Turbulence, displacement, death and worms: a day in the life of a fluvial Carboniferous bivalve

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ABSTRACT

In the Pennsylvanian Rough Rock Flags and Rough Rock of northern England, trace fossils attributed to the non-marine bivalve *Carbonicola* are found. *Carbonicola*, recorded by *Lockeia* and associated trace fossils, lived a semi-infaunal lifestyle and thus were influenced by both the sediment in which they were hosted, and the currents which supplied their nutrients and oxygen. A number of palaeocurrent indictors are commonly associated with *Lockeia* and are confirmed by this study: (a) downstream inclination of vertical burrows; (b) palaeoflow-parallel orientation of long axes. Additional palaeocurrent indicators include: (c) steeper scouring and higher sediment surface on the upstream side; (d) diffuse lamination downstream of the trace, or, more widespread downstream erosion. These semi-infaunal bivalves were partly exposed to the prevailing flow and acted as bed defects, disturbing flow over an otherwise relatively smooth surface; flow separation and acceleration enhanced flow turbulence around the bivalve leading to erosion and the development of a variably developed fan shaped zone of scour immediately downstream. Disturbance and destabilisation of sediment in this way may affect bivalves immediately downstream, plausibly explaining the relatively regular spacing pattern of individual *Lockeia*, or clusters of *Lockeia*, exposed on bedding planes and revealed by nearest neighbour analyses. Bivalves that did not survive high energy flow events were either trapped within the sediment, or transported downstream and deposited in lower-energy environments within the otherwise high-energy deposits of the Rough Rock. These are often associated with *Planolites* and *Cochlichnus*, trace fossils of scavenging worms which radiate around the imprints of dead bivalves. This assemblage of trace fossil s indicates that areas suitable for bivalve colonisation occurred in upstream areas.

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Introduction

The recognition and interpretation of trace fossils can be critical to our understanding of ancient sedimentary successions, particularly where body fossil preservation is rare. Although tracks, trails and burrows have been recognised in Carboniferous strata since the mid nineteenth century (Binney 1852, on the Westphalian strata of Lancashire), it was the pioneering work on Westphalian strata of Germany which established the relationship of trace fossil assemblages to sedimentary and faunal cyclicity (Jessen 1949; Jessen et al. 1952; Seilacher 1963, 1964). Continental invertebrate ichnology has become increasingly important in sedimentary geology, particularly in terms of the interpretation of palaeoenvironmental conditions, and hence prediction of facies associations and distributions, the identification of key stratigraphic surfaces in the absence of temporally distinctive body fossils, and also in our understanding of the evolution, behavioural characteristics and environmental distributions of the trace makers (e.g. Buatois & Mángano 2004, 2007 and references therein). Bivalves were one of the major trace fossil producers present throughout the Phanerozoic; their environmental adaptability has seen them conquer a diverse range of habitats during their long evolutionary history (e.g., Stanley 1970; Eagar 1978; Savazzi 1982; Seilacher 1990).

The bivalves trace fossils reported herein belong to a transitional Skolithos-Mermia ichnofacies, being produced dominantly in subaqueous conditions which may be subject to variability in flow conditions and periodic emergence, e.g. channel bars, floodplain areas, crevasse splays (see discussion in Lawfield and Pickerill 2006, and references therein; see also Eagar et al. 1985, p.133 “Scoyenia association”).

Within the Late-Mississippian and Pennsylvanian of the British Isles, trace fossils attributed to the burrowing, vertical “escape” and horizontal locomotion of bivalves have long been recognised (e.g. Binney 1852, Eagar 1974, Hardy & Broadhurst 1978, Eagar et al. 1985). Inferences of palaeoenvironmental conditions, including palaeocurrent directions have been made from these. Numerous biogenic sedimentary structures have previously been identified within the Rough Rock and Rough Rock Flags at Cracken Edge, Derbyshire (Hardy 1970; Miller 1986). The present study reports the occurrence and distribution of traces attributed to the non-marine bivalve *Carbonicola* with the aim of answering the following questions: (1) What features of *Lockeia* and associated traces are indicators of palaeoflow direction, and what do these features tell us about the hydraulic regime? (2) What factors might induce the observed regular spacing of *Lockeia*? (3) How are *Lockeia* associated with other traces? (4) Collectively, can interpretation of these observations provide generic insights for palaeoenvironmental analysis of other systems? (5) Can these insights provide areas for further study of the Rough Rock and Rough Rock Flags?

The ichnogeneric name *Lockeia* is here used, for the hypichnial moulds and epichnial casts interpreted as bivalve resting traces, following the discussion by Maples

& West (1989). Prior to this, the junior synonym *Pelecypodichnus* had been used alongside or replacing *Lockeia*, which was regarded incorrectly as a nomen oblitum. For this reason it should be noted that many of the key papers reported herein refer to *Pelecypodichnus* rather than *Lockeia*, but that the two are largely interchangeable. Crucially however, '*Lockeia*' does not presume formation through the activity of bivalves, or any other creature, which is an important aspect of the general approach to ichnology.

Carboniferous Rough Rock and Rough Rock Flags

The Carboniferous (Pennsylvanian, Regional Stage: Yeadonian G_1) (Fig. 1) Rough Rock Flags and the overlying Rough Rock are considered to be the deposits of a progradational fluvio-deltaic system deposited within the Pennsylvanian Pennine Basin of northern England (Heath 1975; Bristow 1987, 1988, 1993; Hampson et al. 1996). The Rough Rock has received much attention over the years (Hull & Green 1864; Gilligan 1920; Wray 1929; Shackleton 1962; Wright 1964; Heath 1975; Bristow 1987, 1988, 1993; Holdsworth & Collinson 1988; Maynard 1991; Hampson et al. 1996). The pioneering work of Gilligan (1920) on the petrography of the Rough Rock led to his conclusions that deposition was from fluvio-deltaic systems analogous to the modern Mississippi, Ganges and Brahmaputra Rivers under a monsoonal climate, with sediment sourced from a distant northern granitoid gneiss with additional metamorphic and sedimentary rocks. These ideas were refined by Heath (1975) who suggested that the major Rough Rock channels were braided with extensive crevasse splay and overbank deposits. Bristow (1993) describes the Rough Rock as a coarse-grained multi-storey, multi-lateral braided river sheet sandstone and also proposed the Brahmaputra (Jamuna) River (Bangladesh) as an analogue.

The underlying fine-grained sandstones and siltstones of the Rough Rock Flags have received less attention, although they occur at the approximate stratigraphic level of the better known Upper Haslingden Flags (Collinson & Banks 1975; Collinson 1988) (Fig. 1). Typically, the Rough Rock Flags consist of variably well-developed coarsening upwards packages. South of the present study area, at Ridgeway, Bristow (1988) describes the Rough Rock Flags as consisting of alternating fine-grained ripple laminated sandstones and siltstones, laterally extensive and of consistent thickness over tens of metres. At Cracken Edge, Miller (1986) described the unit as fine-grained cross-laminated and planar-laminated sandstones; further north, at Elland, a similar facies association is overlain by minor coarse-grained channel sandstones within the Rough Rock Flags. Bristow (1988) describes a southwards fining of the Rough Rock Flags with the deposits interpreted as that of a lobate, fluvial dominated delta, analogous to the modern Atchalafaya Delta, USA.

The study area, Cracken Edge (Fig. 1), is a north-south trending escarpment dominated by the quarried Rough Rock and underlying Rough Rock Flags which are exposed discontinuously over a distance of 5 km. Cracken Edge runs along the eastern face of Chinley Churn, a 451m high hill between Birch Vale and Chinley in the High Peak of Derbyshire. The principal exposures are Cracken Edge Quarry (disused) and Foxholes Clough 1 km to the north. The underlying sequence is exposed in the valley immediately to the east of Chinley Churn and is marked at the base by shales containing the *Reticuloceras gracile* marine band. These are overlain by the fluvial Chatsworth Grit, Simmondley Coal, and shales containing the *Gastrioceras cancellatum* and *Gastrioceras* *cumbriense* marine bands respectively (Maynard 1991; Waters et al. 2008). The Rough Rock Flags and the overlying Rough Rock form Cracken Edge and are overlain by the *Gastrioceras subcrenatum* marine band marking the boundary between the European Namurian and Westphalian stages.

Trace fossil assemblage

The Rough Rock Flags feature plentiful trace fossils of the *Skolithos*-*Mermia* ichnofacies (Seilacher 1967; Buatois and Mángano 1995, 2004; Lawfield & Pickerill, 2006) including *Planolites*, *Cochlichnus*, *Palaeophycus*, *Didymaulichnus* and *Lockeia*, aspects of which were described at the locality by Hardy (1970) and Miller (1986). Whilst the previous work forms the basis of this study, the observations and interpretations presented herein comprise a comprehensive review of implications for palaeocurrent analysis and certain aspects of bivalve development and behaviour. *Lockeia* (*L. siliquaria* James, 1879) of the Yeadonian at Cracken Edge, and other Carboniferous sandstones of northern England have previously been attributed to *Carbonicola* although shells are rarely preserved (Hardy 1970; Eagar 1974; Hardy & Broadhurst 1978; Eagar et al. 1985; Miller 1986). However, rare examples of *Carbonicola* have been found at the tops of sub-vertical trace fossils similar to those described herein, and from similar aged strata (Hardy 1970; Eagar 1974; Broadhurst et al. 1980; Eagar 1983, Eagar et al. 1985). Moulds and casts of bivalve shells are more commonly found, preservation of shell material was probably rare due to the high energy nature of the environment, compaction of the sediment, and dissolution of carbonate within the vados or phreatic zone (e.g., Bridge et al. 1986; Lawfield & Pickerill 2006). Hardy (1970) suggested that dissolution of bivalve shells may have provided the carbonate found within the common carbonate concretions within the Rough Rock, although this was disputed by Miller (1986).

Lockeia and genetically associated traces

Lockeia siliquaria James, 1879

These characteristically almond-shaped traces are 8-30mm in length, preserved as epichnial hollows and hypichnial expressions, sometimes with a more pointed end, which generally has a common orientation, ‘pointing’ upstream, based on its preserved relationship to underlying and overlying ripple cross-lamination and trough cross-bedding (Figs. 2 and 3). Rare casts resembling cross-sections through sand-filled bivalve shells are found in some *Lockeia* traces (Fig. 2). Where more than one trace is found, there may be a strong degree of ellipse (and palaeoflow) parallelism, smaller groups of individuals may form an en-echelon pattern on the bedding plane, again parallel to palaeoflow (Fig. 3).

Lockeia may be found clustered on individual bedding planes, with maximum recorded population densities of up to 1000 per m^2 (Fig. 3), however they may be associated with smaller groups, although in general terms where one trace is found within a bed it is likely that they there will be associated traces. Large bedding plane exposures reveal a relatively regular spacing pattern, although *Lockeia* may be ‘paired’ or found in clusters (Fig. 3). Nearest neighbour analysis, following the technique of Pemberton & Frey (1984) was applied to *Lockeia* distributions at two localities (Fig. 3). Within a 200 × 200 mm quadrant, the distance from each *Lockeia* to its nearest neighbour was measured (r), the sum (Σr) and the mean distance (r_A) was then calculated (Fig. 3). The mean value is compared with the mean distribution expected in a randomly distributed population (r_E)

given by: $r_E = 1/2\sqrt{p}$; where p is the density of individuals per unit area. Departure of the observed distribution from a random distribution is given by the ratio (R) of r_A/r_E. Where R<unity, the distribution may be aggregated; where R = unity the distribution is random, and where R>unity the distribution is approaching maximum spacing. Distributions varied from conditions approaching uniform spacing (maximum spacing) (Fig. 3A), to aggregated (Fig. 3B). In Fig. 3B it is apparent that clustered or ‘aggregated’ individuals occur in densely populated bands.

Lockeia have a bimodal size distribution, with each mode having a relatively narrow size range: large traces, representing about 20% of the population, with a mean length and width of 24.1 mm and 14.8 mm respectively; small traces, representing about 80% of the population, with a mean length and width of 12.5 mm and 9.7 mm wide respectively (100 samples). Large and small traces have mean length/width ratios of 1.6 and 1.3 respectively.

This trace fossil appears in large numbers within two distinct horizons in the Rough Rock Flags, the lower horizon is laterally extensive covering at least 0.5 km in the lower section of the quarry (also noted by Miller 1986, his localities 3-9). The preserved extent of the upper unit is truncated by the channelised base of the overlying Rough Rock. In both cases a thin (80-120 mm) siltstone horizon very rarely containing vertical traces is overlain by thicker fine-medium grained planar-laminated sandstone which is often extensively marked by subvertical burrows, the tops of which are marked by these almond shaped traces. The base of the sandstone has a different character, being poorly-sorted, organic-rich and lacking sedimentary structure (Fig. 4). Epichnial impressions of *Lockeia* are associated with sub-vertical traces cutting through underlying sediment, and hypichnial expressions on bed bases (Fig. 5).

Interpretation

These *Lockeia* traces have previously been attributed to resting traces of the unionid bivalve *Carbonicola* (Hardy 1970; Eagar 1977; Miller 1986); this study finds no reason to disagree. The presence of two distinct size-classes suggests that the bivalves in each class were of approximately the same age. Modern unionids produce larvae which live as a parasite attaching themselves to the gills of fish (Ellis 1978). Whether this mode of dispersal was developed in the Carboniferous is unknown, although freshwater fish became more common and diversified considerably throughout the Carboniferous (Long 2007). It is likely that dispersal of larvae was probably more general, utilising currents and settling out of suspension in areas of lower flow energy. This method of distribution is used today by marine bivalves which typically have a planktonic larva known as veliger (Ellis 1978), and often leads to the development of colonies of bivalves of distinctive size-classes. However, planktonic distribution is problematic as a method of reproduction and colonisation in a fluvial regime, as strong currents may wash veliger out to sea, although the lower density of fresh water (relative to sea water) may allow more rapid settling. Today the only freshwater bivalve with a planktonic stage is *Dreissena*, a comparatively recent coloniser of the freshwater environment (McMahon 1996). In Sphaeriidae, young are kept in brood pouches and extruded in low numbers (6-30) as relatively large miniatures of the adult (Ellis 1978). The bimodal distribution and association with a chaotic organic-rich sandstone deposit, interpreted as a flood deposit, suggests that the colony arrived as mature adults, carried from upstream, and was dominated by one year group, with lesser mature individuals. The ‘spread’ of larger sizes of *Lockeia* supports the conclusion that bivalves were transported in flood conditions, and that progressively a year-class would be found farther downstream. This could lead to entire mature year-classes in upstream localities being represented by only a few individuals, as survivors of an earlier community (Broadhurst, et al. 1980), compared to a younger year class which may be well represented.

Eagar (1978) and Hardy & Broadhurst (1978) recorded ellipse parallelism of *Lockeia* traces within Lower Westphalian sediments and attributed it to parallel alignment, along the commissural plane, of the bivalve *Carbonicola*. The larger of the *Lockeia* type traces commonly have a stronger degree of ellipse parallelism than the smaller traces, perhaps because larger bivalves presented a larger obstacle to flow necessitating alignment; additionally, the data presented in Fig. 3 show that larger specimens tended to be more elliptical. The upstream ‘pointing’ of *Lockeia* (Fig. 2) has previously been attributed to the upstream positioning of the inhalant siphon typical of filter feeding bivalves (Eagar 1974, 1977; Wildish et al. 1987; Vincent et al. 1988; Monismith et al. 1990), and agrees with other sedimentary palaeocurrent indicators within the section (Fig. 3A). Additionally, this orientation reduces the risk of inhaling matter that should only ever be exhaled.

Spacing of *Lockeia* analysed using the nearest neighbour technique revealed a combination of aggregated and well-spaced distributions. The technique was not pursued at length as suitably large exposures were not available; and the character of distribution varied greatly on individual surfaces, for example in Fig. 3B clusters of *Lockeia* appear as ‘bands’ of individuals, presumably related to some sort of flow alignment and flow sheltering. The distribution between clusters and individuals appears to be more uniform; clusters tend to be close-knit groups suggesting that they acted as an individual within the flow, allowing them to shelter and avoid erosion; this is analogous to mussel banks in modern marine environments (Gascoigne et al. 2005). The effect of turbulence on individuals and clusters is discussed in a little more detail below. The nearest neighbour technique may therefore work better if clusters of *Lockeia* were counted as individuals, and the spacing between clusters and individuals be taken into account.

Burrow traces

Sub vertical 'burrows' are common, recorded as sub-vertical and curved endichnia, reaching up to 650 mm in length (Figs. 4, 5 and 6). Where the bedding plane is exposed, the burrow top of is marked by an epichnial impression and the base by a hypichnial expression (attributed above to *Lockeia*). The burrows are generally infilled by the same sediment as the host bed, typically fine-medium sand forming menisci laminae, but commonly with small <1 mm mudstone flakes, coarser grains and heavy minerals found in the deepest parts. Where burrows are apparently abandoned, it is common for the last stage of fill to be coarser-grained (Fig. 5). The centre of the burrow may be marked by v-shaped meniscae, cone like in three dimensions, associated with dark-coloured zones of sediment and/or cement; the 'burrow' is a composite of these nested cones. Lamination upstream of the trace is commonly slightly higher than downstream, with lamination warped steeply into the burrow, downstream lamination is generally less steeply warped and returns to horizontal more gradually.

The burrow wall, and sediment surrounding the burrow often has a proud weathering profile suggesting differential cementation (Fig. 4). The width of the burrow tends to increase upwards, in some places more rapidly than others. The traces cut through lamination and bedding. In some areas there is a curvature of the entire trace, or part of the trace, which shows slight down-current movement of the trace producer (Fig.

4). In several sections there is a diffusion of lamination immediately downstream of the trace (Figs. 5 and 6). In one particular bed this is a relatively common feature, with the development of diffuse lamination and more heavily scoured surfaces on the downstream side of the traces (discussed in more detail below).

Interpretation

Heath (1975) refers to these traces as 'internally symmetrical vertical burrows' and Miller (1986) terms them 'escape shafts'. Increase in burrow width from the base to the tops of the traces suggests that the bivalves grew in the space of time taken to deposit the bed; however, no discernible trends have been recorded from these traces. Bivalve growth does indicate that sedimentation was relatively slow but episodic and that these are not true escape traces. Bromley (1996) terms such traces 'Equilibichnia' as movement was an effort to keep in equilibrium with the sediment/water interface. Equilibichnia are distinct from Fugichnia which *are* escape traces and are created in response to a rapid influx of sediment. Additional evidence of these traces representing upwards movement, rather than burrowing, is their length: it is unlikely for bivalves to burrow to 650 mm depth, Stanley (1970) reported that the deepest burrowers known today reach only 250 mm and are marine, although M. Amler (pers. comm.) reports estuarine *Mya arenaria* of the Brittanic coast burrowing down to 400 mm. Ellipse parallelism was interpreted above to represent palaeoflow alignment of bivalves a view which is supported here; alignment of incurrent/exhalent siphons with tidal currents has also been documented from *Mya arenaria* in tidal flat areas (Vincent et al. 1988). This is an important point in the interpretation that the traces were produced by upwards movement, as the ellipse parallelism is found wherever sub-vertical traces cut through bedding; there is no obvious reason for bivalves to maintain this alignment beneath the sediment-water interface.

Eagar (1977) noted that burrows often commence obliquely, curving upwards to near vertical in their upper parts. Thoms & Berg (1985) also described basal curvature in much larger traces in the Devonian Catskill Formation (Pennsylvania, USA), which they attributed to forcing by unidirectional currents and sediment accretion on the upstream side. In this case, and apparently those reported by Eagar (1977), it would be reasonable to assume that the curvature is prominent at the base of the trace as currents may have been stronger at earlier times, but through time flow energy waned. Alternatively, growth of the trace maker through time, potentially combined with increasingly ellipsoid shell morphologies, may have provided it with extra stability so that it was progressively less affected by current activity (assuming relatively uniform current velocities).

The slightly higher sediment surface and steep scouring on the upstream side of the trace is typical of erosional scour around denser/larger (and hence more stable) objects on a finer grained mobile bed (Allen 1971). Erosion and diffusion of lamination downstream of the traces suggests that the bivalves were locally enhancing flow turbulence. This scenario could lead to destabilisation of bivalves downstream – potentially leading to the relatively regular spacing patterns of *Lockeia* reported above. This is discussed in more detail below.

Turbulence and erosion

Evidence of erosion of bivalves is revealed in several palaeocurrent-parallel sections where sub-vertical burrows are exposed. As noted above, extensive subvertical burrows typically occur in parallel laminated, micaceous sandstones, however, in some sections the sediment downstream of the burrows is either devoid of sedimentary structure, or lamination has become diffuse or highly irregular (Fig. 6). In some cases, there is a repetitive disturbance, i.e., throughout the stratigraphy, of the sediment in the lee of an individual subvertical trace. On bedding planes, similar structures are expressed as low amplitude hummocky surfaces on the lee side of *Lockeia*. These may have a fan-like shape but are generally indistinct.

Interpretation

The close relationship between traces and disruption of sediment on their lee sides suggests that the burrow aperture, or protruding bivalve was acting as an obstacle to flow, or bed defect (e.g., Allen 1971). Flow line convergence on either side of the bivalve would cause local acceleration, whist downstream flow separation may enhance turbulence, leading to localised scour around the shell. The effect of the scour is to further induce upstream flow separation and enhance erosion, as part of a positive feedback loop. The result is that a zone of erosion forms, being steep sided upstream of the bivalve but shallowing and flaring out downstream. The fact that some localities seem to have been particularly prone to this, or that the same trace created this effect repeatedly suggests that the bivalves were often close to the threshold limit for the bed shear stress they could withstand, either due to their positioning (e.g., close to an overspill point) or due to disequilibrium between their size/form and the prevailing flow conditions. The enhancement of turbulence in the wake of the bivalve may trigger bed erosion at lower shear stresses than typically required for plane bed erosion.

Sediment destabilisation in the turbulent wake of the bivalve may lead to the erosion and entrainment of the bivalves' contemporaries. This potentially could explain the relatively regular spacing patterns between individual and clusters of *Lockeia* within large colonies (Fig. 3A). Modern bivalves have developed strategies to avoid acting as a focus of bed scour, including the development of shell ridges (Stanley 1975a, 1975b, 1981; Watters 1994), and the ability to burrow to a depth great enough to preclude erosion (Thoms & Berg 1985).

Lateral movement traces

Epichnial grooves, 5-6 mm wide with slightly raised ridges on either side of the central furrow are found on the tops of fine-grained sandstone but are relatively uncommon, and only known from fallen blocks (Fig. 7). Lateral movement traces consist of straight to slightly sinuous trails which sometimes cross but never branch. The longest trails seen were just over 500 mm in length, but this is a product of limited exposure, potentially they are much longer. Some examples show a range of orientations but most are roughly aligned with each other. Similar trails were reported by Hardy (1970), Hardy & Broadhurst (1978) and Miller (1986).

Interpretation

These traces are here attributed to the ploughing movement of bivalves in response to a drop in water level. The bivalves most-likely inhabited shallow water environments such as sand-banks, sand-flats or crevasse splay areas, such environments are prone to emergence during low flow stage and changes in river course; during these times the bivalves would need to move to submerged areas. The approximate alignment of traces suggests movement following a receding water-line, such behaviour has been noted in modern day bivalves during drought conditions and reservoir draining (Fig. 9; also see

Lawfield and Pickerill 2006, Fig. 4 C, E, F). The prominent ridges (epichnial expressions) developed in non-cohesive sediment suggest that the sediment was probably sub-aerially exposed for some period and that the bivalves were able to withstand this. Modern day bivalves are able to withstand days or weeks of desiccation (Miller & Payne 1998). Hardy (1970) reported that these trails may cross cut laminae and were made endichnially up to the sediment surface; this has not been noted in the present study but presumably reflects movement from a slightly deeper burrow occupied during times of submergence.

Death and worms

Planolites, Cochlichnus and *Didymaulichnus* were described by Miller (1986) at Cracken Edge. The present study has found *Didymaulichnus* to be rare, but *Palaeopyhcus* is more common, although not reported by Miller (1986). Most typically, these traces occur within finer-grained intervals in the Rough Rock channel bodies, although they do occur to a lesser extent within the Rough Rock Flags (similar to Miller's (1986) Type A facies association). *Planolites* and *Cochlichnus* dominate and are commonly found in association with *Lockeia*; however where *Lockeia* is widespread, for example on individual bedding planes, they are less common. However, on certain bedding planes, particularly those of relatively fine-grained intervals within the Rough Rock, preserved as hypichnial expressions on sandstone beds, the above assemblage occurs with *Lockeia* and the two often have an intimate relationship (Fig. 8). *Lockeia* traces may be of the characteristic almond shape discussed above, or may be gradational to more rounded forms, suggestive of the inferred bivalve trace maker lying on its side, i.e., an imprint of part of the side of the bivalve rather than the narrower ellipse imprint indicative of a 'life-position'; around these traces, *Planolites* and *Cochlichnus* may be particularly abundant, in some cases radiating from a central *Lockeia* type trace (Fig. 8B-E).

Interpretation

Hardy (1970) and Eagar et al. (1985) documented the occurrence of this assemblage of trace fossils with *Lockeia* type traces, and attributed the relationship to the scavenging of dead and decaying bivalves by polychaete worms (*Planolites*) and probably nematode worms (e.g., Elliott 1985; see discussion in Uchman et al. 2009). A similar assemblage has been recorded from the Lower Cretaceous Tunbridge Wells Sand (southern England) where the relationship was attributed to nematodes or annelids feeding on dead in-situ bivalves (Goldring et al. 2005). This scavenging fauna was truly opportunistic and able to establish itself very rapidly, as they are only found in significant numbers in close association with *Lockeia*. It is common for such opportunistic faunas to be found in high densities but low diversities (Bromley 1996). Traces of this fauna generally are not present amongst the life assemblages of bivalve traces, with the exception of small numbers of *Cochlichnus*. It is suggested that the fauna tended to live within quieter environments of the main river channels, feeding off organic material within the sediment. When these quiet areas were inundated during flood events, potentially carrying bivalves, they took advantage of the situation, migrating to scavenge off the dead or dying bivalves. Traces of the scavenging fauna are generally absent in overlying sandstones.

This relationship most commonly occurs at the upper interface of finer grained intervals (e.g. the fallen block of Fig. 8) within the more typically coarse-grained Rough Rock braided river facies. The occurrence of *Lockeia* within this interval suggests that suitable environments for bivalve habitation occurred in the immediate upstream area. In turn, this suggests that similar environments to that where the Rough Rock Flags accumulated, which were demonstrably suitable for bivalve life, also occurred laterally to the Rough Rock braided river channels, probably as crevasse splays or other marginal environments subject to periodic emergence.

Discussion

Lockeia are interpreted as the traces of bivalves which lived an semi-infaunal lifestyle, maintaining equilibrium with the sediment-water interface, and able to burrow to shallow depths to avoid erosion from the substrate. A number of features have previously been described as diagnostic of palaeocurrent trend or direction. Parallelism of the commissural planes of bivalves, in response to the prevailing current direction, gives *Lockeia* its characteristic ellipse parallelism (Eagar 1977; Hardy & Broadhurst 1978). As such, where enough measurements may be taken to establish a reliable sample population, it may be possible to infer the trend of palaeoflow. In the case of the Rough Rock Flags, the local palaeoflow indicated by alignment of commissural planes and direction of inhalant siphons suggests flow towards the SE. Local sedimentary palaeocurrent indicators (ripple cross-lamination) above and below suggest the same. This is opposed to the typical palaeocurrents reported for the Rough Rock Flags, which suggest flow towards the SW (Bristow 1987, 1988) (although Miller (1986) reported some palaeocurrents towards the east). The sedimentary and ichnological flow indicators may reflect deposition in an area where flow was locally diverging from the axial flow, such as a crevasse splay, or point bar.

Thoms & Berg (1985) hypothesised that basal curvature of subvertical bivalve burrows may be related to downcurrent forcing of the bivalve; this study confirms that the inclination of burrows is generally linked to the palaeoflow history of the sediments in which they are found, with flow indicated by those swinging from NE to SE. These burrows typically straighten as they reach the upper parts, suggesting either that flows waned through time, or that bivalve growth provided extra stability allowing the bivalve to maintain its position within the sediment. Additionally, *Lockeia* and associated burrows tend to have steeper scour margins on their upstream side, and in some cases the lamination surface is higher on the upstream trace. Sediment on the downstream side of the trace may be deflated through erosion, or may reflect lower depositional rates associated with increased flow energy and turbulence induced by flow around the bivalve.

Erosion of sediment immediately downstream of the trace may occur through the localised enhancement of turbulence as the bivalve acts as a bed defect (Allen 1971); scour further enhances flow separation, turbulence generation and lead to increased scour. This may ultimately lead to erosion of the bivalve from the substrate (Fig. 10A T3). The resultant sedimentary record includes of scour around a bivalve includes diffuse lamination, or even more irregular scour topography, downstream of the burrow (Fig. 6). Although dominantly found as individuals within larger colonies, *Lockeia* are commonly clustered, either in pairs, or greater numbers; this close association may allow the cluster to behave as a single ‘defect’ within the flow. For this reason, the spacing pattern between clusters and individuals may be fairly uniform, although within the clusters they may be closely spaced. For this reason, nearest neighbour analysis is problematic, as depending on the focus of the study, bivalves may be ‘aggregated’ in a palaeoflow parallel cluster, or uniformly spaced as individuals or smaller clusters (Fig. 10B). The effect of turbulence enhancement is of importance as it plausibly explains the reasonably uniform spacing pattern of individual or clustered bivalves within large colonies. Evidence of bivalves being dislodged from their substrate is abundant (Fig. 5C-D), which is perhaps unsurprising given the periodically high strength flows and the non-cohesive nature of the sediment.

The size distribution of *Lockeia* suggests domination by at least two year-classes, with larger individuals forming a less tightly associated group, suggesting that they may represent several year classes. Such a distribution may be expected in a unidirectional flow regime where transport of individuals is generally downstream; accordingly, older year-classes may be more evenly distributed along a given river length than younger year-classes, so that in a given locality the older year-class would be less well represented. This has been interpreted by other workers to imply high rates of infant mortality (e.g. Eagar, 1978). In contrast, bivalves that live on a stable substrate in fluvial environments may be characterised by colonies of bivalves with much more complex age and size range structures (Payne et al. 1989).

Lateral movement traces are rare within the Rough Rock Flags, suggesting that bivalves tended to be submerged at a depth great enough to maintain their position year round. Additionally, traces tend to occur on surfaces that appear to have been subaerially exposed; preservation potential of these surfaces was probably fairly low, as they would be particularly prone to erosion during the arrival of the next flood event.

The food source that made this environment attractive to bivalves was most-likely the large quantities of organic material transported by the Rough Rock braided river system. Evidence of this includes thick accumulations of carbonaceous material and coalified plant fragments at Cracken Edge, and within many Rough Rock outcrops in the inferred upstream area (e.g., Bristow 1987). At Cracken Edge, plant imprints within the Rough Rock are numerous and include *Calamites*, *Sigillaria*, *Cordaites*, *Lepidodendron*, *Stigmaria*, *Bothrodendron*, and *Alethopteris*. In the Rough Rock Flags, plant fragments are typically comminuted and largely unidentifiable.

In quiet backwaters of the Rough Rock river system, in areas such as abandoned channel-fills, polychaete and nematode worms scavenged on decaying vegetation within the sediment, and on the flesh of dead, decaying bivalves transported during flood events. The preservation potential of sedimentary units within sandy braided rivers is generally low (e.g., Ashworth et al. 1999), implying that most bivalves will not be preserved in-situ after their death, but will be reworked along with their host sediment. *Planolites*, thought to be the trace of polychaete worms, are the predominant trace of this association and often radiate around the *Lockeia*, which are thought to represent dead bivalves. Nematodes are thought to create *Cochlichnus* traces, which has been demonstrated experimentally; although there has been some debate that *Cochlichnus* may also be formed by insects, or insect larvae (Uchman et al. 2009, and references therein). This scavenging association does not occur in the Rough Rock Flags, suggesting that bivalves which were eroded and entrained from their substrate were carried with the main channel flow and deposited either in the channel or carried to coastal areas; however, as suggested above, preservation potential of shell material was probably rare; thus accumulations of dead bivalves are under-recorded in the stratigraphy (e.g., Bridge et al. 1986; Lawfield & Pickerill 2006). The association suggests that environments similar to those populated by bivalves during Rough Rock Flags times were present during Rough Rock times, and that the Rough Rock Flags is probably a lateral as well as distal equivalent of the Rough

Rock. The existing subdivision is based on lithofacies, but the two lithofacies may simply reflect depositional sub-environments of the same system (Fig. 11).

Conclusions

The bivalves which created *Lockeia* and associated locomotion trails and subvertical burrows lived an semi-infaunal lifestyle and thus were influenced by both the sediment in which they were hosted, and the currents which supplied nutrients and oxygen. Conclusions are subdivided into those which may be of general importance and applicable to other systems, and those which allow further interpretation of this particular setting.

These trace fossils have received scientific attention over the last two centuries but several new insights from this study further demonstrate the importance of these traces in terms of palaeoenvironmental analysis:

(1) A number of palaeocurrent indictors are commonly associated with *Lockeia* and are confirmed by this study: (a) downstream inclination of near-vertical burrows. The angle may hint at sedimentation rates and also the size of the individual. (b) Long axes of *Lockeia* are commonly oriented parallel to palaeoflow, presumably with inhalant siphons pointing upstream. Additional palaeocurrent indicators include: (c) steeper sided scour and higher sediment surface on the upstream side of the trace; (d) diffuse lamination downstream of the trace, or, more widespread downstream erosion.

(2) Enhancement of turbulence by flow around individual or clusters of bivalves may lead to the development of a fan-shaped zone of increased erosion immediately

downstream; this may lead to disturbance and destabilisation of sediment, and hence other bivalves, downstream. This effect may plausibly explain the relatively uniform spacing pattern of *Lockeia* and provides an additional indication of palaeoflow.

(3) Scavenging of transported bivalves (killed prior to, or during transport) by polychaete and nematode worms, marked by *Planolites* and *Cochlichnus* traces respectively which often radiate towards the imprints of dead bivalves. These assemblages indicate that areas which were suitable for bivalve colonisation occurred in upstream areas.

These conclusions may provide generic insights into systems with similar settings. In terms of the Rough Rock and the Rough Rock Flags, the trace fossils provide further insights into this well-studied system: (a) palaeocurrent analysis of the traces suggests that a significant component of the flow which deposited the Rough Rock Flags was towards the north-east to south-east; this is confirmed by detailed observation of sedimentary current indicators within the section but is counter to previous interpretations of palaeoflow dominantly to the south-west. This may reflect a different source, as postulated for the Haslingden Flags, or may reflect flow divergence associated with overbank flow, crevasse splays or point bars (potentially supported by Miller's 1986 data). (b) The occurrence of *Lockeia-Planolites-Cochlichnus* scavenging horizons within the Rough Rock braided river sandstones suggests that suitable environments for bivalve colonisation existed in upstream localities, suggesting that Rough Rock Flags type facies are probably lateral, as well as distal equivalents to the Rough Rock.

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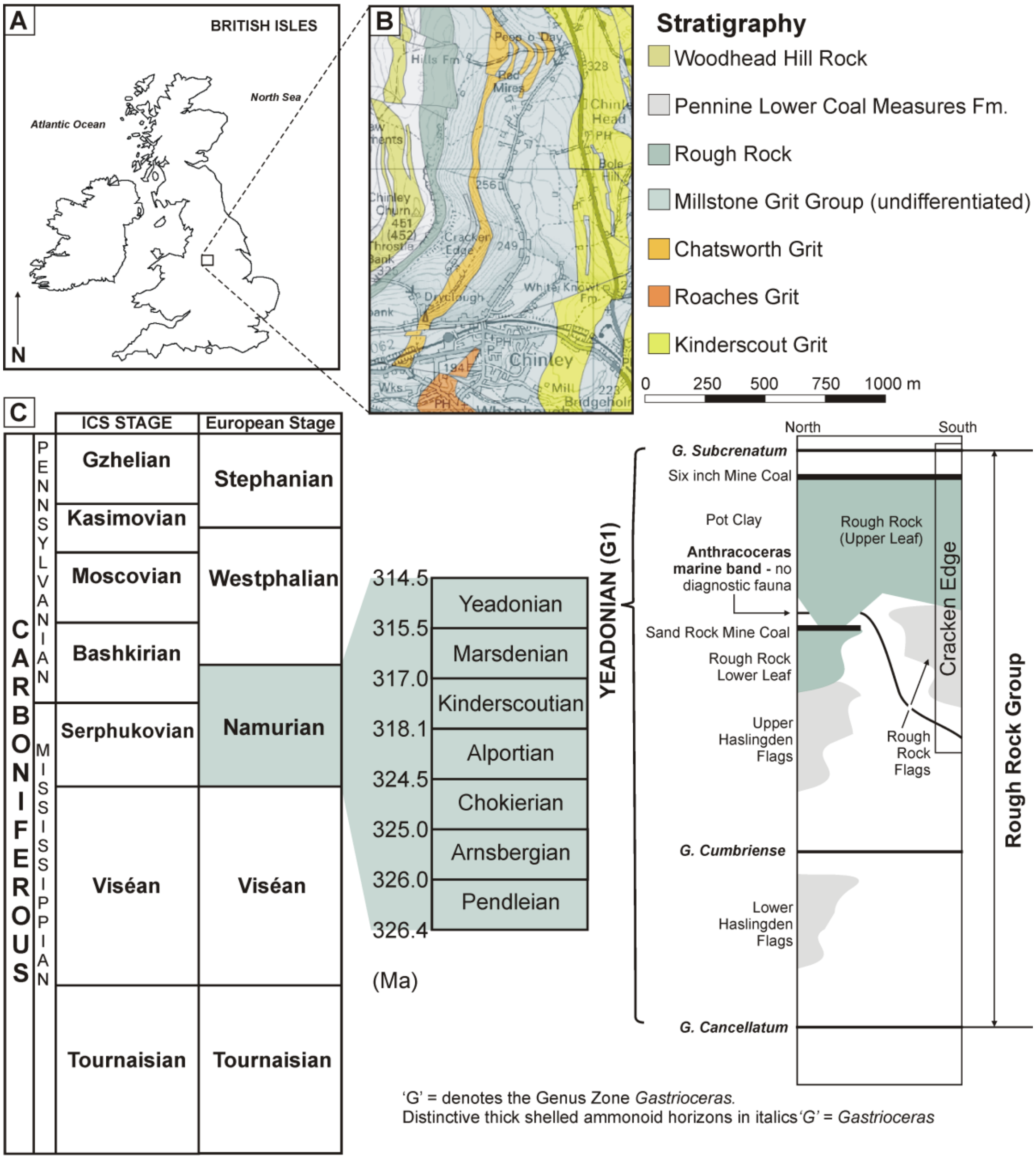

Figure 1 – (A) Location of the study are in the UK; (B) Geological map of the area around Cracken Edge, near Chinley in the High Peak of Derbyshire (Geological Map Data©NERC 2009); (C) Stratigraphy of the Rough Rock Group, showing the defining ammonoid zones (*Gastrioceras cancellatum* and *Gastrioceras subcrenatum* at the base and top respectively). The location of Cracken Edge is shown schematically. Partly modified from Hampson et al. (1996).

Figure – 2. *Lockeia* epichnial depression with sand-filled cast of bivalve shell. Several specimens are revealed at the tops of burrows (Fig. 5) but no well-preserved examples of the trace maker have been found. Hardy (1970) and Miller (1986) attribute this bivalve to *Carbonicola* based on its occurrence at other localities. Note the pointed end of the shell (top) marking the position of the inhalant siphon.

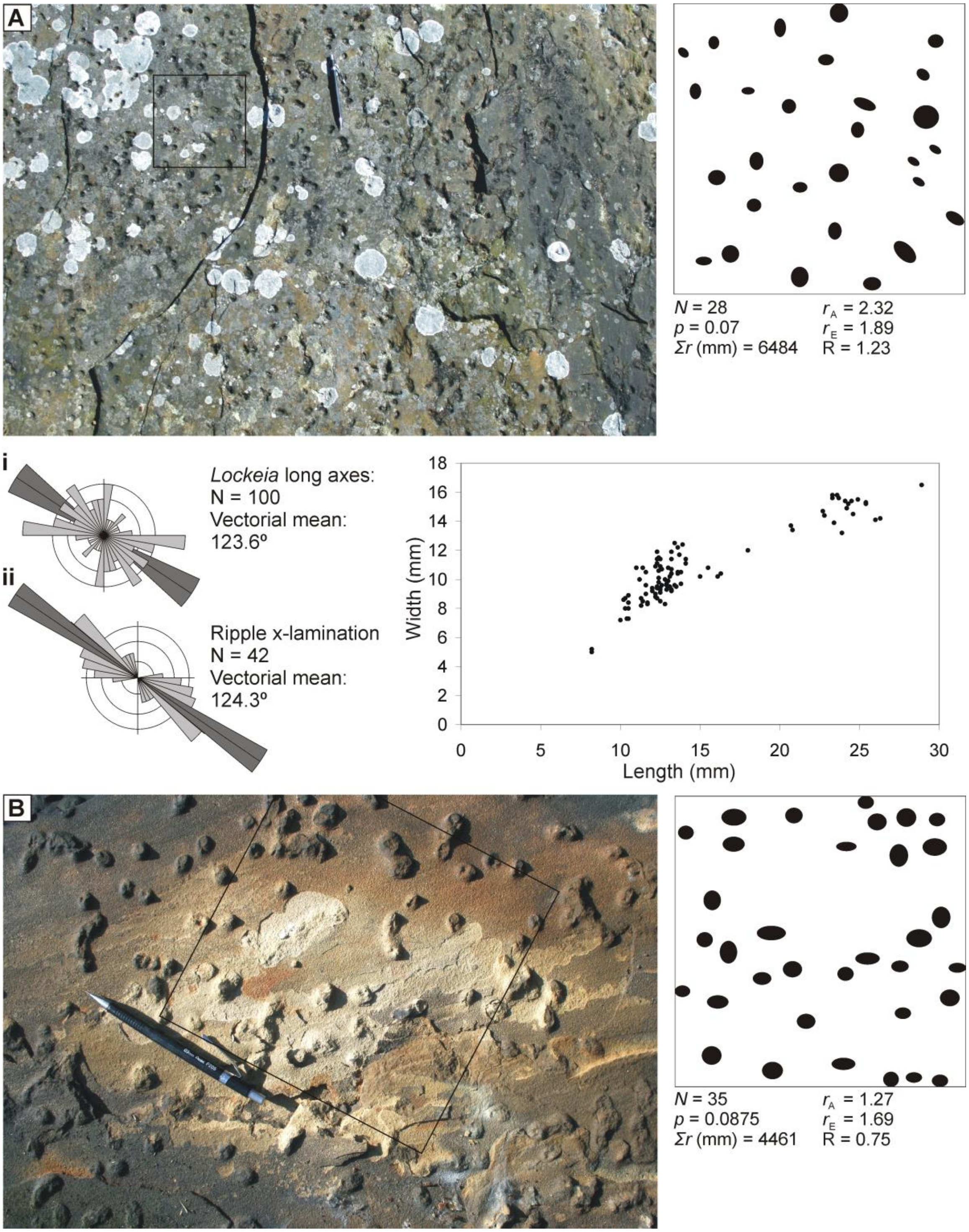

Figure 3 – (A) *Lockeia* as epichnial impressions (negative traces) on an in-situ upper bedding plane surface, which overlies the subvertical burrows of Fig. 4. *Lockeia* has a relatively regular spacing pattern; it is however common to find clusters of two or more individuals, often with an 'en echelon' alignment with palaeoflow (see 'i' and 'ii'). Nearest neighbour analyses reveal that *Lockeia* in has a non-random distribution (R=1.23) (values above unity suggests distribution is approaching maximum spacing). Long-axes trend approximately NW-SE, directional information suggests alignment with palaeoflow towards 123.6°. Size distribution analysis reveals two distinct size classes.

(B) Hypichnial expressions of *Lockeia* with central apertures (on a loose slab). *Lockeia* also have a non-random distribution but their low value (R=0.75) suggests that they are aggregated, which is clear to see in the image. Quadrants are 200 × 200 mm; pencil is 145 mm long. Note the central 'apertures' of *Lockeia*, which may reflect foot withdrawl; these are not a common feature of *Lockeia* in the present study, although they resemble some of the *Lockeia* found at the bases of 'escape shafts' illustrated by Broadhurst et al. (1980, Fig. 8).

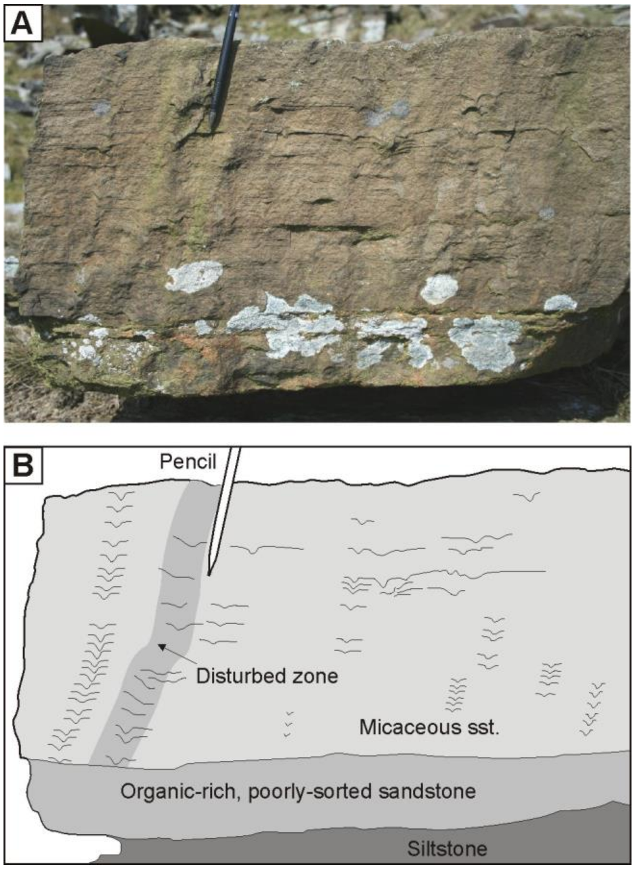

Figure 4 – (A) Vertical 'burrow' traces preserved as endichia, marked at their tops and bases by epichnial and hypichnial *Lockeia* respectively. Prominent traces are highlighted in (B). These traces are referred to Equilibichnia, as they represent the response of the organisms (bivalves) to episodic sedimentation, rather than true escape traces, or downwards burrowing traces. The traces appear to originate from the organic-rich structureless sandstone at the base, interpreted to be a flood deposit.

Figure 5 – Sliced sections. (A) Opposing sections through Equilibichnia trace associated with hypichnial expression (white arrows) and epichnial impression of *Lockeia*. In this

case the bivalve appears to have burrowed into the sediment in response to erosion of the substrate (demonstrated by the scour topography overlying the burrow aperture); this has subsequently been filled by micaceous and muddy sediment; the outline of the sand filled shell is marked by dark-coloured cement (circled in lower image). The protrusion of the bivalve is marked in the top image (black arrow). (B) Sub-vertical burrows with basal *Lockeia* hypichnial expressions marked (white arrows). Black arrows indicate the change in sediment surface relief across one of the burrows, indicating palaeoflow from right to left. The dashed line indicates downward burrowing of an unknown organism, note sharply down-warped sediment on RHS of line. (C) Burrow arrowed in white suggests progressive downstream dislodging of bivalves; however, it cannot be said for certain whether this is the progressive downstream movement of one individual or more, i.e., successive colonisation surfaces. Note the uppermost white arrow shows a large trace with no apparent underlying precursor. The black arrow points to an abandoned burrow, the relief of which was progressively healed by later flows. Dashed oval line indicates the outline of a sand-filled shell indicating death in-situ (e.g. Broadhurst et al. 1980) (D) Black arrow indicates an abandoned burrow trace. Centre of sample is marked by an intensively burrowed fabric, entirely created by bivalve movement. (E) Steep upstream burrow margin with diffuse laminae and shallow margin on the downstream side. (F) Burrow tops, i.e., *Lockeia* epichnia, infilled with coarse-granular sand.

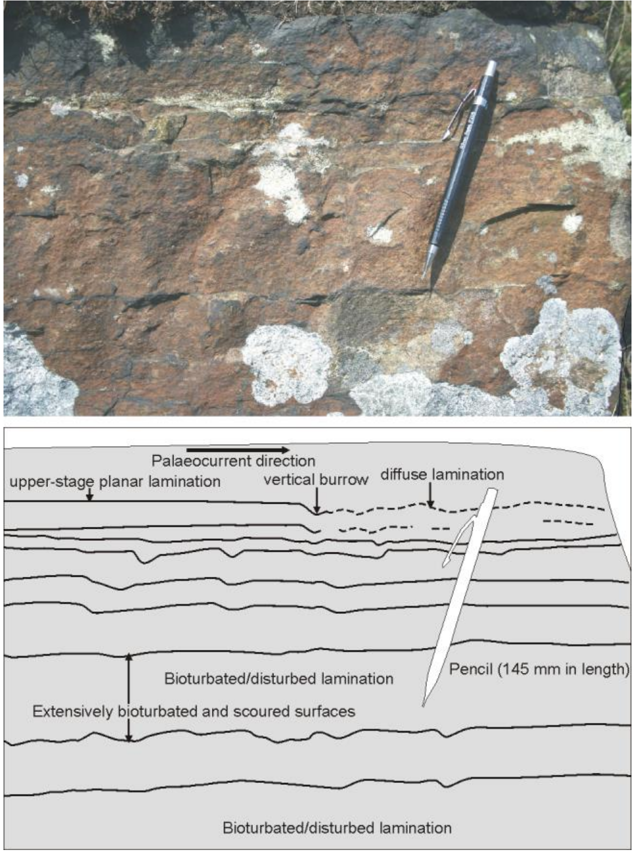

Figure 6 – Relatively impersistent subvertical burrows within an exposure approximately parallel to palaeoflow. There are a number of clear examples of downstream erosion on the lee-side of the vertical traces, which are attributed to bivalve equilibichnia. On the lee-side of the trace, lamination which is clear and defined by micaceous layers on the upstream side, is replaced by diffuse lamination, or an apparently massive appearance. This feature is here attributed to downstream erosion of the substrate. This effect may be

a critical factor in the spacing of bivalves within colonies (Fig. 3). The impersistence of traces in this locality suggests that it was subject to regular high energy flow events (lower 8 m of the Rough Rock Flags recorded by Miller 1986).

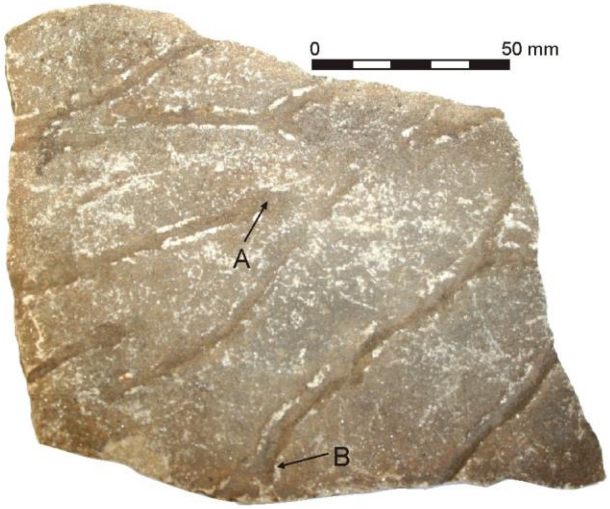

Figure 7 – Locomotion tracks are uncommon at Cracken Edge. These “plough marks” take the form of epichnial grooves, 5-6mm wide with slightly raised ridges on either side of the central furrow, and often terminate in a *Lockeia* trace (A). Traces are straight to slightly sinuous trails which sometimes cross but never branch, these have only been found on loose slabs from the lower 8 m of the Rough Rock Flags recorded by Miller 1986, the longest trail revealed was 500 mm in length. These were probably created in subaerially exposed sediment, necessary to maintain their steep sides and ridges (B), and reflect movement of the (bivalve) trace maker towards a receding waterline (see Fig. 9).

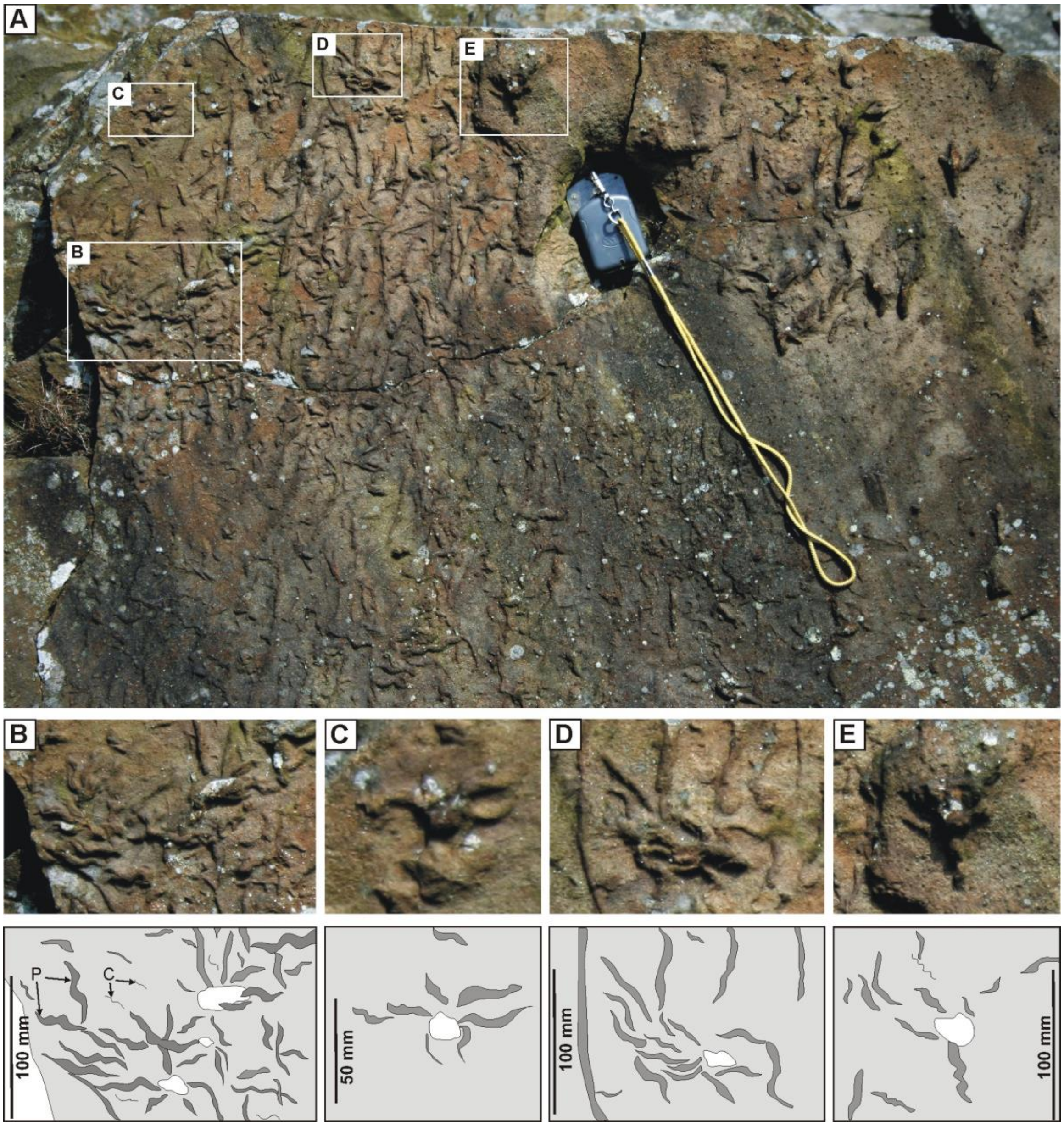

Figure 8 – Scavenging association typically includes *Planolites*, *Cochlichnus*, *Didymaulichnus* and *Palaeophycus*. (A) Basal bedding plane of a fallen block. The horizon from which the block fell is consistently marked by this ichnocoenoses and overlies a thin (100 mm) siltstone interval, overlying which a relatively finer-grained sandstone lens within the Rough Rock. Long traces are commonly aligned from the top to bottom of the block, corresponding to ENE-WSW on the in-situ bedding planes; Hardy (1970) recorded NW-SE orientated *Coclichnus* in the Rough Rock Flags. Insets B-E show predominantly *Planolites* (P) and *Cochlichnus* (C) traces radiating towards central hypichnial mounds interpreted to be *Lockeia* (pale grey colour), casts of dead and decaying bivalves carried by flood waters to a previously quiet environment (e.g., a small abandoned channel).

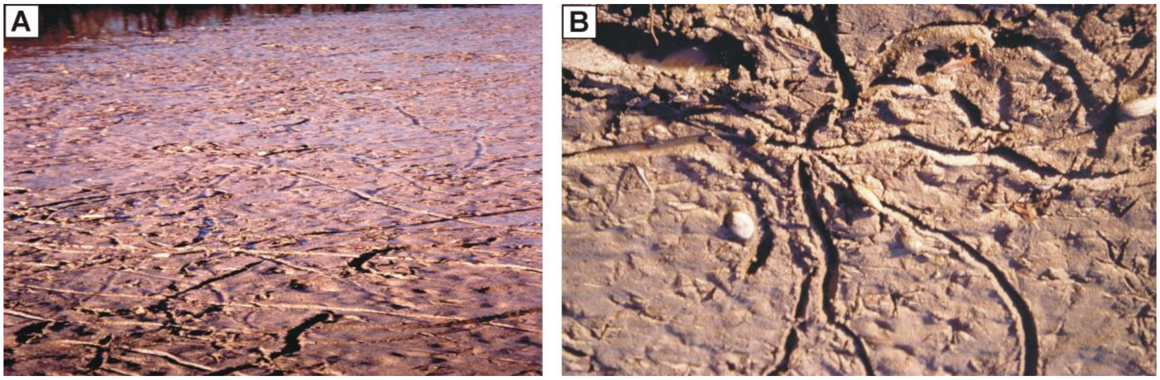

Figure 9 – Lateral movement traces (epichnial grooves) created by bivalves following a receding water line during reservoir draining (Mapperley Reservoir, Derbyshire, England). traces are generally sub-perpendicular to the receding water-line Photographs courtesy of Dr Andrew Johnson.

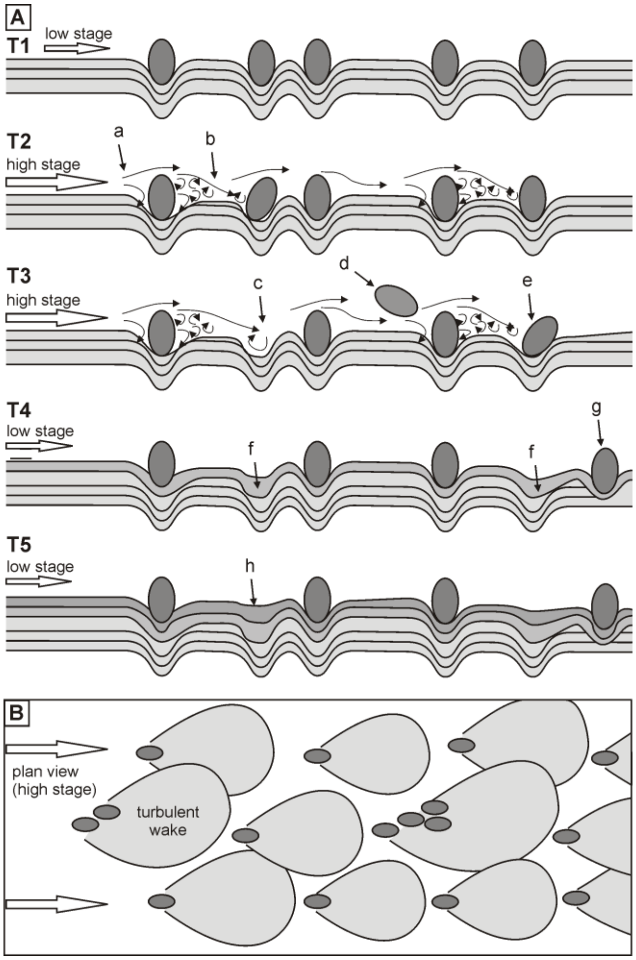

Figure 10 – A relatively regular spacing pattern of *Lockeia* has been noted. Evidence of erosion and scouring downstream of *Lockeia* has also been recorded. (A) A model is presented whereby erosion and scour associated with flow around individual, or clusters, of semi-infaunal bivalves on a non-cohesive substrate induces further flow separation and

creates a turbulent wake downstream of the organism. This turbulence leads to enhanced erosion and the destabilisation of bivalve in the immediate downstream vicinity. This mechanism may plausibly explain the relatively uniform spacing pattern of *Lockeia* often observed within the Rough Rock Flags and elsewhere. (a) steeper side to burrow on upstream side of bivalve; (b) deflation of sediment surface downstream of bivalve; (c) abandoned burrow, due to destabilisation associated with turbulent wake of upstream bivalve; (d) bivalve transported downstream; (e) bivalve destabilised within sediment; (f) ponding of sediment within hollow begins to heal the topography (compare to Fig. 5D); (g) bivalve relocated downstream (compare to Fig. 5C); (h) sediment surface nearly entirely healed (compare to Fig. 5D). (B) Plan view of the generation of turbulent wakes around individual or clusters of bivalves.

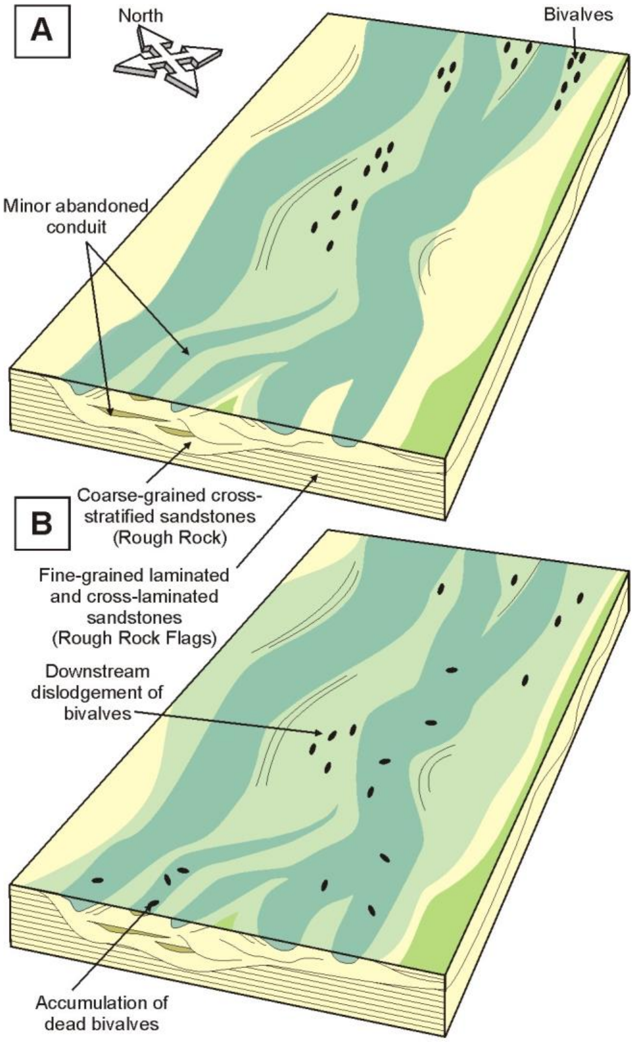

Figure 11 – Braided river setting of the Rough Rock during normal flow stage (A) and high stage (B). Bivalves are thought to have colonised areas of relatively lower energy flow, such as sand-flats developed on bar tops or crevasse splay areas. As such environments are prone to erosion, bivalves were periodically dislodged from their burrows and either managed to re-establish themselves soon after, or were transported down system, either being deposited in quieter areas, in this case a minor abandoned conduit, or transported further downstream. Dead bivalves deposited in these

environments within the Rough Rock channel system were scavenged by polychaete and nematode worms. In unidirectional flow regimes, bivalve year-classes may be transported progressively further downstream, with the result that the oldest bivalve year classes may be poorly represented in upstream localities.