopteridalean
	Protolepidodendropsis pulchra in situ	2-4 m arborescent lycopsid in forests
Mimerdalen Subgroup (Givetian)	*Actinopodium* - the anatomy of *Svalbardia polymorpha*	Medium size leafy and woody archaeopteridalean tree (branches)
	Caulopteris sp.	Trunk (up to 10 cm), with leaf scars, likely of *Svalbardia* or *Enigmophyton*
	Protolepidodendropsis pulchra	2-4 m arborescent lycopsid
	Prototaxites	Upright ?fungi
Wijde Bay Formation (Eifelian)	*Protocephalopteris praecox*	Shrub, unknown affinity
	Large ‘sulcate stems’ 170 mm wide	Unknown tree
	Psilophyton arcticum	Spiny, ?herbaceous, unknown affinity
	Hostimella sp.	Smooth branching axes, small, anatomically preserved
Grey Hoek Formation (Eifelian)	*Arctophyton gracile*	Small shrub, possibly cladoxylopsid
	Large ‘sulcate stems’ up to 155 mm wide	Unknown tree
	Psilodendrion spinulosum	Spiny small ?non-woody plant of shrub-like habit, unknown affinity
	Psilophyton arcticum	Spiny, ?herbaceous, unknown affinity
	Noisia ramosa	?Herbaceous, unknown affinity
Wood Bay	*Barinophyton* sp	?Herbaceous

Formation (Pragian-Emsian)	*Zosterophyllum longum*	Herbaceous zosterophyll
	Hostimella	Small naked axes
	Psilophyton sp.	?Herbaceous

Red Bay Group (Lochkovian)	*Prototaxites*	Upright ?fungi
	Pachytheca	Ball-shaped ?algae
	Hostinella	Small naked axes
	cf. *Zosterophyllum*	Herbaceous, clumped, zosterophyll
	cf. *Gosslingia*	Herbaceous zosterophyll

		Fossil Plant Material			**Biologica**
Age	**Units**	**Comminuted debris**	**Fragmentary remains**	**Standing fossils**	**Alluvial mudrock**
Frasnian	Plantekløfta, Planteryggen	●	●	●	●
Givetian	Tordalen	●	●		●
Eifelian	Grey Hoek, Wijde Bay	●	●		●
Pragian-Emsian	Wood Bay	●	●		●
Lochkovian	Red Bay	●	●		●
Silurian	Siktefjellet	●			●

lly Influenced Phenomena		Biologically Dependent Phenomen			
Palaeosols	IHS-LA	Putative VISS	Hydrodynamic VISS	Decay-related VISS	Woody debris
●	●	●	●	●	●
●	●				●
●	●	●		●	●
●	●				
●	●				

a	
Driftcretions	**Cannel coal**
●	●

figure 1

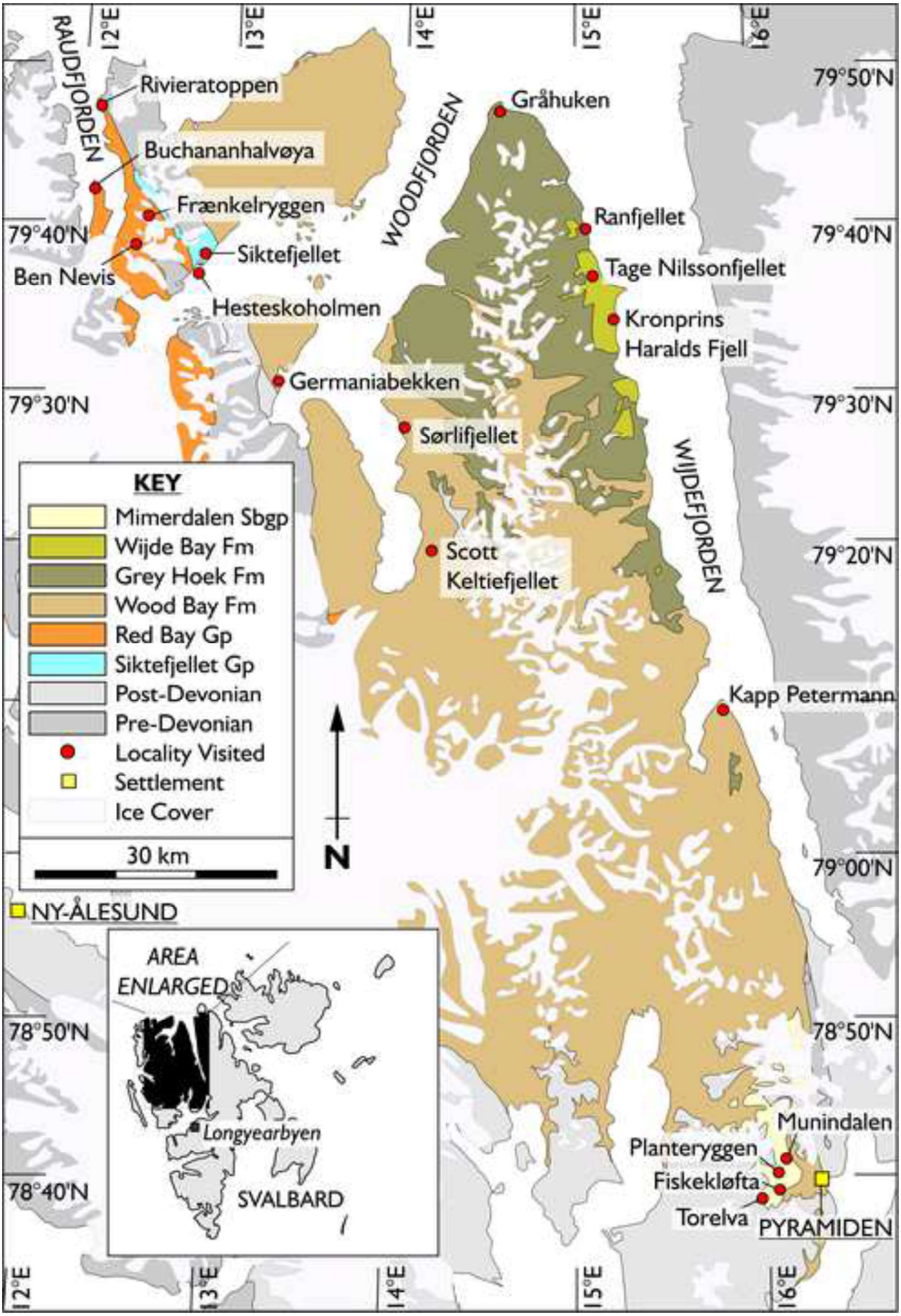
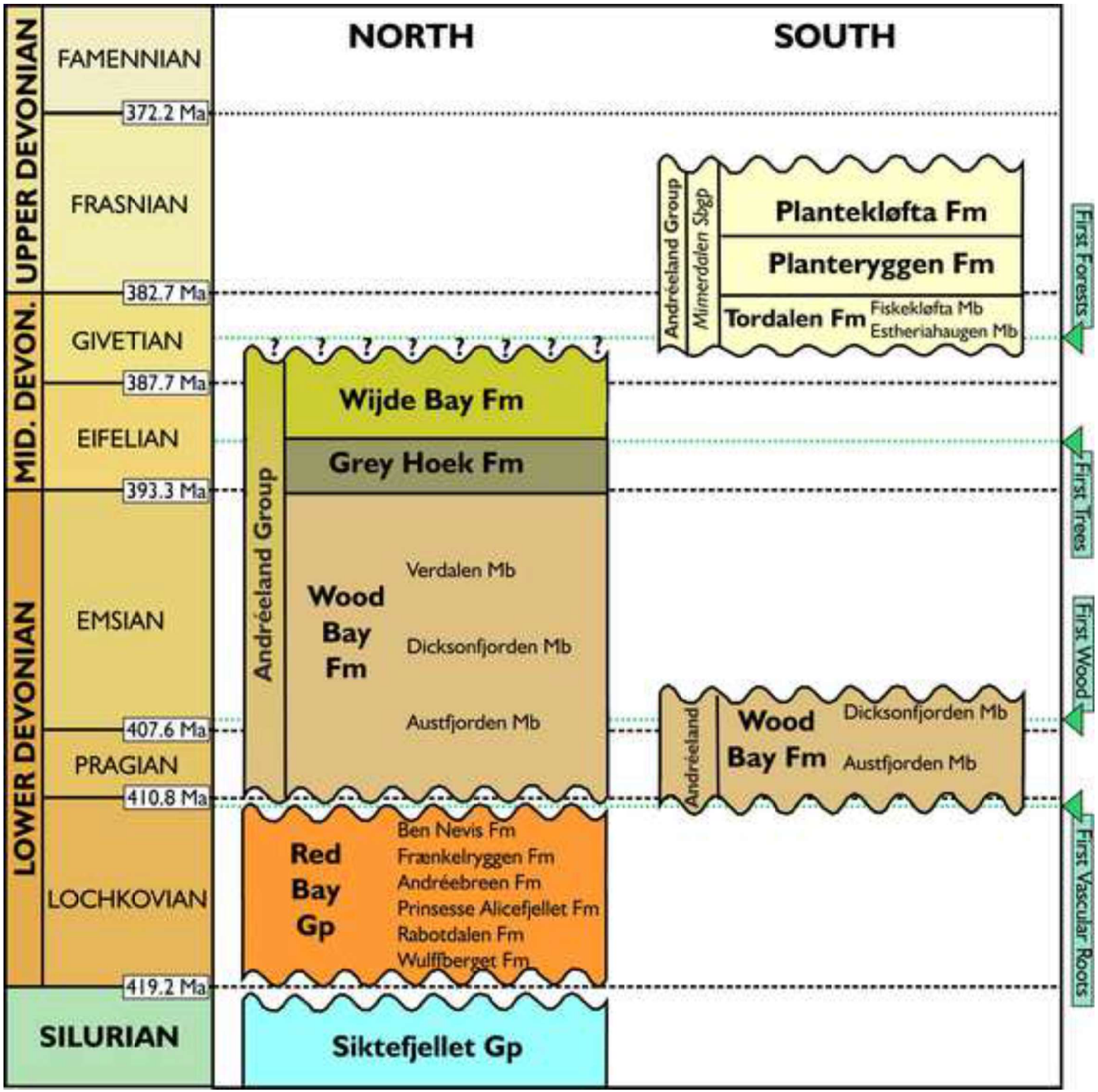

12°E
13°E
14°E
15°E
16°E
79°50'N
79°40'N
79°30'N
79°20'N
79°00'N
78°50'N
78°40'N
RAUDFJORDEN
Rivieratoppen
Buchananhalvøya
Frænkelryggen
Ben Nevis
Siktefjellet
Hesteskoholmen
Germaniabekken
WOODFJORDEN
Gråhuken
Ranfjellet
Tage Nilssonfjellet
Kronprins Haralds Fjell
Sørlifjellet
Scott Keltiefjellet
WIJDEFJORDEN
Kapp Petermann
KEY
Mimerdalen Sbgp
Wijde Bay Fm
Grey Hoek Fm
Wood Bay Fm
Red Bay Gp
Siktefjellet Gp
Post-Devonian
Pre-Devonian
Locality Visited
Settlement
Ice Cover
30 km
N
NY-ÅLESUND
AREA ENLARGED
Longyearbyen
SVALBARD
Munindalen
Planteryggen
Fiskekløfta
Torelva
PYRAMIDEN

figure 2


UPPER DEVONIAN
MID. DEVON.
LOWER DEVONIAN
SILURIAN
FAMENNIAN
372.2 Ma
FRASNIAN
382.7 Ma
GIVETIAN
387.7 Ma
EIFELIAN
393.3 Ma
EMSIAN
407.6 Ma
PRAGIAN
410.8 Ma
LOCHKOVIAN
419.2 Ma
NORTH
SOUTH
Andréeland Group
Wijde Bay Fm
Grey Hoek Fm
Wood Bay Fm
Verdalen Mb
Dicksonfjorden Mb
Austfjorden Mb
Red Bay Gp
Ben Nevis Fm
Frænkelryggen Fm
Andréebreen Fm
Prinsesse Alicefjellet Fm
Rabotdalen Fm
Wulffberget Fm
Siktefjellet Gp
Andréeland Group
Mimerdalen Sbgp
Plantekløfta Fm
Planteryggen Fm
Tordalen Fm
Fiskekløfta Mb
Estheriahaugen Mb
Andréeland
Wood Bay Fm
Dicksonfjorden Mb
Austfjorden Mb
First Forests
First Trees
First Wood
First Vascular Roots

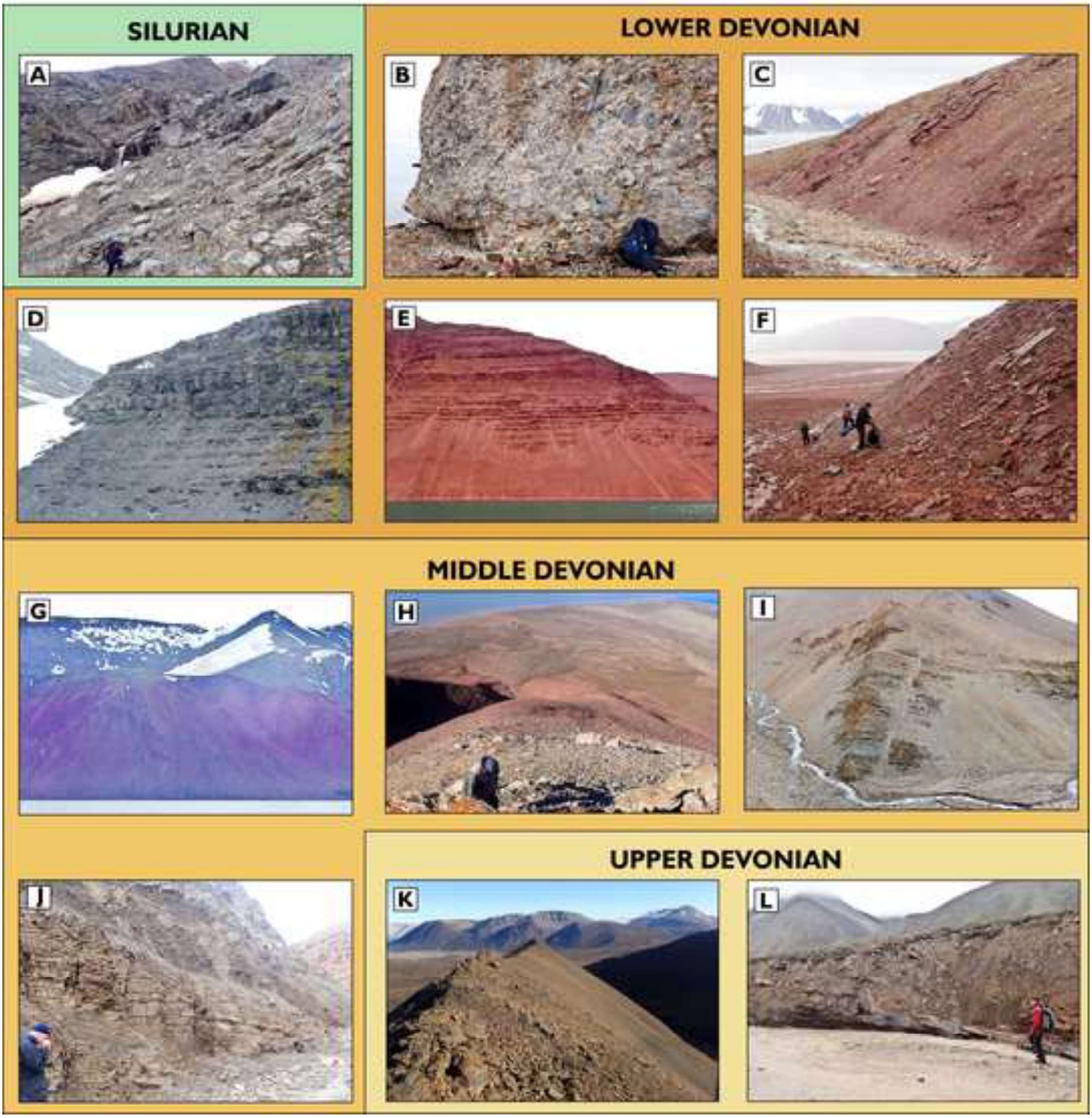

SILURIAN
LOWER DEVONIAN
A
B
C
D
E
F
MIDDLE DEVONIAN
G
H
I
UPPER DEVONIAN
J
K
L

figure 4

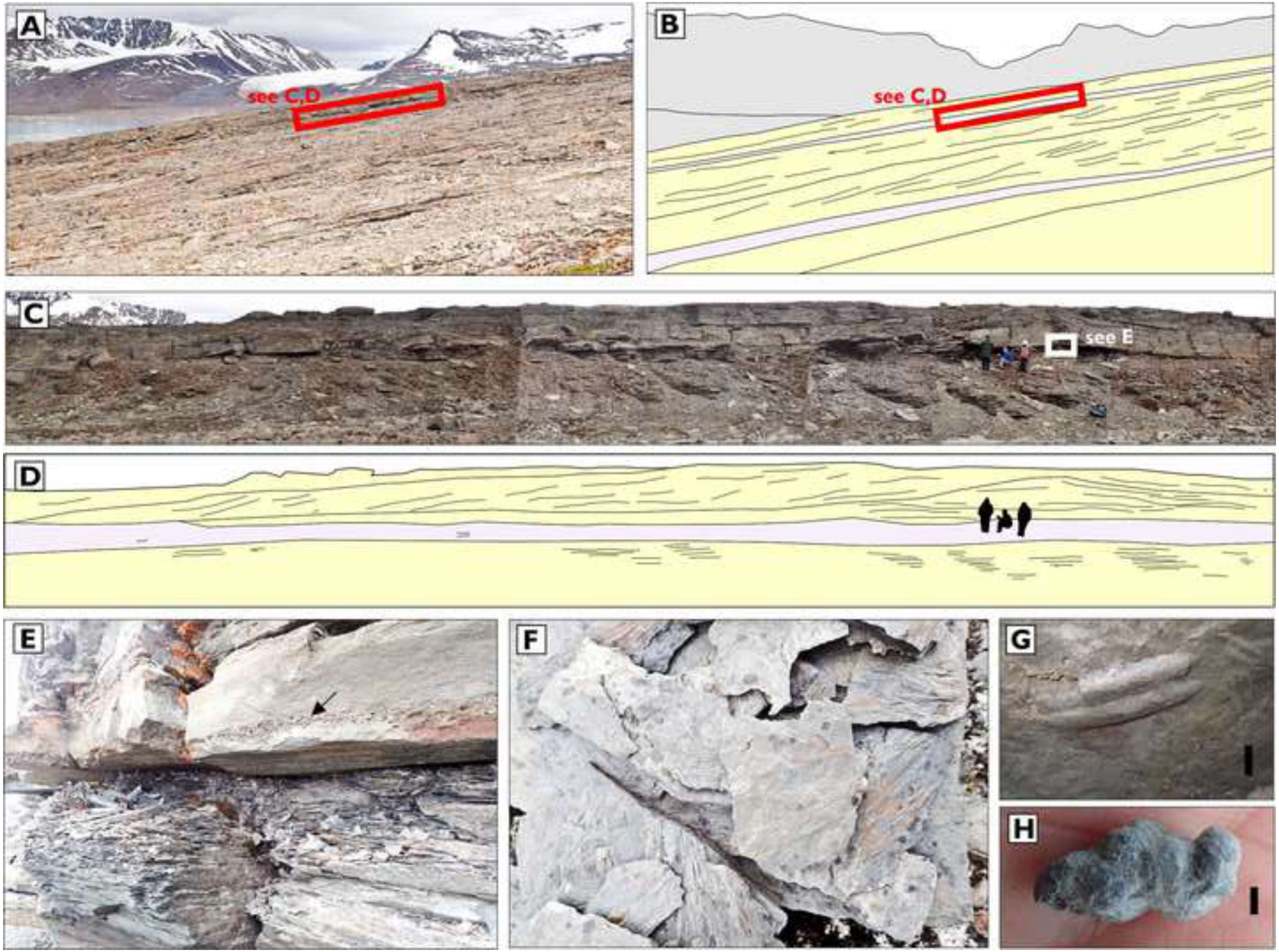


figure 5

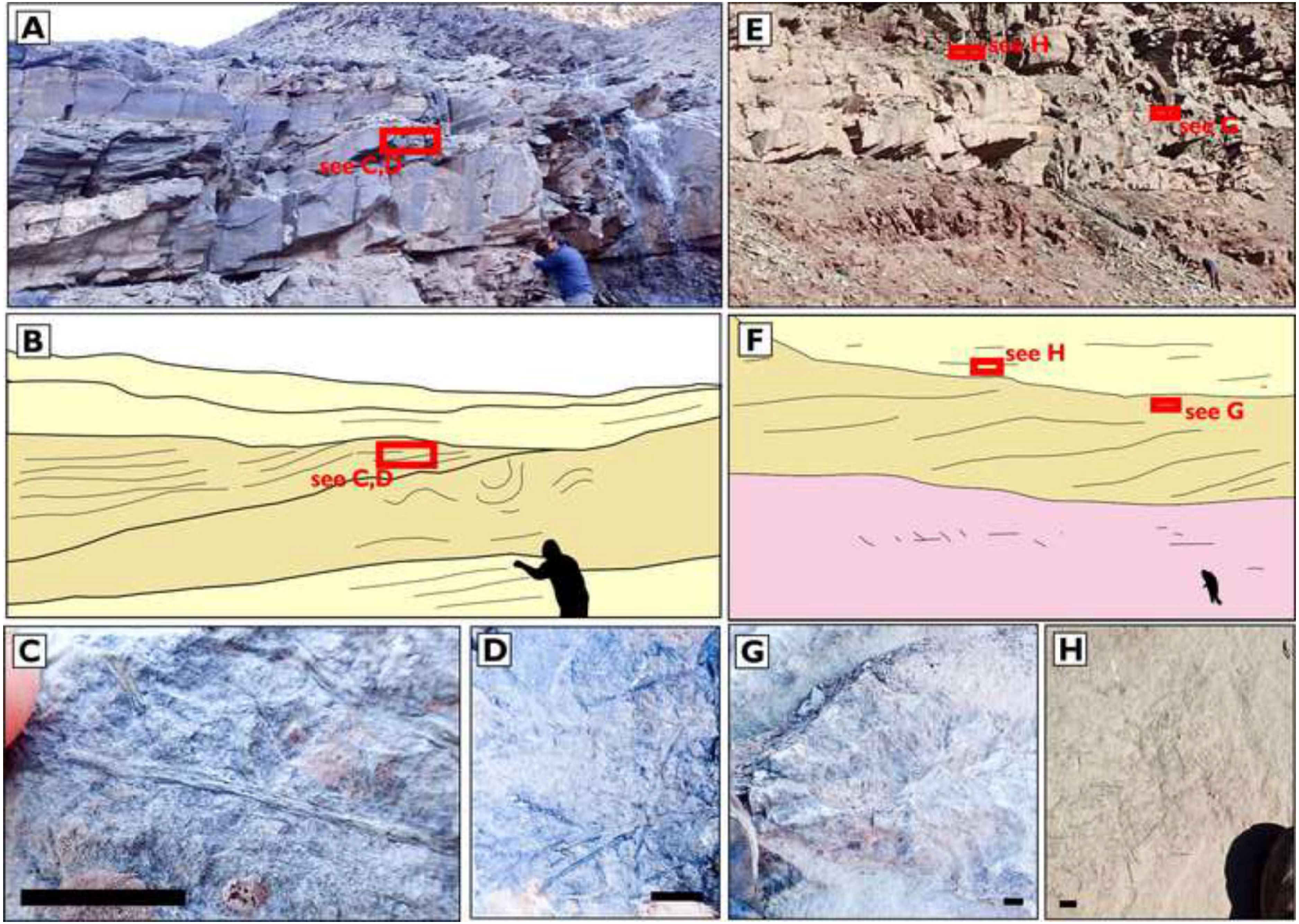


figure 6

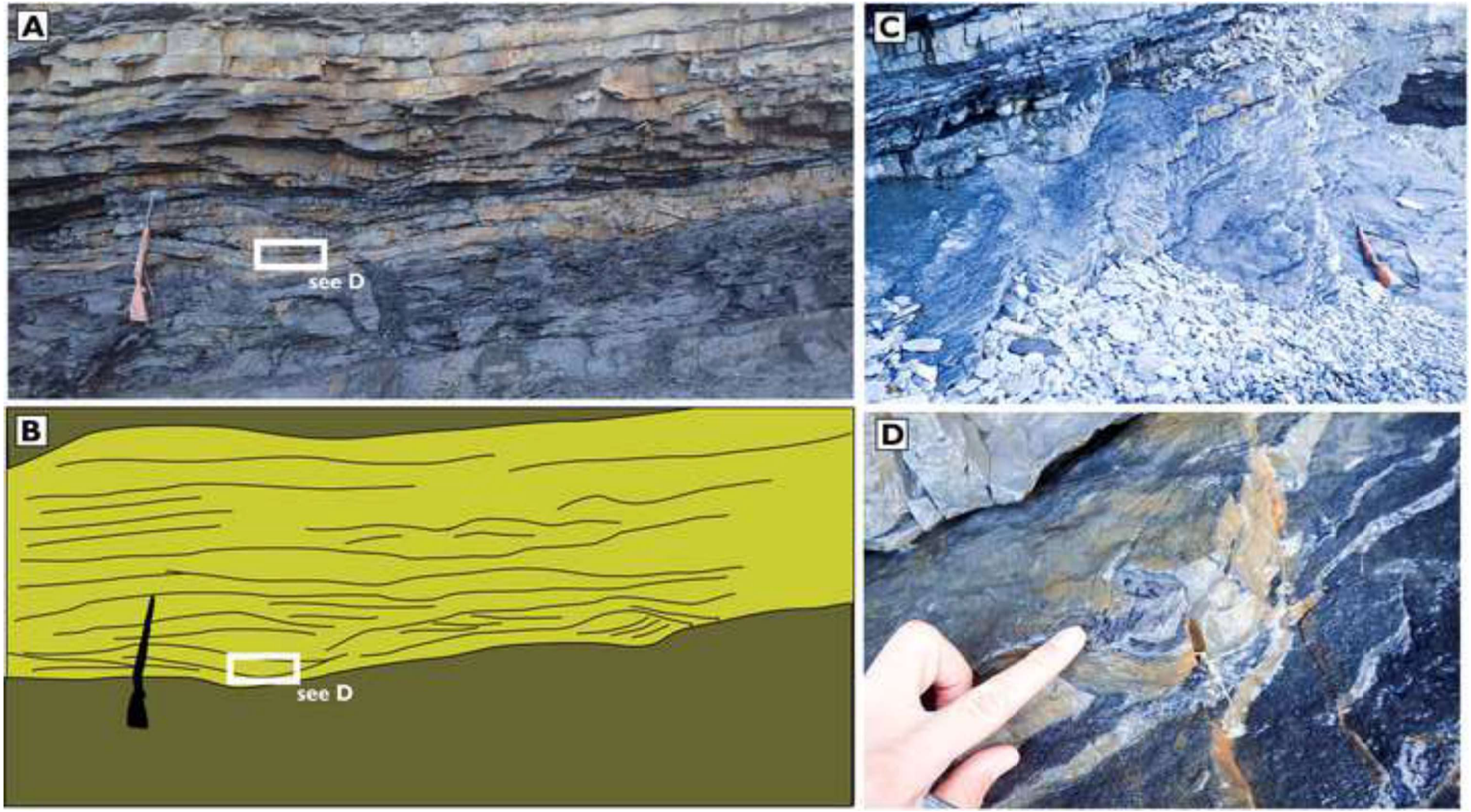


figure 7

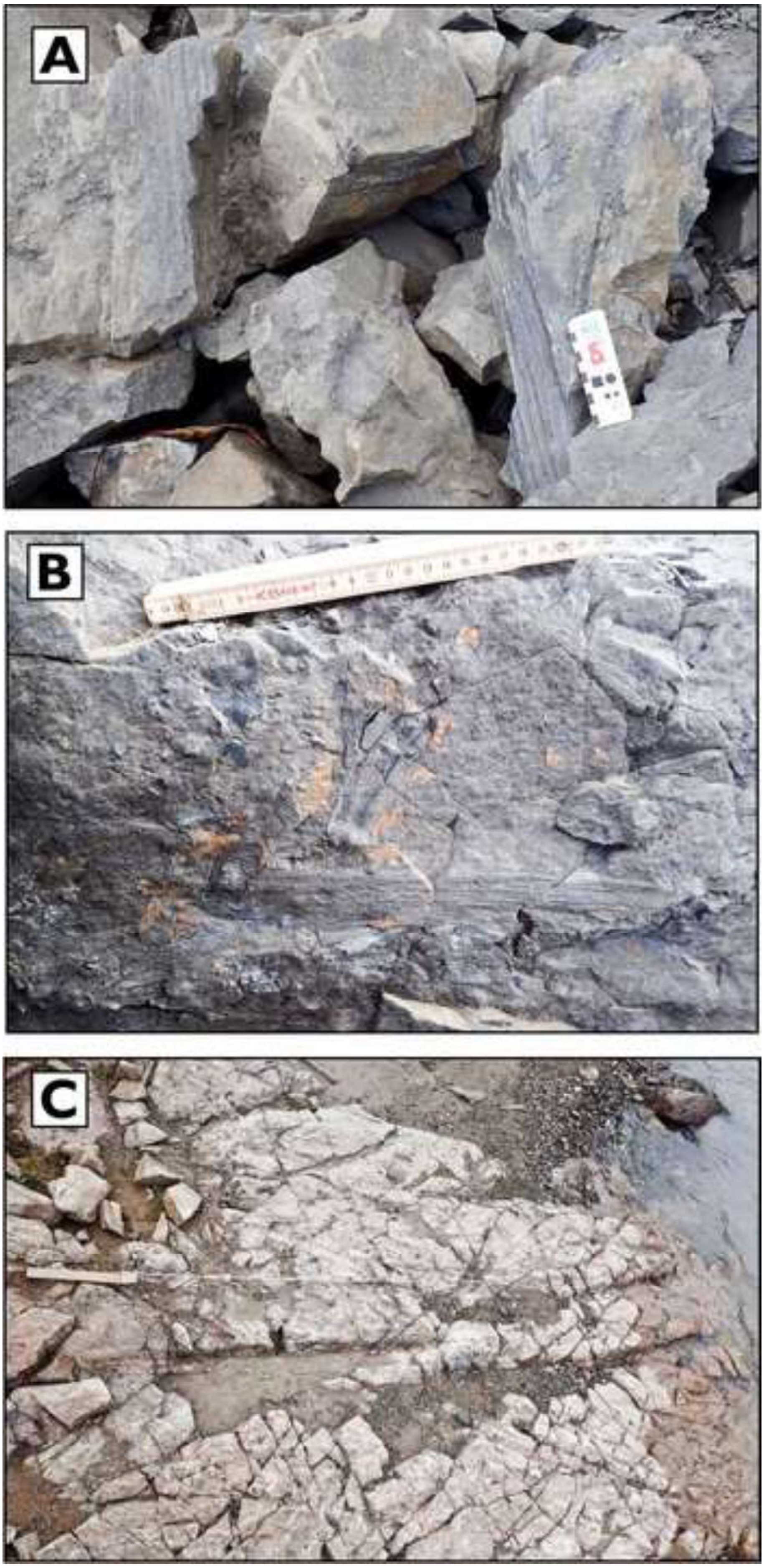
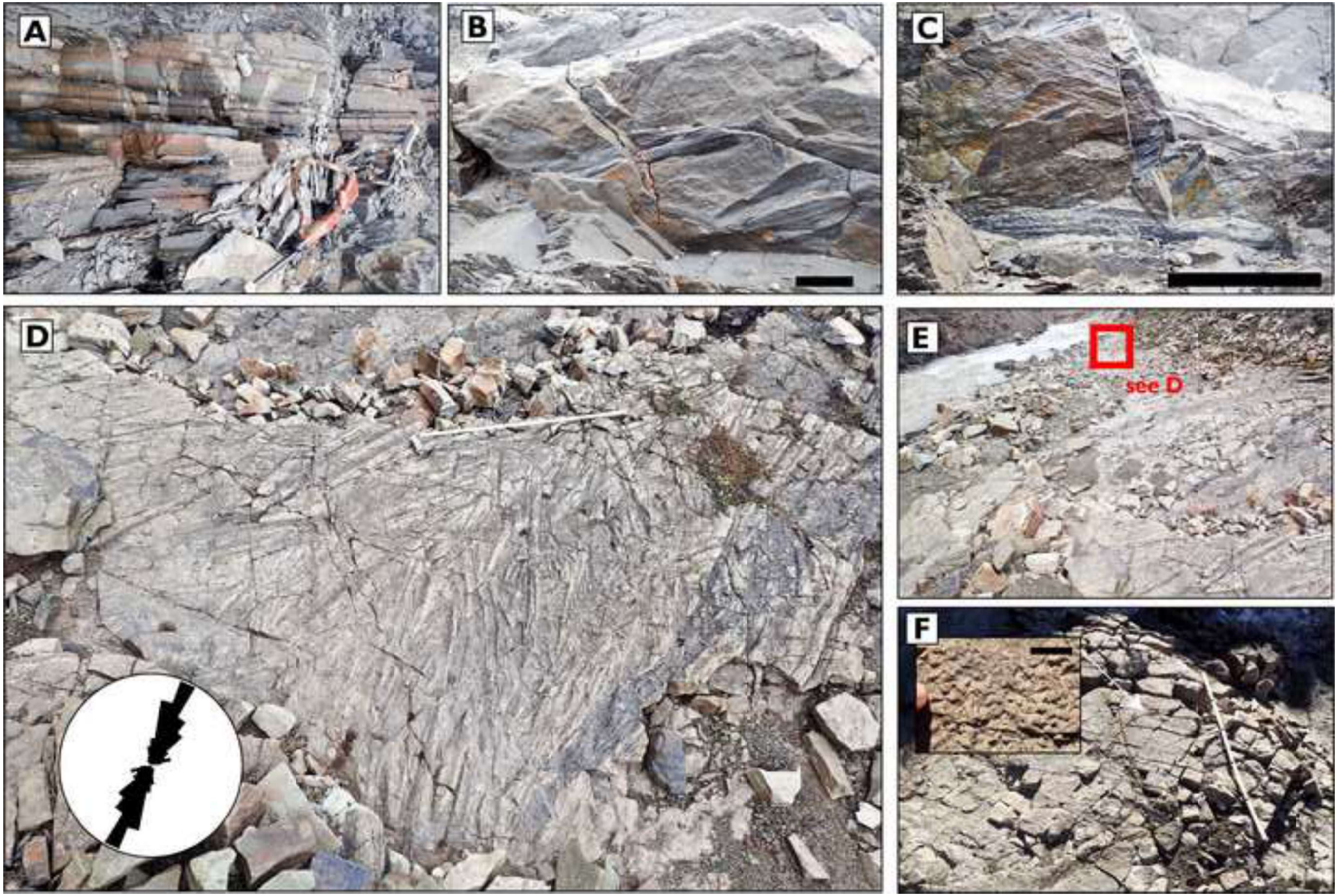
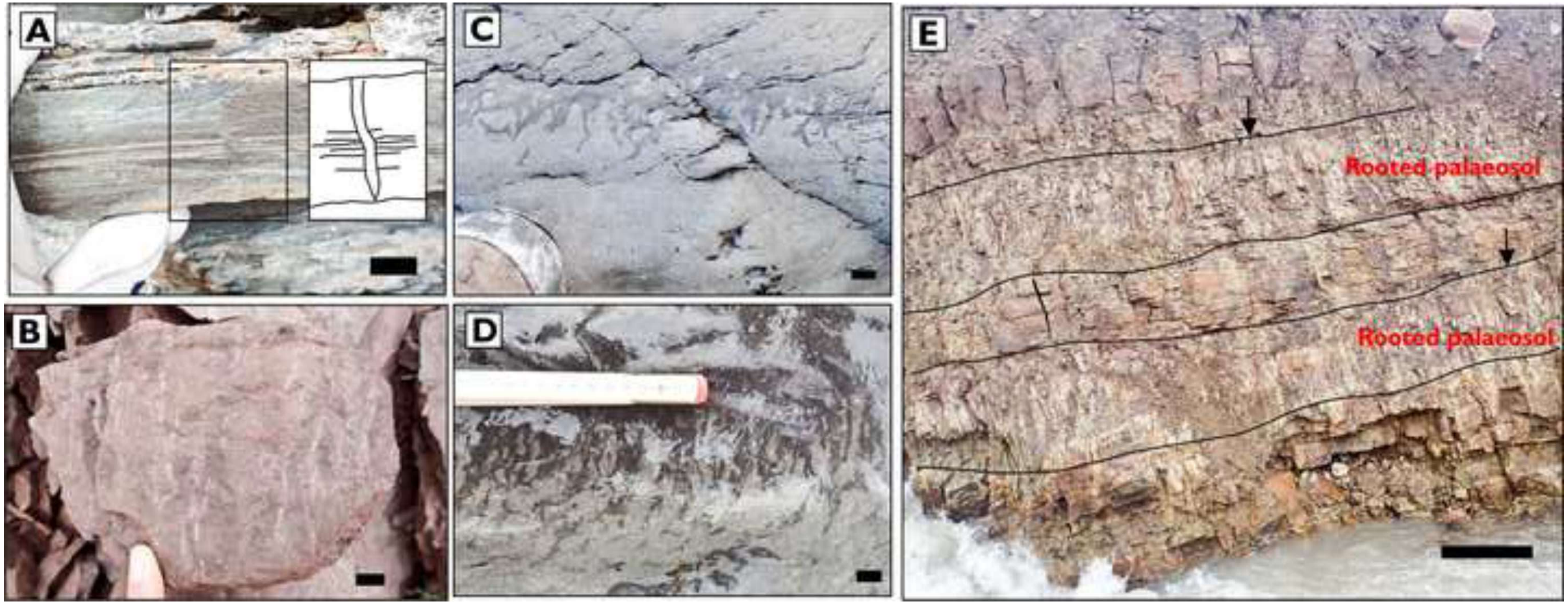


figure 8




A
B
C
D
E
Rooted palaeosol
Rooted palaeosol

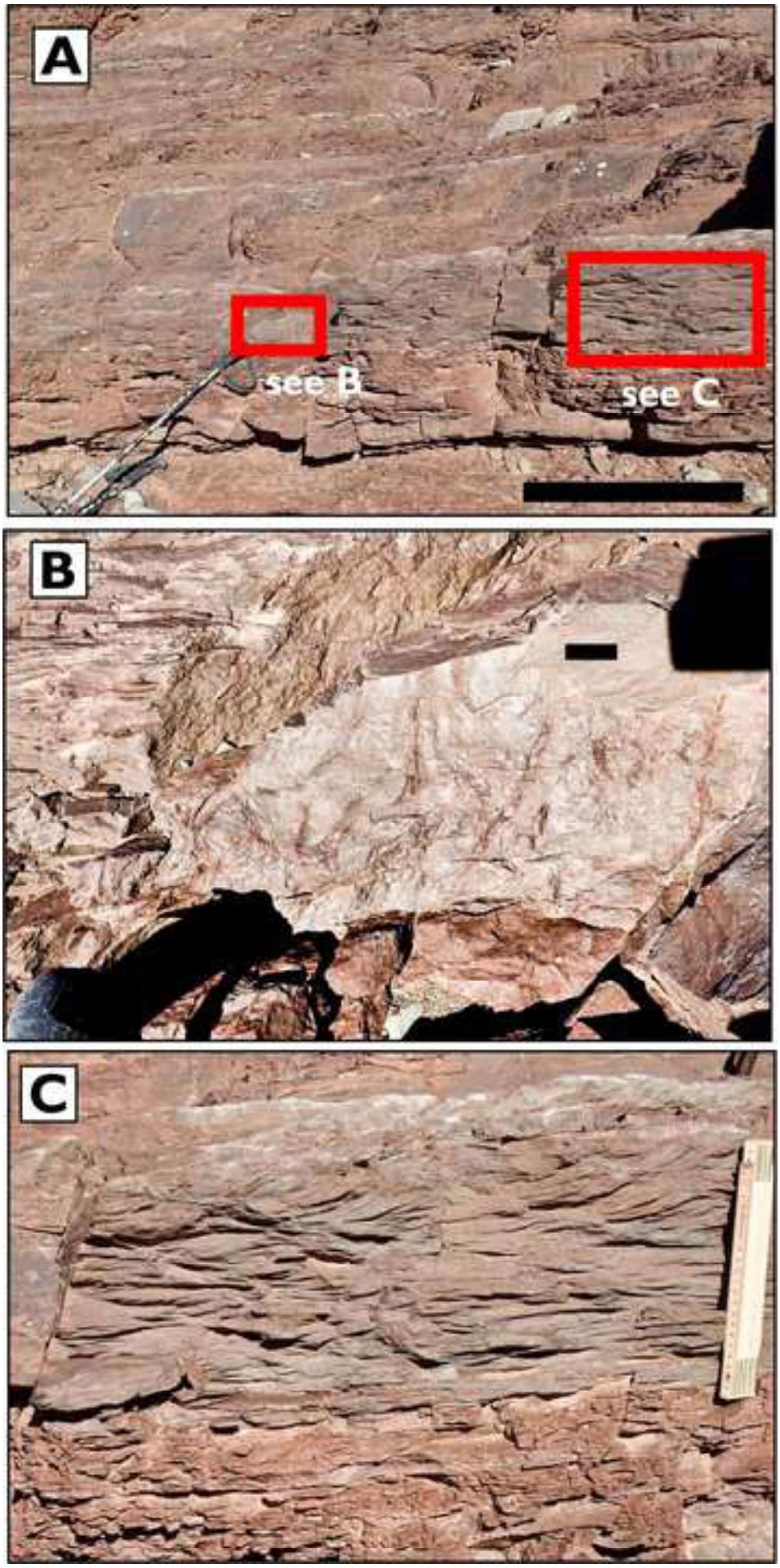
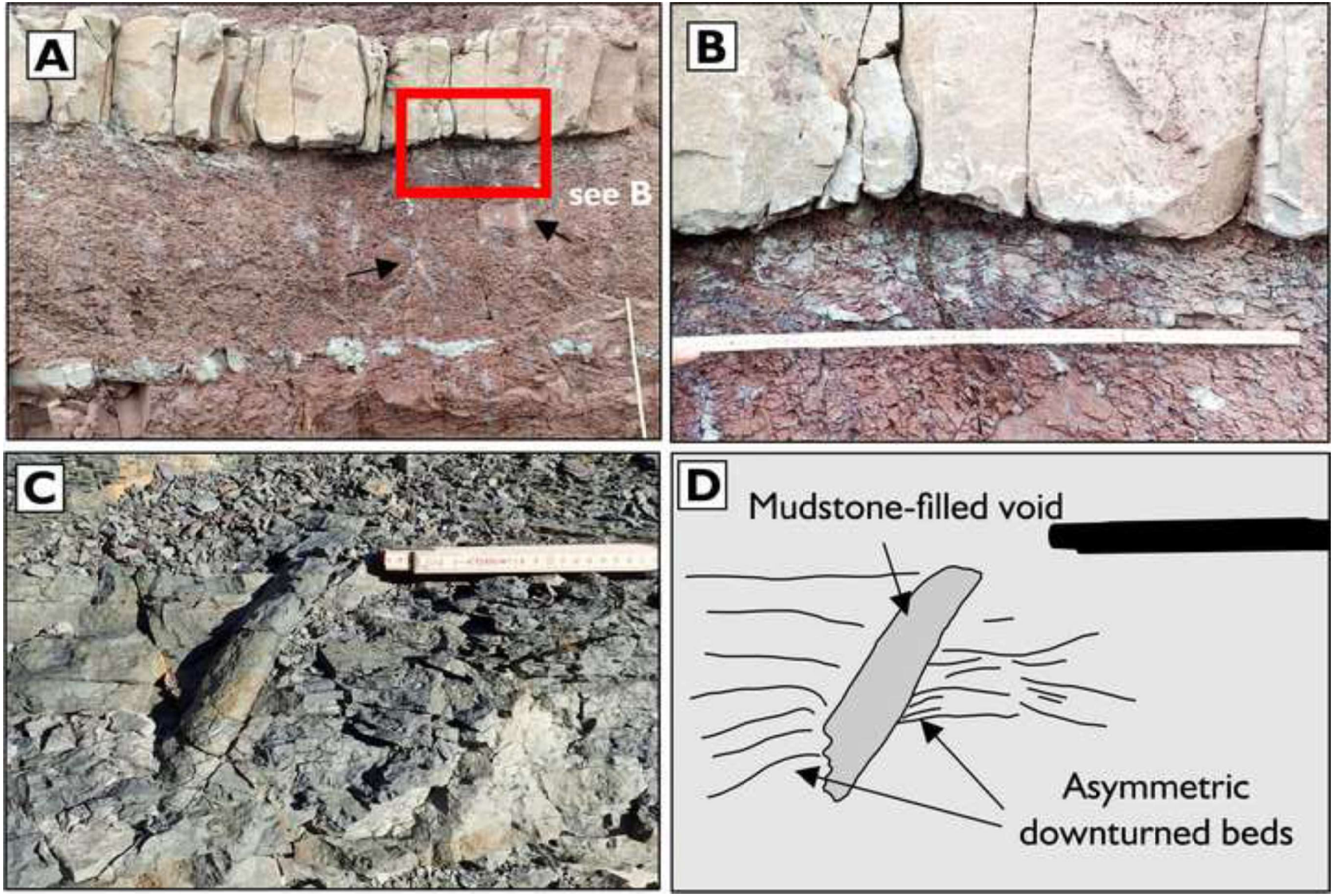
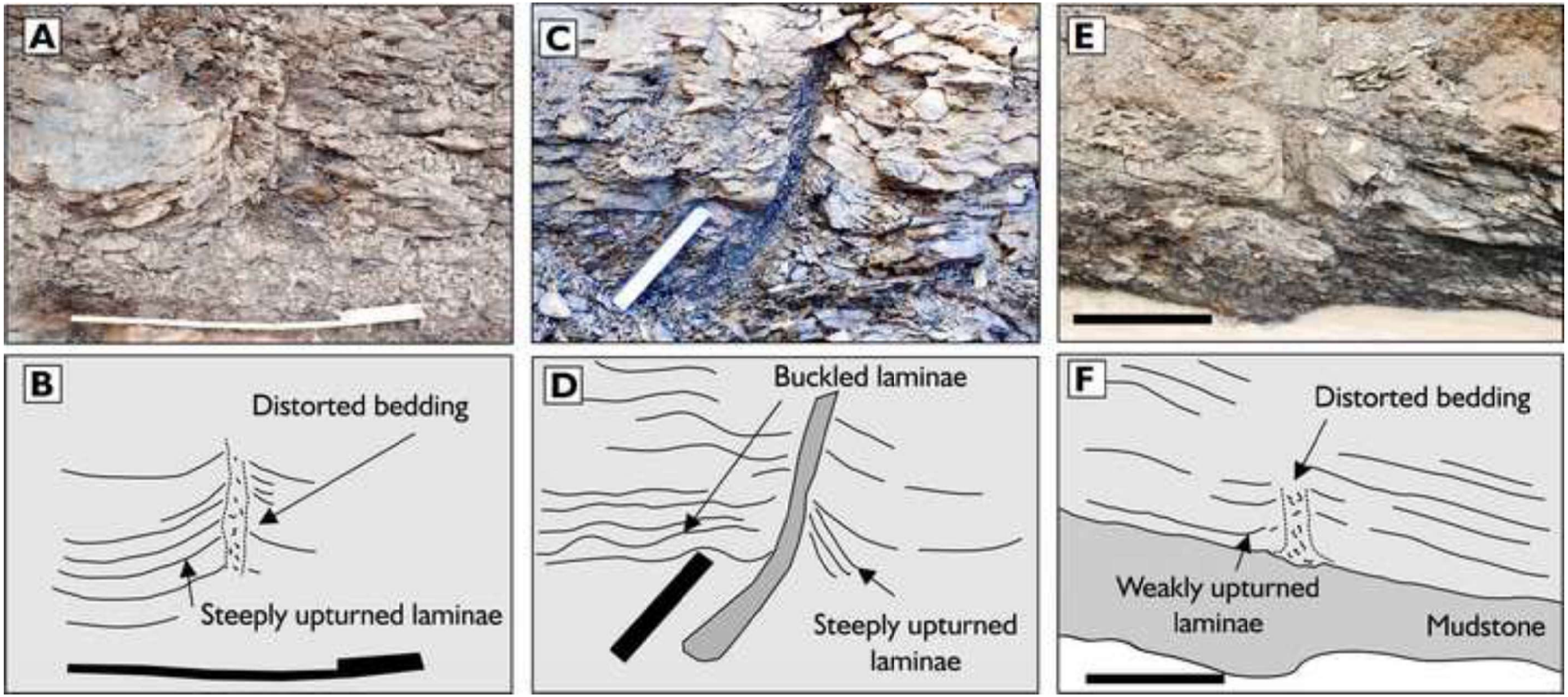

A
see B
see C
B
C

figure 11


A
see B
B
C
D
Mudstone-filled void
Asymmetric
downturned beds


A
C
E
B
Distorted bedding
Steeply upturned laminae
D
Buckled laminae
Steeply upturned laminae
F
Distorted bedding
Weakly upturned laminae
Mudstone

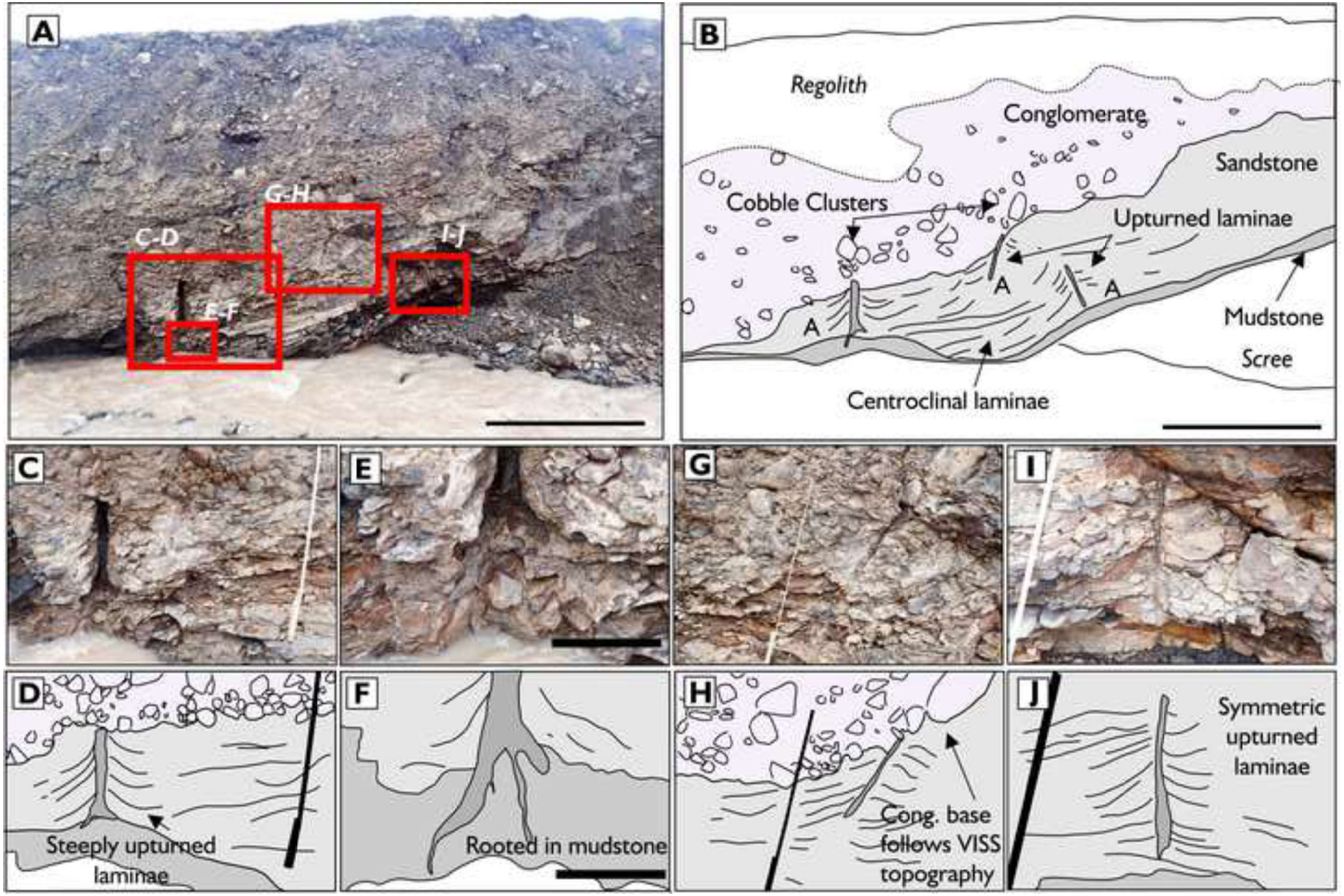

A
C-D
G-H
I-J
E-F
B
Regolith
Conglomerate
Sandstone
Cobble Clusters
Upturned laminae
A
A
A
Mudstone
Scree
Centroclinal laminae
C
E
G
I
D
Steeply upturned laminae
F
Rooted in mudstone
H
Cong. base follows VISS topography
J
Symmetric upturned laminae

figure 14

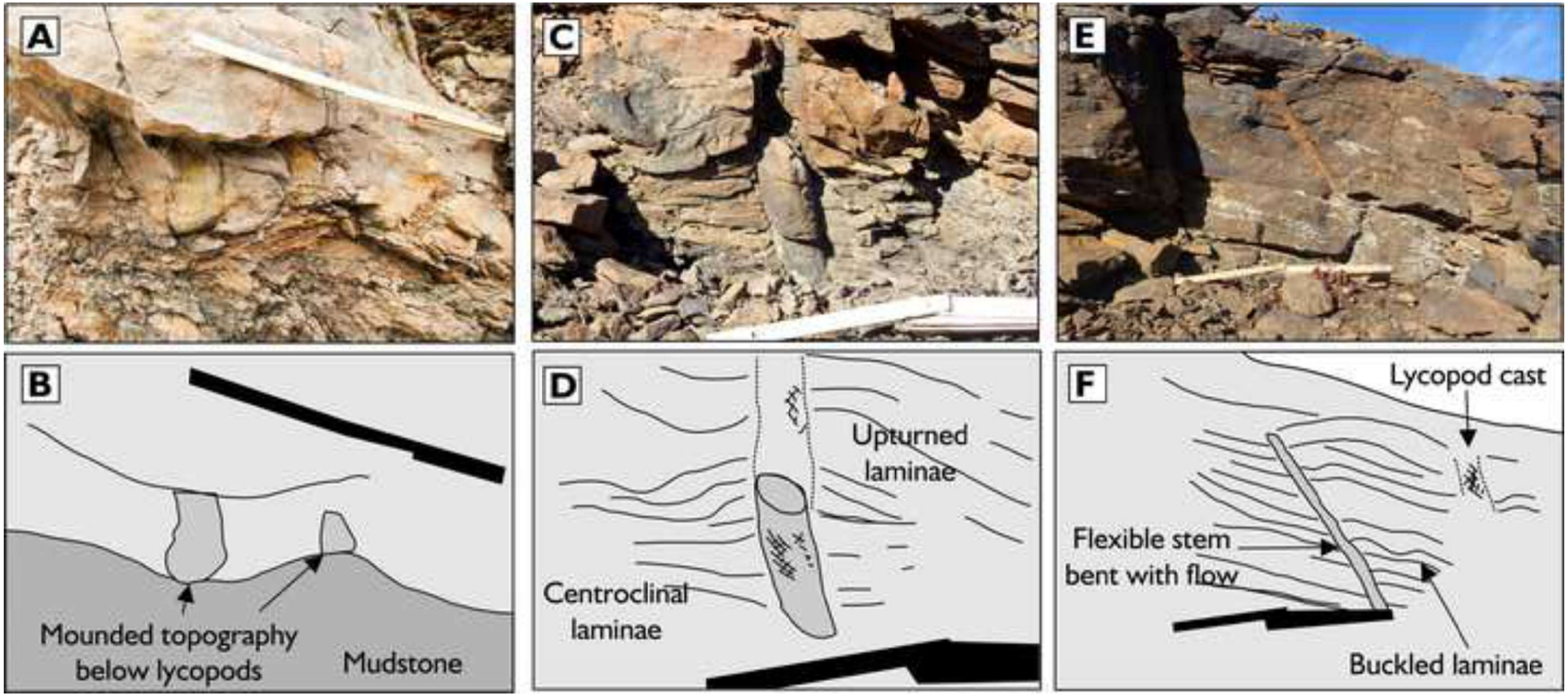
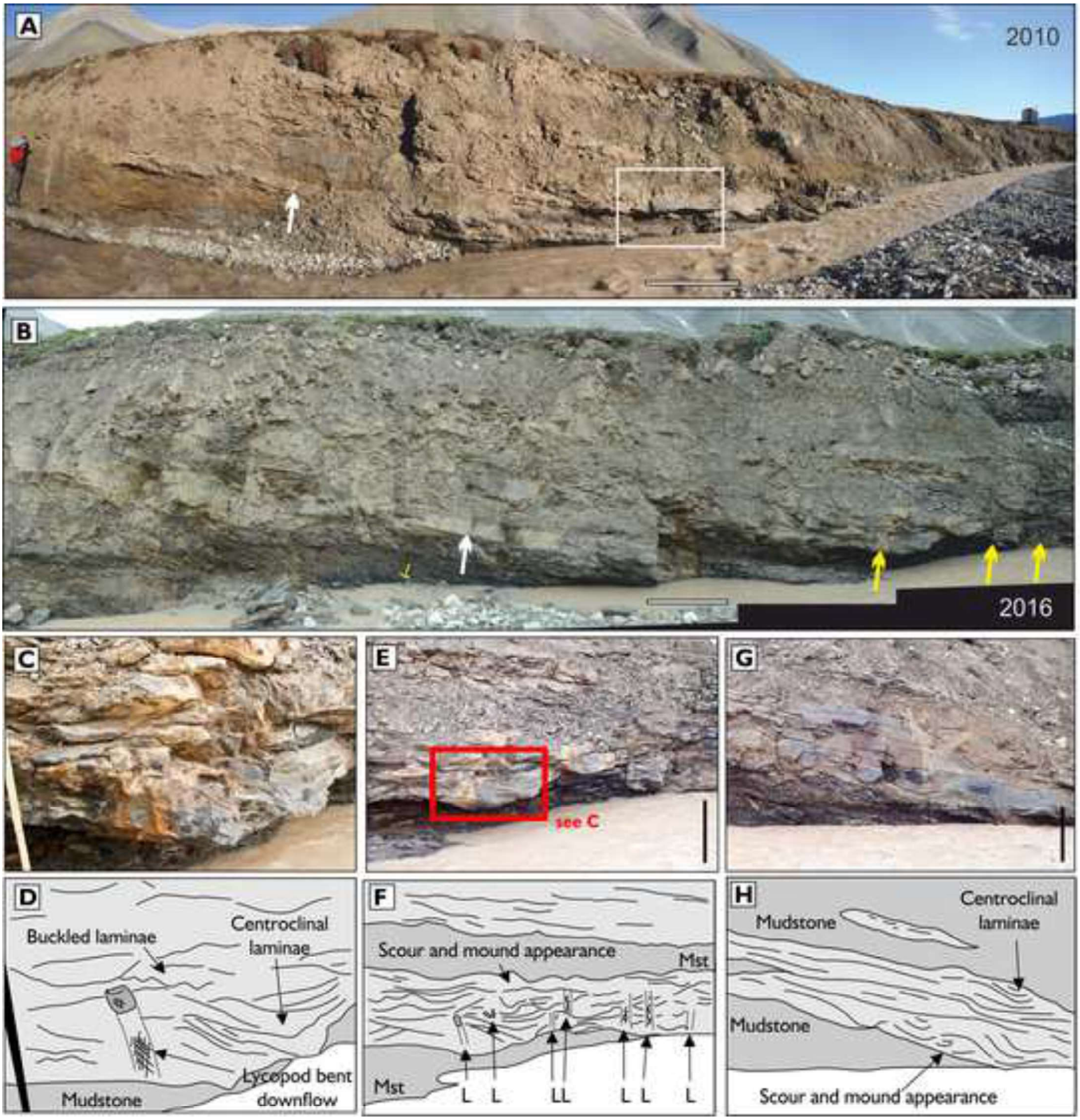

A
C
E
B
Mounded topography
below lycopods
Mudstone
D
Centroclinal
laminae
Upturned
laminae
F
Lycopod cast
Flexible stem
bent with flow
Buckled laminae

figure 15


A
2010
B
2016
C
E
see C
G
D
Buckled laminae
Centroclinal laminae
Lycopod bent downflow
Mudstone
F
Scour and mound appearance
Mst
Mst
L
L
LL
L
L
L
H
Mudstone
Centroclinal laminae
Mudstone
Scour and mound appearance

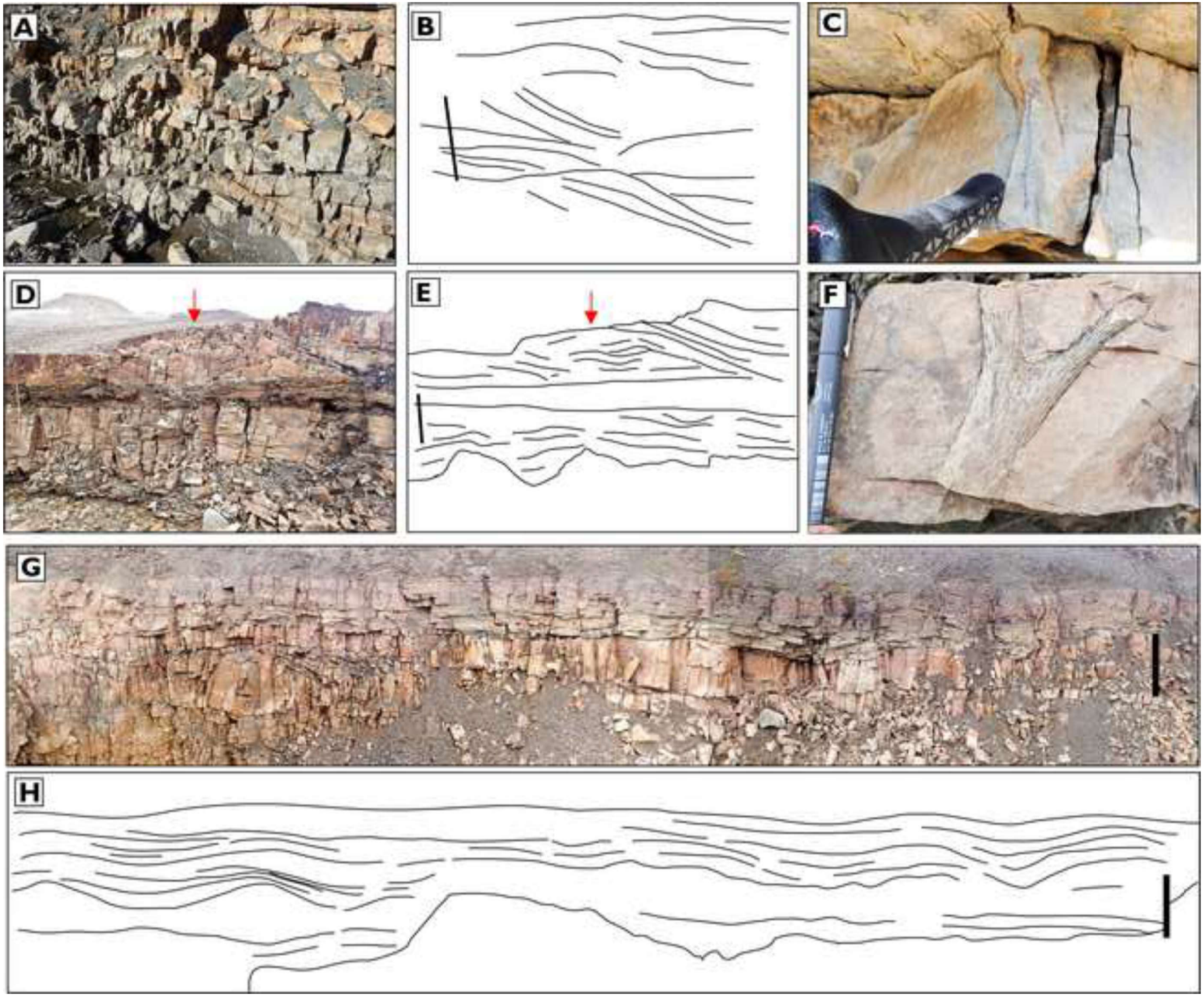

A
B
C
D
E
F
G
H

figure 17

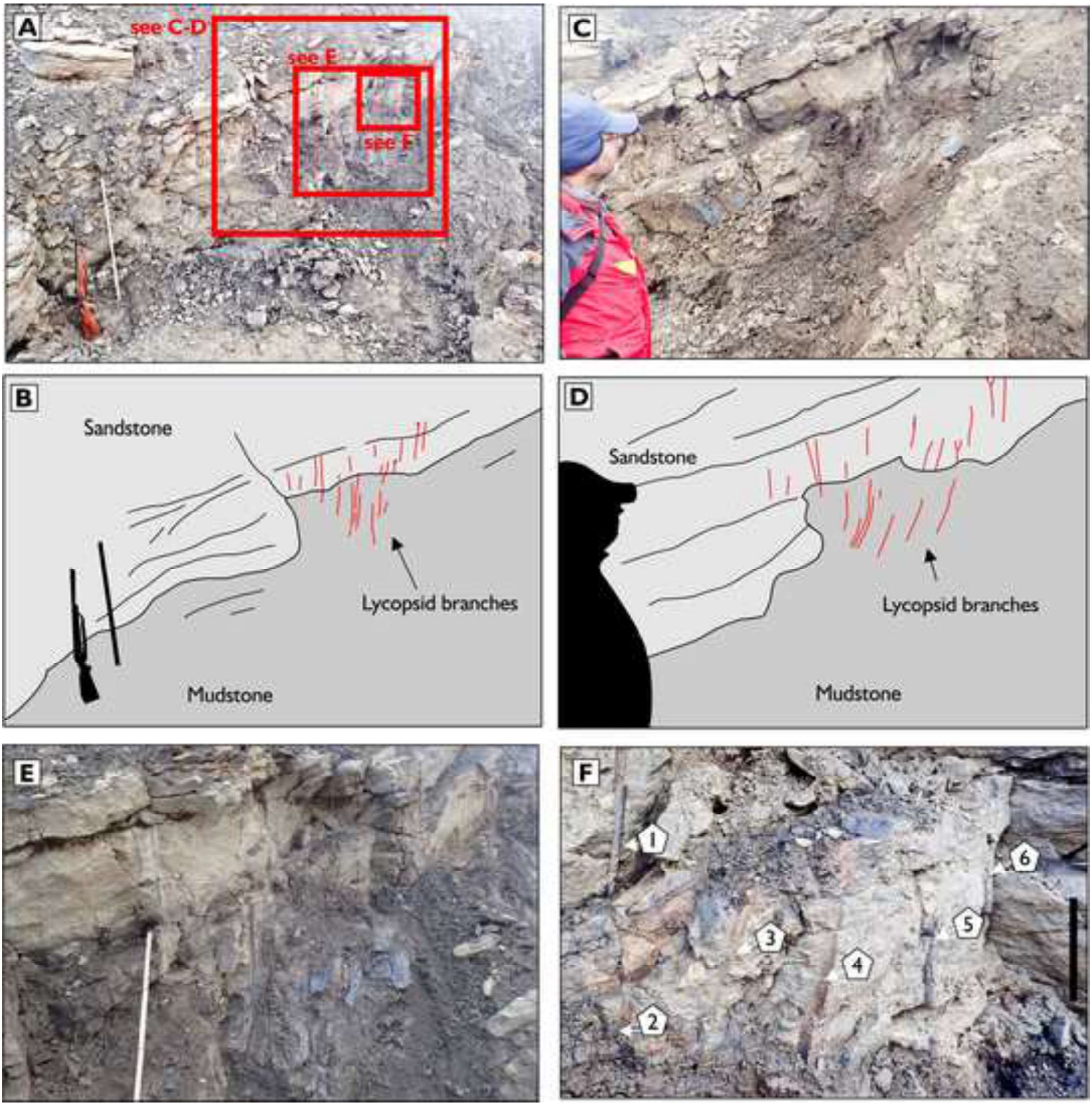

A
see C-D
see E
see F
C
B
Sandstone
Lycopsid branches
Mudstone
D
Sandstone
Lycopsid branches
Mudstone
E
F
1
6
5
3
4
2

figure 18

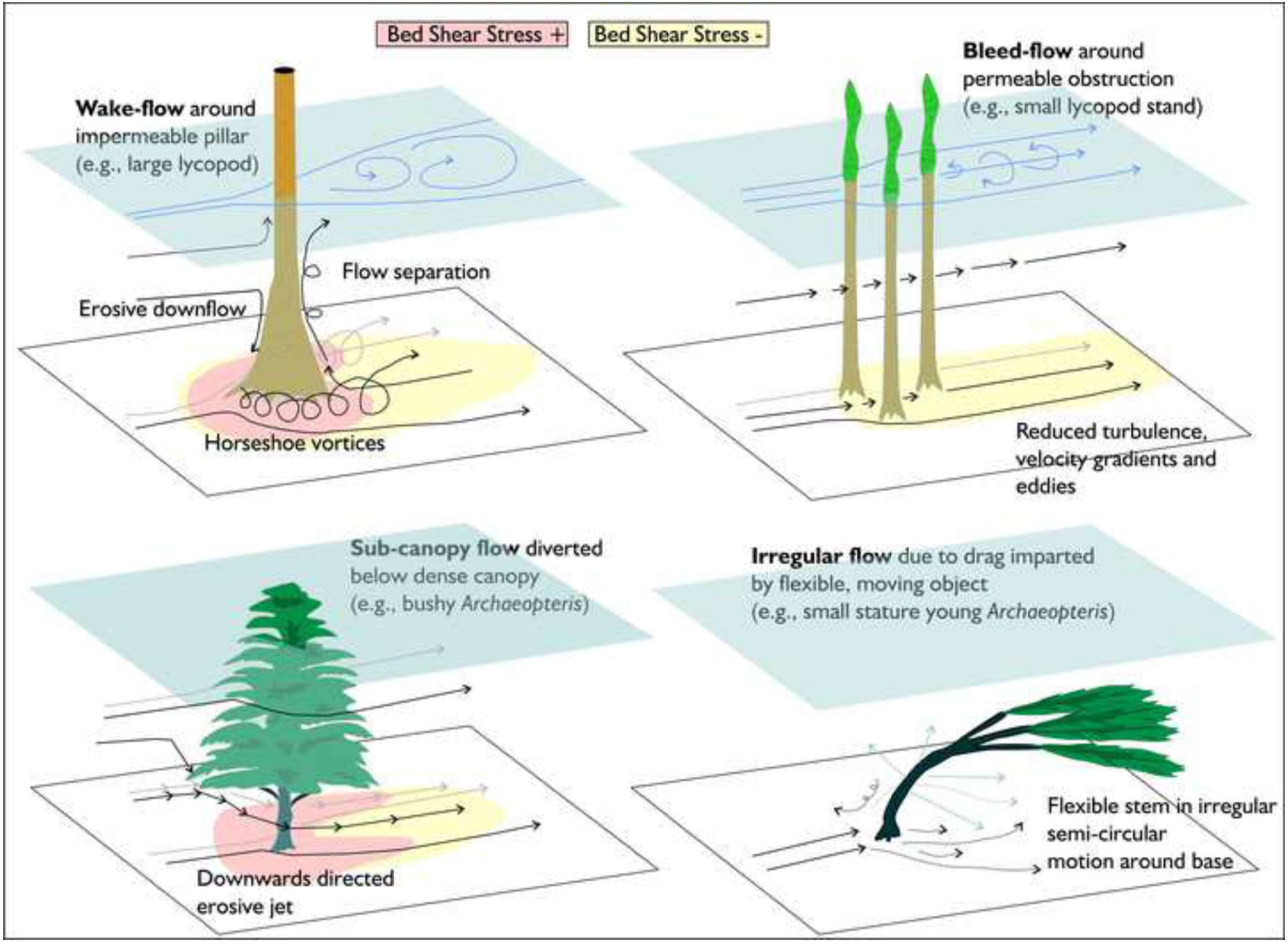

Bed Shear Stress +
Bed Shear Stress -
Wake-flow around
impermeable pillar
(e.g., large lycopod)
Flow separation
Erosive downflow
Horseshoe vortices
Bleed-flow around
permeable obstruction
(e.g., small lycopod stand)
Reduced turbulence,
velocity gradients and
eddies
Sub-canopy flow diverted
below dense canopy
(e.g., bushy *Archaeopteris*)
Downwards directed
erosive jet
Irregular flow due to drag imparted
by flexible, moving object
(e.g., small stature young *Archaeopteris*)
Flexible stem in irregular
semi-circular
motion around base

figure 19

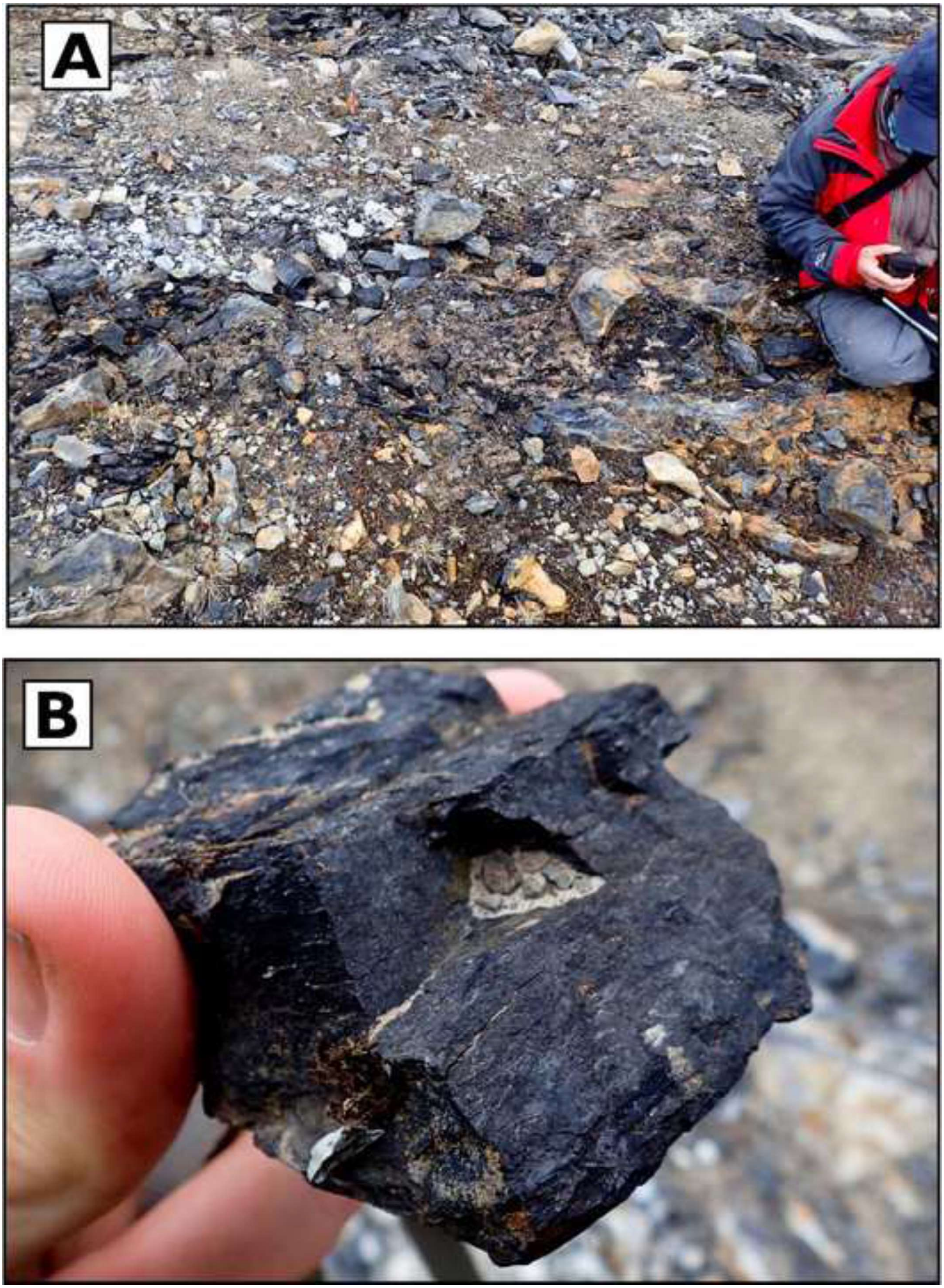
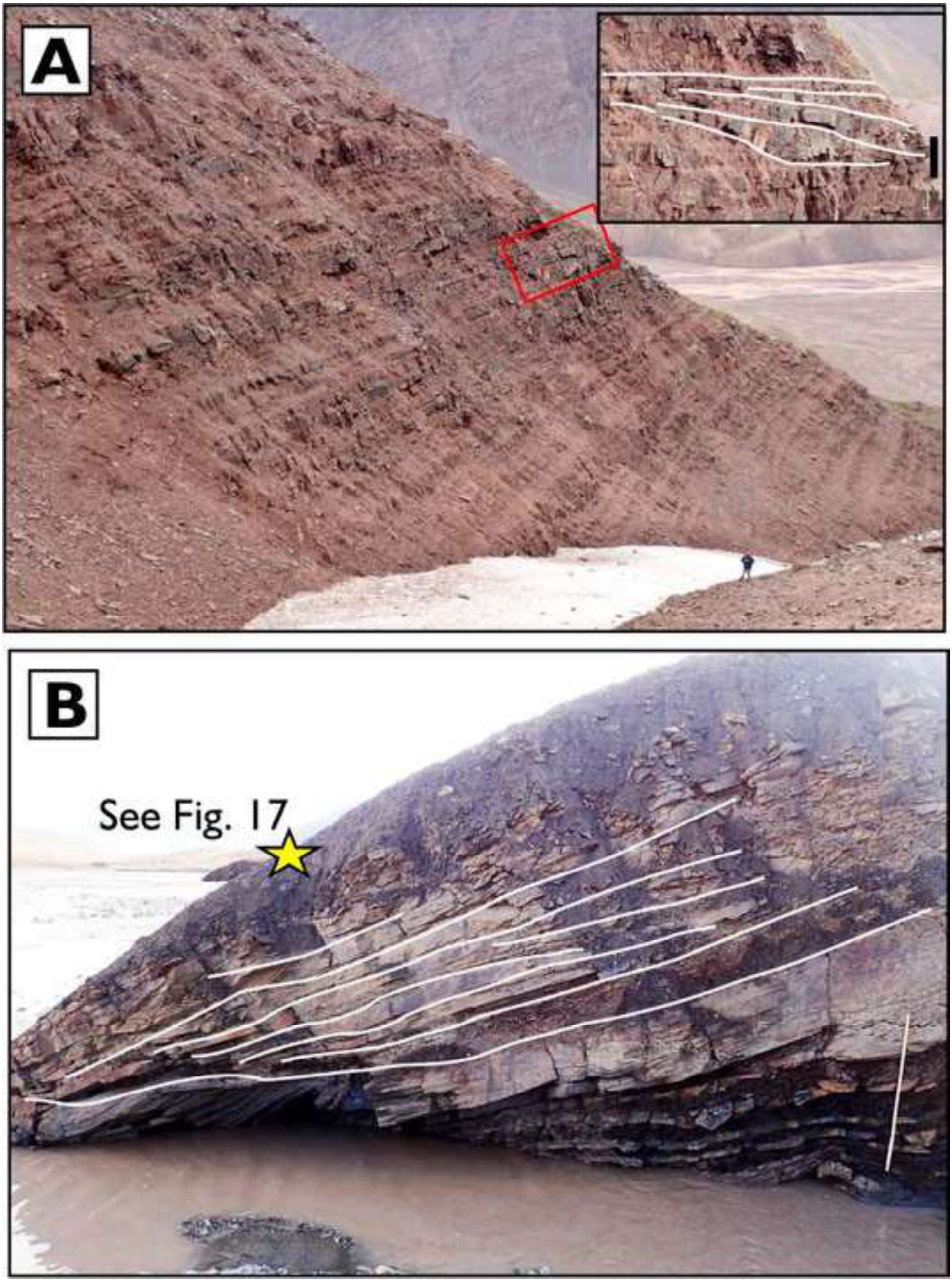
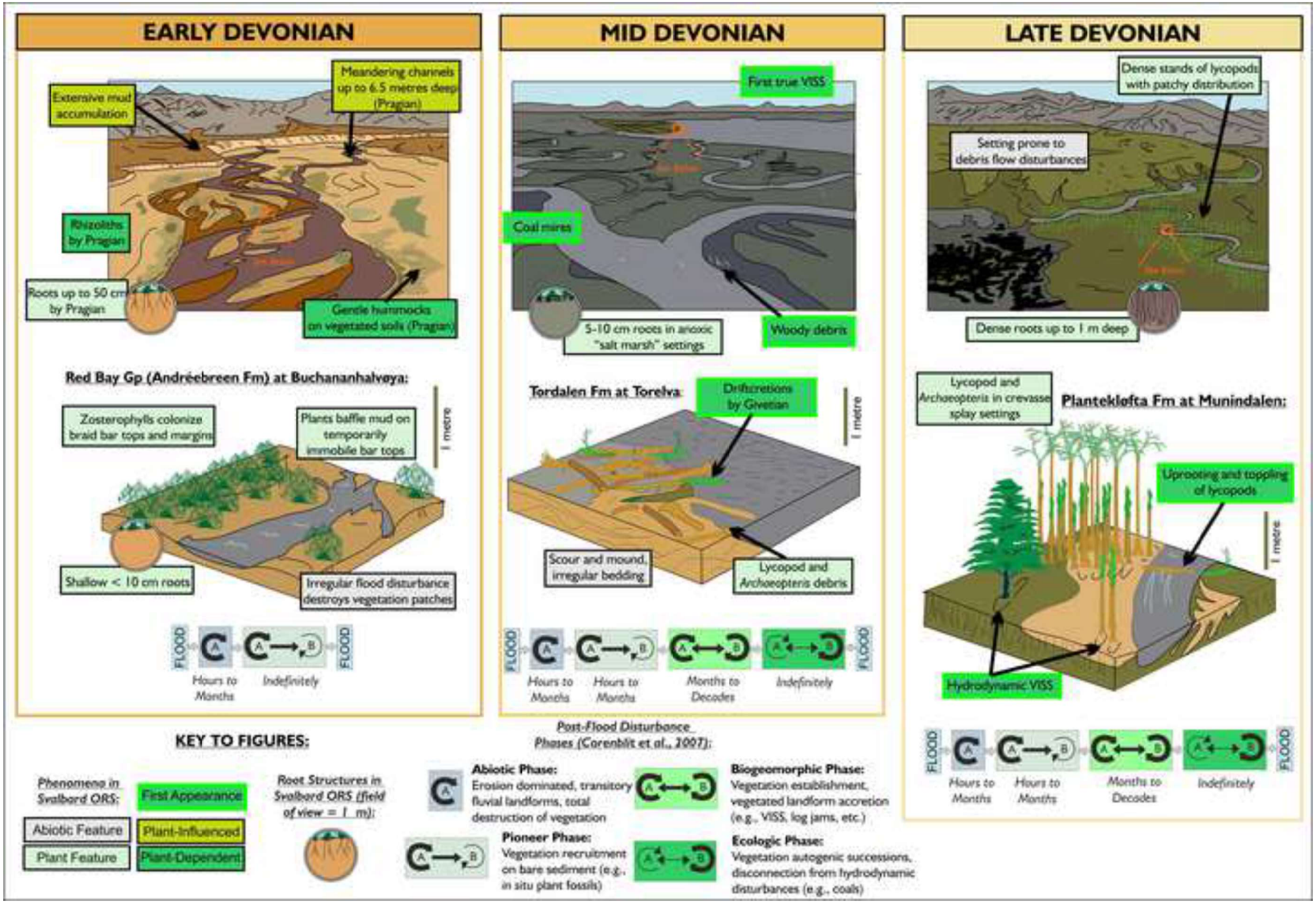


figure 20




EARLY DEVONIAN
MID DEVONIAN
LATE DEVONIAN
Extensive mud accumulation
Meandering channels up to 6.5 metres deep (Pragian)
Rhizoliths by Pragian
Roots up to 50 cm by Pragian
Gentle hummocks on vegetated soils (Pragian)
Red Bay Gp (Andréebreen Fm) at Buchananhalvøya:
Zosterophylls colonize braid bar tops and margins
Plants baffle mud on temporarily immobile bar tops
1 metre
Shallow < 10 cm roots
Irregular flood disturbance destroys vegetation patches
FLOOD
Hours to Months
Indefinitely
First true VISS
Coal mires
5-10 cm roots in anoxic "salt marsh" settings
Woody debris
Tordalen Fm at Torelva:
Driftcretions by Givetian
Scour and mound, irregular bedding
Lycopod and Archaeopteris debris
Months to Decades
Dense stands of lycopods with patchy distribution
Setting prone to debris flow disturbances
Dense roots up to 1 m deep
Lycopod and Archaeopteris in crevasse splay settings
Plantekløfta Fm at Munindalen:
Uprooting and toppling of lycopods
Hydrodynamic VISS
KEY TO FIGURES:
Phenomena in Svalbard ORS:
Abiotic Feature
Plant Feature
First Appearance
Plant-Influenced
Plant-Dependent
Root Structures in Svalbard ORS (field of view = 1 m):
Post-Flood Disturbance Phases (Corenblit et al., 2007):
Abiotic Phase:
Erosion dominated, transitory fluvial landforms, total destruction of vegetation
Pioneer Phase:
Vegetation recruitment on bare sediment (e.g., in situ plant fossils)
Biogeomorphic Phase:
Vegetation establishment, vegetated landform accretion (e.g., VISS, log jams, etc.)
Ecologic Phase:
Vegetation autogenic successions, disconnection from hydrodynamic disturbances (e.g., coals)
A
B