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Non-palimpsested crowded *Skolithos* ichnofabrics in a Carboniferous tidal rhythmite: Disentangling ecological signatures from the spatio-temporal bias of outcrop

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ABSTRACT

A heterolithic tidalite succession yielding spring–neap bundles is newly reported from a mid-Carboniferous (Serpukhovian) section of the Alston Formation of Northumberland, England. The rhythmite records deposition over an interval that can be confidently calibrated to at least 84 lunar days, and attests to a non-negligible tidal range in parts of the Northwest European Seaway in the late Mississippian. The tidalite is notable for the presence of a striking crowded *Skolithos* ichnofabric on both bedding planes and in vertical section. Bedding plane expressions of the ichnofabric reveal true substrates of sand piles excavated during burrow construction, in addition to an apparently remarkable equal spacing between individual burrows that is shown to be genuine through pair correlation function analysis. These characteristics show that the burrowed horizons were registered by contemporaneous ichnocoenoses, with no palimpsesting of burrows. The irregular vertical distribution of burrow horizons, despite a near-continuous semi-diurnal record of sedimentation, is suggested to be an artefact of spatial patchiness of burrowing communities in the depositional environment; imperfectly registered in a vertical profile with high-temporal, low-spatial resolution. The succession proves that burrow palimpsesting is not an inevitable ichnological conclusion of sedimentary stasis, and attests to intermittent palaeoecological fidelity of the stratigraphic record at the small spatio-temporal scales recorded at outcrop.

INTRODUCTION

The diurnal or semi-diurnal tidal deformation of marine waters manifests in coastal regions as a dominant incoming flood tidal current and subordinate outgoing ebb tidal current, each punctuated by a tidal stillstand at high and low tide (e.g. De Boer *et al.*, 1989; Dalrymple *et al.*, 1991; Archer & Johnson, 1997; Mazumder & Arima, 2005; Kvale, 2012). Sedimentary signatures ascribed to these bidirectional currents and repeated fluctuations in current energy are collectively referred to as tidalites and include features such as herringbone/bipolar cross-stratification, reactivation surfaces and cyclic rhythmites (e.g. Nio & Yang, 1991; Wells *et al.*, 2005; Davis, 2012). Tidalites that comprise flat-laminated or laterally-accreted rhythmite successions, consisting of heterolithic laminae of varying thickness, have special value as they can preserve continuous sedimentary records on timescales from the semi-diurnal to annual; archiving spring–neap and longer tidal cycles in addition to daily tides (e.g. Kvale, 2012) and providing insights into the long-term evolution of the Earth–Moon system (e.g. Williams, 1989; Coughenour *et al.*, 2013). Yet, considering that these processes have been ubiquitous and continuous in coastal waters throughout Earth history, tidal rhythmites are relatively uncommon in the global sedimentary-stratigraphic record. This is because not all flood/ebb currents in nature attain (or attain sufficiently distinct) critical velocities to create heterolithic rhythmites, in addition to the propensity for rhythmic laminae to be disrupted or destroyed by other common nearshore sedimentary processes including storm/wave action and bioturbation (e.g. De Boer *et al.*, 1989; Davis, 2012). When instances of ancient tidal rhythmites can be unequivocally identified, having escaped such reworking to become interred in the sedimentary–stratigraphic record, they have extreme value as high-resolution sedimentary chronometers that permit the recognition of signatures that can be accurately chronicled on timescales of days to months.

This study presents evidence for previously unrecognized subhorizontal-laminated heterolithic tidal rhythmites, cropping out in mid-Carboniferous strata of the Northumberland Basin, northern England. The rhythmites act as high-resolution records of sedimentation over a continuous interval of at least 84 days and are especially notable for the presence of crowded *Skolithos* ichnofabrics at several horizons, stochastically distributed throughout tidal bundles, and with no evidence for palimpsesting of burrows. The accuracy of this semi-diurnal sedimentary–stratigraphic chronometer, coupled with evidence for contemporaneous communities of burrowing organisms active during temporally constrained intervals of a few days, renders this outcrop an

exceptional window onto high-frequency palaeoecological processes in the mid-Carboniferous and provides general insight into the significance of non-palimpsested ichnofabrics at outcrop.

GEOLOGICAL SETTING

The outcrop described here is found at Saltpan How (55° 44' 03.5"N, 01° 57' 42.7"W) at the north end of Cocklawburn Beach, 4 km south-east of Berwick-upon-Tweed, Northumberland (Fig. 1), and has only relatively recently become exposed. It occurs directly below the remains of an old cliff top road, truncated by a cliff collapse in the 1950s [dated from historic records (Carlton & Summerling, 2017) and Ordnance Survey maps]. Extensive landslip debris from the collapse created soft earth cliffs that concealed any outcrop for decades; however, accelerated coastal erosion between 2012 and 2018 has removed this (and further bedrock), exposing the present outcrop (Fig. 1; Northumberland County Council, 2012, 2020).

The exposed cliff face comprises strata of the Mississippian-aged Alston Formation, which is the middle of three units of the mid-Carboniferous Yoredale Group (Fig. 1; Dean *et al.*, 2011). All the formations of the Yoredale Group are characterized by repeating cyclothems that can comprise sandstones, shales, coals and limestones, but are differentiated by their age and an upwards-decreasing frequency of carbonates as the units become dominated by terrigenous strata (Reynolds, 1992; Frank & Tyson, 1995; Dean *et al.*, 2011; Booth *et al.*, 2020). The strata were deposited within the Tweed Sub-Basin (Northumberland Basin), in the foreland region of the Variscan orogenic belt, at a subequatorial palaeolatitude (Leeder *et al.*, 1989; Chadwick *et al.*, 1995; Fraser & Gawthorpe, 2003; Torsvik & Cocks, 2017).

Named limestone marker horizons occur throughout the Yoredale Group, recording transgressive cyclicity on frequencies of 100 ka or less, and governed by both glacio-eustasy and local tectonics (Tucker *et al.*, 2009; Waters *et al.*, 2014; Booth *et al.*, 2020). They are biostratigraphically correlated to regional substage level throughout northern Britain, using miospore and foraminifera assemblages (Turner & Spinner, 1992; Cózar & Somerville, 2012, 2020, 2021; Ingrams *et al.*, 2020). The tidalite beds described here occur above the Eelwell Limestone, which is dated to the late Brigantian regional substage (*ca* 329 Ma; early Serpukhovian) (Cózar & Somerville, 2020, 2021; Ingrams *et al.*, 2020). Although the stratigraphy immediately overlying the Eelwell Limestone is complicated and repeated by a series of minor thrust faults, the presence of the 'Acre

Coal' seam at the base of the studied outcrop (Turner & Scrutton, 1995) stratigraphically locates it to within 10 m above the marker limestone.

SEDIMENTARY CHARACTERISTICS OF THE SALTPAN HOW OUTCROP

Description

The studied section commences near the Acre Coal (Fig. 2), which rests on top of fine-grained sandstones with prominent stigmarian root casts. The 30 cm thick coal seam is succeeded by a 2.5 m thick heterolithic package of dark grey-coloured siltstone with 0.5 to 2.0 mm thick laminae and lenses of very fine-grained sandstone. In the uppermost 80 cm of this package, the sandstone laminae are organized into the rhythmic bundles that are the focus of this study (Fig. 3). The upper part of the package is truncated by 50 cm of amalgamated sandstone laminae with prominent wave ripple lamination, soft-sediment deformation, and an erosive base, which itself passes upwards into further heterolithic packages that lack regular bundles of sandstone laminae (Fig. 2).

The studied heterolithic package (Fig. 3) comprises an apparently continuous package of horizontal to sub-horizontal laminae, but close inspection reveals that it is frequently interrupted with minor disconformities that are marked by faint changes in lamina dip or shallowly erosive bounding surfaces (Fig. 3D). The subtlety of the disconformities means that they can remain cryptic at a small scale in the weathered natural outcrop, so it is problematic to confidently divide the succession into conformable packages. Yet despite this, the uppermost 80 cm of the heterolithic package can clearly be seen to be organized into 2 to 5 cm thick bundles that typically consist of individual 0.1 to 3.0 mm thick sandstone and siltstone laminae, punctuated by 1 to 3 cm thick intervals of vertically-continuous siltstone (Figs 3 and 4).

The apparent number of sandstone laminae in each bundle is dependent on the precise vertical profile along which they are counted, because even over a lateral distance of a few millimetres some laminae can be seen to be lenticular and discontinuous, and some have shallowly erosive bases (Fig. 5). Additionally, accurate counts can occasionally be hindered by post-depositional micro-thrusts internal to the rock package (Fig. 5C).

To mitigate against both the lamina-scale and bundle-scale lateral discontinuity, counts and measurements of laminae were restricted to one *ca* 20 cm thick vertical interval of six bundles, which could confidently be traced uninterrupted along the length of the outcrop (Figs 3 and 5).

Tallies of number of laminae and thickness of individual laminae were taken in 15 vertical transects of these six bundles; as five groups of three vertical counts, spaced 5 cm horizontally, across the 11 m wide outcrop. Ignoring instances where the uppermost bundle had been erosionally-truncated, these counts revealed that each bundle consists of between nine and 20 discernible sandstone laminae, with the majority consisting of 12 to 16 laminae (mean *ca* 14; Fig. 6A). Measurements of the thickness of individual sandstone laminae reveal that they are thickest (typically 1 to 2 mm) towards the middle of each bundle, and thinner (typically <0.5 mm) towards the top and bottom of each bundle (Fig. 6B).

Interpretation of tidal rhythmites

The heterolithic bundles are interpreted as tidal rhythmites, with cyclic variations in lamina thickness and lithology recording changes in current velocity associated with lunar/solar cycles (e.g. Kvale, 2012). Ideal instances of tidal rhythmites permit the recognition of a hierarchy of semi-diurnal, diurnal, fortnightly (neap–spring), and longer-recurrence tidal events, variably synchronized to the synodic (lunar; 29.52 day) or tropical (27.32 day) month (e.g. Archer *et al.*, 1991; Kvale, 2006, 2012). Such instances can be invaluable in determining palaeotidal range, lunar retreat, or regional palaeogeography, but are dissimilar from the examples described here because: (i) they are most commonly described from core rather than natural rock outcrop, meaning that laminae can be more clearly discerned within a spatially-confined sample; (ii) they can be far more vertically extensive, with additional value for determining longer-term events; and (iii) the best examples contain few disconformities and consist of laterally-continuous laminae.

The bundles from the Alston Formation are imperfectly registered in a naturally-weathered rock outcrop of limited spatial extent (for example, Fig. 4), where the propensity for lateral discontinuity of individual laminae and bundles is more apparent than in a core sample. Despite this, they exhibit four regular and repetitive characteristics that strongly indicate that they are deposits arising from cyclic neap–spring variability in current strength: (i) the bundle laminae are always evident as couplets of sandstone and siltstone, analogous to modern rhythmites where the flood, or flood and ebb, tidal currents are sufficient to move sand, and intervening episodes of tidal stillstand are marked by the settling of mud from suspension (e.g. Nio & Yang, 1991); (ii) despite local variability, the bundles never contain fewer than nine sandstone laminae, and never more than 20: a consistent range of sand laminae as would be expected from a semi-diurnal tidal system in which not every subordinate tidal current surpassed the critical velocity for the tractional

movement of sand (e.g. Kvale, 2012). In addition, the lenticular nature of some of the sand laminae (Fig. 5A) indicates that some may be the deposits of sediment-starved ripples: thus, lamina deposition may have been less frequent than the motion of tidal currents due to limited local sediment budgets; (iii) there is consistency to the thickness of both the bundles (2 to 5 cm) and the siltstone intervals (1 to 3 cm) that separate them, attesting to a regularity in the variation of depositional energy that is attained in few non-tidal sedimentary settings. There is weak evidence that there may be a pattern of alternation between thicker and thinner bundles (for example, compare bundles 1, 3 and 5, versus bundles 2 and 4, in Fig. 4), as could be expected from the high spring tide versus the low spring tide in any one synodic or tropical month; and (iv) sandstone laminae are thicker in the middle of bundles than the top and bottom of bundles, comparable with patterns observed in definitive tidal rhythmites, where peak lamina thickness is incrementally attained commensurate with the dominant current of the peak spring tide (e.g. Kvale, 2012).

The sedimentological context of the surrounding strata is supportive of a tidal role in deposition. The Alston Formation near Saltpan How has previously been investigated in detail from a facies model perspective by Reynolds (1992) and Booth et al. (2020), who both interpreted the presence of tidally-influenced sedimentary facies [Reynolds' (1992) Facies II tidal channel and Booth et al.'s (2020) Facies D1 interdistributary bay tidal flats]. However, neither noted the presence of rhythmite bundles, suggesting that this facies motif may be very spatially-restricted and only apparent in the most recently exposed outcrop. The positioning of the rhythmite immediately above a transgressive surface onto the Acre Coal, within a succession that locally also contains evidence for fluvio-deltaic and storm-induced hummocky cross-stratification (e.g. Reynolds, 1992; Booth et al., 2020), suggests deposition within the shallow subtidal realm (Dashtgard et al., 2021). The restricted vertical and lateral extent of the rhythmite is compatible with suggestions that deposition occurred in an interdistributary bay, between some of the many localized delta lobes that typify facies models for the cyclothems of the Yoredale Group (e.g. Reynolds, 1992; Frank & Tyson, 1995; Dean et al., 2011; Jones, 2011; Booth et al., 2020; Fielding, 2021). It appears to be a rare and fortuitously surviving record of tidal conditions within the Tweed Sub-Basin, because most such deposits that once existed were destined to reworking and replacement by higher energy deltaic and shallow marine facies signatures.

The limited extent and imperfect rendering of the tidal rhythmites in the Alston Formation mean that they are unsuited for detailed analysis of palaeotidal regime, and whether they were deposited

on synodic or tropical rhythms (e.g. Kvale, 2006, 2012) remains uncertain. Nonetheless, several spring–neap packages can be recognized to varying degrees of certainty and estimates of sedimentation duration can be applied to individual disconformity-bounded packages of bundles (Fig. 4: where each spring–neap–spring-neap cycle is approximated as 28 days, between the synodic and tropical tidal rhythms). This attests to sedimentation rates of *ca* 15 cm per month, at the scale of the rhythmite package, permitting the succession to be used as an approximate chronometer for assessing the significance of ichnological signatures within it (see *Ichnology of the Alston Formation Tidalites* section).

The localized high sedimentation rate can be explained with reference to the hierarchy of sedimentary phenomena within deltaic environments (e.g. Bhattacharya *et al.*, 2019, 2020; Holbrook & Miall, 2020). Recent stratigraphic models have demonstrated how higher-order hierarchies of larger phenomena generate statistically large volumes of underfilled accommodation space between or within themselves (Ganti *et al.*, 2020). In the case of the deltaic sedimentary setting of the Alston Formation, the generation of higher-order phenomena, such as delta lobes, would sporadically lead to localized areas of underfilled accommodation space (i.e. interdistributary bays), where archived sedimentation rates could be elevated. Most such accumulations would be at high risk of later reworking (for example, during reorganization of the delta), explaining the rarity of the facies signature within the Alston Formation. Yet as such facies would have been intrinsic components of the depositional environment, the random preservational sampling of a fraction, at the small scale of the described outcrop, is expected. It requires no special explanation of extraordinarily rapid sea-level change (e.g. Myrow *et al.*, 2018) and instead is a 'frozen accident' of preservation (Miall, 2015).

Context within the regional record of ancient tidalites

Although of only limited extent, the Alston Formation rhythmites are significant for interpretations of regional palaeogeography at the time of deposition. Pre-Quaternary tidalites are rare in Britain, with only a few putative Cretaceous (Allen, 1981; Wells *et al.*, 2010) and Carboniferous (Read, 1992; Aitkenhead & Riley, 1996; Archer & Kvale, 1997; O'Mara *et al.*, 1999; Brettle *et al.*, 2002; Wells *et al.*, 2005) examples having been previously recorded. Of these, only a single example yields unequivocal evidence for rhythmites with tidal periodicities (Aitkenhead & Riley, 1996; Archer & Kvale, 1997; Brettle *et al.*, 2002; Wells *et al.*, 2005): a 76 cm thick borehole sequence of 95 heterolithic laminae from early Pennsylvanian (Kinderscoutian–

Marsdenian) prodeltaic facies in the Central Pennine Basin of West Yorkshire (Aitkenhead & Riley, 1996; Archer & Kvale, 1997).

The paucity of tidalites in the abundant Carboniferous shallow marine sedimentary record of Britain has been ascribed to its palaeogeographic location on the Northwest European Seaway (NES) (Collinson, 1988; Wells *et al.*, 2005). At the onset of the Carboniferous, the NES connected to the open Panthalassic Ocean both to the north of present-day Scandinavia, and to the south-west, through the Rheic Ocean between Laurussia and Gondwana (Torsvik & Cocks, 2016). As the period progressed the Variscan orogeny resulted in the closure of the Rheic Ocean, meaning that the NES remained open only to the far north and became increasingly epeiric in nature. This led to extremely microtidal conditions in its inner reaches (Collinson, 1988), and later Carboniferous tidal ranges for the British part of the NES have been modelled as reaching only *ca* 5 cm in open water, and up to 1 m in restricted estuaries (Wells *et al.*, 2005).

While the formation of flat-laminated heterolithic tidal rhythmites is possible under reasonably microtidal regimes (Wells *et al.*, 2005), the example from the Alston Formation shows that the early Serpukhovian tidal range in the British part of the NES was not wholly negligible, and so may pre-date full closure of the Rheic Ocean. Further, the local basin setting and pronounced basement topography may have played a role in accentuating tidal range. At the time of deposition, the Tweed Sub-Basin was a narrow basinal low, sandwiched between the buoyant granite-cored highs of the Cheviot Block to the south and Southern Uplands Block to the north (Fig. 1; Leeder *et al.*, 1989; Chadwick *et al.*, 1995; Fraser & Gawthorpe, 2003). Within this basement context, it is plausible that the Tweed Sub-Basin provided the foundations for an open-mouthed embayment and would thus have experienced oceanic tides that were amplified above the regional 'norm' by resonance effects (Reynaud & Dalrymple, 2012).

ICHNOLOGY OF THE ALSTON FORMATION TIDALITES

Description

Diverse trace fossils have previously been documented from the Alston Formation in the Northumberland Basin, including reports of *Arenicolites, Beaconites, Diplocraterion, Neoione, Macaronichnus, Palaeophycus, Planolites, Skolithos, Taenidium, Teichichnus, Thalassanoides* and *Zoophycos* (e.g. Boyd & McIlroy, 2017, 2018; Booth *et al.*, 2020; McLean *et al.*, 2020). Despite this formation-level ichnodiversity, the heterolithic package described here contains only a

monospecific assemblage of multiple short, mud-filled *Skolithos* (Fig. 7). Burrows can confidently be ascribed to *Skolithos* as they have a structureless infill, and lack the concentric lining of other similar vertical ichnotaxa such as *Rosselia*. Individual burrows are 2 to 3 mm in diameter and 4 to 30 mm in length and are oriented vertically to sub-vertically in the strata [some particularly inclined instances may be due to tectonic shear (for example, Fig. 3B)].

The burrows penetrate through both sandstone and siltstone laminae, with no discernible lithological preference for their upper termination, but are exclusively infilled with siltstone. Vertical profile exposures of the traces exhibit no evidence for burrow overprinting and, where the outcrop is exposed as horizontal bedding planes, the burrows are seen to occur as spatially pervasive groupings with strikingly equant spacing between individual burrows (Fig. 7). No overlapping of burrow shafts was witnessed across 41 discrete bedding surface exposures.

A further striking feature of the burrowed horizons is that some of the visible bedding planes clearly record true substrates (i.e. preserved former water–sediment interfaces; Davies & Shillito, 2018, 2021), because the burrow tops are seen to be rimmed by sand that was exhumed from antecedent heterolithic laminae during the registration of the burrow (Fig. 7C and D). The sand rims are demonstrably surficial features that exist only at the burrow aperture, as evidenced by a lack of deformation of adjacent sediment where burrows are seen in vertical section (i.e. attesting that these were not formed by adjustment of the burrow position in response to burial). Within the vertical 80 cm interval of tidal bundles, a total of 538 sandstone and siltstone laminae were counted, 15% of which were penetrated by vertical burrows. Of the laminae, 51 were exposed as horizontal bedding planes and 15 mudstone laminae could be recognized as true substrates by virtue of the rimmed motif to the burrow tops (the remaining 36 were underdetermined due to an absence of trace fossils).The overall bioturbation index of the heterolithic package was 2 (5 to 30% bioturbation intensity), increasing to 3 (30 to 60%) at the scale of individual burrowed laminae (Taylor & Goldring, 1993). Counts of burrow tops in 10 cm^2 quadrants on such true substrates indicate that the density of burrows was up to 14,400 per m^2.

The monospecific *Skolithos* assemblage is restricted to the tidal rhythmite facies, but there are other trace fossils in adjacent strata. In the wave ripple-laminated sandstone packages that overlie the rhythmite, examples of *Planolites* and *Teichichnus* are present (Fig. 2). In the climbing ripple-laminated sandstones below the Acre Coal, multiple escape traces can be recognized (fugichnia; Fig. 9). Escape traces are produced by an animal rapidly migrating upwards through a body of

sediment that was deposited suddenly, resulting in downturned laminae, as sediment collapsed to fill the void left by the tracemaker (Ekdale *et al.*, 1984). In this case, locally rapid sedimentation is attested to by the climbing ripple-lamination through which the escape traces penetrate.

Analysis of burrow spacing

To quantify the apparent mutual avoidance of burrow tops, spatial point process analyses (SPPA) were applied to four bedding plane exposures that each revealed at least 50 cm^2 of true substrate (True Substrates 1 to 4, hereafter T1 to T4; Fig. 8). The SPPA include a suite of different analyses to investigate the spatial distributions of points (here burrows) within a mapped area (Illian *et al.* 2008). They include nearest neighbour analyses which have been previously employed to investigate burrow communities (e.g. Pemberton & Frey, 1984; Davies *et al.*, 2009), whereby the distance from each burrow to its nearest neighbour is measured and plotted on a cumulative frequency curve. However, nearest neighbour analyses only capture local patterns because they are limited by the maximum distance between two burrows: if all specimens occur within 10 mm of each other, for example, then the analyses will not include any patterns greater than 10 mm. This spatial limitation means that large-scale spatial patterns, as well as more complex patterns can be overlooked (Mitchell & Butterfield 2018). To capture more complex patterns over larger spatial scales, pair correlation functions (PCFs) were used, which measure how the density of points (here burrows) changes as distance increases. Where PCF = 1, the pattern is completely spatially random (CSR), and so no underlying processes can be resolved from the observed pattern. If PCF > 1 then the points (burrows) are aggregated or clustered together and if PCF < 1 then the points (burrows) are spaced out or segregated (Illian *et al.* 2008). To test whether the observed patterns are significantly different from CSR, the observed data was compared to a homogeneous Poisson model (which models CSR) using 999 Monte Carlo simulations of CSR with the simulation envelopes defined as the highest and lowest 5% of generated data (Wiegand & Moloney 2013). To further aid comparisons with model fitting, the goodness-of-fit test pd was calculated, where pd = 0 corresponded to no model fit to the data, and pd = 1 corresponded to a perfect model fit. If there were significant excursions outside the stimulation envelope and the homogenous Poisson model was not a good fit for the data (pd >> 0.1), the observed pattern was described as non-random (Diggle 2003).

Where small spatial-scale segregation (spacing out) of points (burrows) was observed, segregation models were fitted to the data (cf. Mitchell & Harris 2020), so that the spatial scale of avoidance

could be quantified, along with the strength of such avoidance. Where points have circles of avoidance which totally exclude other points, this is known as a hard-core model and where the density of points within this circle is reduced and does not totally exclude other points this is known as a soft-core model (Wiegand & Moloney 2013). For a hard-core model (total avoidance), the model parameter p = 0, and for a soft core model with a linear relationship between the circle centre and edge p = 1. These model-fitting analyses were performed in Programita (Wiegand & Moloney 2013).

The PCF analyses found burrow tops on all four true substrates were not-randomly distributed (all pd << 0.001) and exhibited significant segregation (avoidance) at small spatial scales (r < 10 mm) (Fig. 8). T1, T2 and T3 exhibited significant aggregation between 10 mm and 15 mm and T4 between 8 mm and 12 mm. The best-fit segregation model for T1 had an avoidance radius of 5 mm, with a parameter of 0.5 (pd = 0.446), T2 had an avoidance radius of 13 mm, with a parameter of 0.3 (pd = 0.645), T3 had an avoidance radius of 6 mm, with a parameter of 0.05 (pd = 0.814) and T4 had an avoidance radius of 4 mm, with a parameter of 0.05 (pd = 0.290). These analyses show that T1, T3 and T4 all exhibited strong avoidance behaviour (demonstrated by the parameter ~ 0) around the burrows, with varying degrees of distance from the burrows (4 to 6 mm). This behaviour is consistent with strong restrictions for the burrow-makers on proximity to each other. T2 exhibited a weaker segregation behaviour (parameter = 0.3) over a larger spatial scale of 13 cells, which could suggest that the constraints on proximity/avoidance for the T2 community were more diffuse, but may more likely be an artefact of imperfect recent erosion and exposure, with some burrow tops being masked by remnants of overlying laminae.

Interpretation

Tracemakers

Skolithos is a facies-crossing trace fossil with a Phanerozoic range, and the ichnogenus most likely exemplifies behavioural convergence amongst a wide range of invertebrate tracemakers (Curran & Frey, 1977; Knaust, 2017; Knaust *et al.*, 2018). However, some dense, monospecific assemblages of *Skolithos* have previously been ascribed to the activity of communities of phoronids ('horseshoe worms') (Sundberg, 1983; Emig, 2010; Knaust *et al.*, 2018). Phoronids are one of the smallest phyla of invertebrates, closely related to brachiopods, and have an evolutionary history extending back from the present until at least the Devonian (Emig, 1982; Santagata, 2015). In the case of the

Alston Formation burrows, modern analogue is strongly supportive of tracemaker organisms that behaved similarly to phoronids. Recent examples of the phylum construct mud-lined burrow tubes in soft-sediment, which have equivalent dimensions (1 to 3 mm diameter, <15 cm length: Larson & Stachowicz, 2009) and densities (for example, the modern species *Phoronis psammophila* are seen up to 15 to 18,000 per m^2: Emig, 1982) to the ichnofossils. Phoronids also have a strong environmental preference for intertidal to shallow subtidal habitats, and are mostly found at 0 to 70 m water depth (Ronan, 1978; Emig, 1982; Larson & Stachowicz, 2009). Additionally, as recent phoronids filter-feed from burrow apertures with lophophore nets, they exhibit mutual avoidance to deter overlying of lophophores, thus encouraging equant burrow spacing (Ronan, 1978; Emig, 1982; Frey & Pemberton, 1986). Finally, recent phoronids can retreat into their tubes during intervals when sediment is actively being deposited on their colonized substrate, and their re-emergence after sedimentation events is known to produce rims of sediment around their burrow apertures (Sundberg, 1983), with a strong similarity to the aperture rims seen in the Alston Formation.

Tracemakers similar to other known vermiform taxa appear less likely candidates. Nemerteans are known to produce simple vertical burrows with a passive fill, amongst a range of other, more complex burrow morphologies (Knaust, 2010). However, as nemerteans are largely predatory and have burrows that typically occur in low densities (Thiel & Kruse, 2001), there is little analogy with the dense associations of non-randomly spaced burrows, which are most easily explained through mutual avoidance of filter feeding organisms. Terebellid polychaetes typically produce burrows with walls consisting of concentric muddy laminae (such as in *Rosselia*) in which brick-like parcels of sediment can sometimes be observed (Schäfer, 1972; Aller & Yingst, 1978; Nara, 1995). Such features are not present in the Alston Formation *Skolithos*, suggesting that tracemakers similar to terebellid polychaetes were unlikely.

The tracemakers of the ichnofossils from adjacent strata were likely different organisms due to the different dimensions and morphologies of the burrows. *Planolites* and *Teichichnus* have each been ascribed to a cosmopolitan range of marine invertebrate tracemakers (Keighley & Pickerill, 1995; Knaust, 2018), though the large dimensions of the former (Fig. 2) suggests that molluscs (bivalves) were most likely the tracemakers (Keighley & Pickerill, 1995). Escape traces similar to those seen in Fig. 9 are known to be created by semi-sessile bivalves or vermiform organisms (Ekdale *et al.*, 1984).

Ichnocoenoses

The term 'ichnocoenosis' has been variably applied in trace fossil studies (see Keighley & Pickerill, 2003; McIlroy, 2004) and taken to mean either an approximation of a single community of traces that co-existed (e.g. Bromley & Asgaard 1979), or a simultaneous community of traces that co-existed on the same substrate (Ekdale *et al.*, 1984; Ekdale,1985). Pickerill (1992), Keighley & Pickerill (2003) and McIlroy (2004) objected to the latter usage on the basis that it can be impossible to determine burrow synchronicity. However, in the case of the Alston Formation traces, the recognition that burrows have upper terminations on preserved true substrates (Davies & Shillito, 2018, 2021), the lack of overprinting of burrows, and the evidence for continuous daily sedimentation, implies that burrows which occur on the same bedding surfaces were produced during the same short colonization windows, forming discrete contemporaneous ichnocoenoses in the sense of Ekdale *et al.* (1984) and Ekdale, (1985). This means that each individual burrowed horizon was formed by a simultaneous community of tracemakers living on the same substrate, rather than being formed through repeated and palimpsested burrow activity throughout an extended colonization window. The dominant characteristic of the Alston Formation tidalite ichnoceonoses is that they are monospecific, recording communities solely consisting of the *Skolithos* tracemaker, to the exclusion of other benthic fauna.

This ichnological signature contrasts with that seen in other tidalites of similar age, such as the Tonganoxie Sandstone of Kansas, USA. There, vertical burrows are rare within the tidalite facies and the associations are dominated by surficial trackways and trails (Buatois *et al.*, 1998). This difference is explained as in the Tonganoxie tracemakers arrived from neighbouring environments during colonization windows (Buatois *et al.*, 1997), whereas the Alston tracemakers may have settled directly from the water column, and hence were able to exploit the full colonization window.

Ichnofabric and Bioturbation Index

Although the burrowed horizons exhibit a crowded *Skolithos* ichnofabric, the bioturbation index of the horizons is relatively low (BI 2 to 3; Taylor & Goldring, 1993). In part this is an artefact of the equant burrow spacing, which may have had a minimum separation distance. It is also a result of the fact that no convincing overprinting can be observed in the section: wherever vertical burrows are seen, they share a common upper termination layer. Additionally, the irregular

vertical distribution of burrowed laminae, separated by non-burrowed stratigraphic intervals, means that no instances of palimpsesting into antecedent burrowed layers were witnessed. These traits imply that, while the sedimentary environment in which the tidalite was deposited was clearly amenable to the tracemakers, burrowing was never pervasive everywhere. The vertical expression of intermittent burrowed laminae, colonized to their maximum possible extent, but separated by laminae that lack burrows, is explainable as a stratigraphic translation of an uneven spatial distribution of burrowed patches within the depositional environment (Miller & Smail, 1997; Dashtgard, 2011; Marenco & Hagadorn, 2019; Davies & Shillito, 2021). Supporting analogue comes from comparison with modern substrates dominantly colonized by vertically burrowing filter feeding organisms. Modern phoronid burrows are known to occur in dense patches, spatially segregated by uncolonized regions of substrate (Ronan, 1978). More generally, Dashtgard (2011) analysed the substrates of Boundary Bay, Canada, and observed that there the total area occupied by organisms rarely exceeded 3%, which would correspond to a Bioturbation Index of only 1 if translated to the rock record. Attaining greater bioturbation intensities requires an extended colonization window, which would not have been afforded by the semi-diurnal sediment accrual of the Alston Formation tidalite.

Ichnofacies

The overall trace fossil assemblage of the Alston Formation (Boyd & McIlroy, 2017, 2018; Booth *et al.*, 2020; McLean *et al.*, 2020) is comparable to the recently described *Phycosiphon* and *Rosselia* ichnofacies (MacEachern & Bann, 2020). These ichnofacies have been erected to describe prodelta and delta front trace fossil assemblages and may be especially useful in subdividing Carboniferous cyclothem successions (Fielding, 2021). However, while the ichnofauna of the Alston Formation as a whole is reasonably diverse, and dominated by abundant deposit feeding traces (for example, *Teichichnus*, *Zoophycos*), these traces typically occur in low diversity or monospecific trace fossil associations (Booth *et al.*, 2020), similar to the *Skolithos* assemblage discussed here. As such it is likely that different parts of the Alston Formation cover the full range of deltaic subenvironments typified by the *Phycosiphon* and *Rosselia* ichnofacies (MacEachern & Bann, 2020). The monospecific segregation of ichnogenera suggests that the broader depositional setting was partitioned ecologically (Shillito & Davies, 2020), with filter-feeding organisms preferentially inhabiting sheltered areas (for example, as recorded by the

tidalite), and deposit feeding organisms occupying wave dominated regions and offshore carbonates, where interstitial food sources were plentiful.

INTEGRATING TEMPOS OF SEDIMENTATION AND ECOLOGY

Trace fossils can be used to add definition to our understanding of sedimentation rates at outcrop, both in terms of an understanding of the time taken for burrows to be excavated (Gingras *et al.*, 2008) and a recognition that burrows are commonly registered during intervals of sedimentary stasis (Tipper, 2015), when the temporary cessation of local sediment accrual opens a colonization window for infaunal organisms (Pollard *et al.*, 1993). These attributes can reliably be combined to estimate a minimum time duration of burrowed true substrates, prior to their burial (Davies *et al.*, 2019; Davies & Shillito, 2021). However, estimates are commonly underdetermined by an absence of evidence for the maximum duration of time over which the burrowed substrate could have persisted as the lithic surface. The Alston Formation example of synchronous ichnocoenoses and true substrates within a tidalite circumvents such limitations because they enable the comparison of timescales of burrowing activity against the tidal sedimentation rhythms recorded by the host strata. In this way, they provide an example of how the tempos recorded by sedimentary strata, extensive to the burrows that they host, can inform on the duration of burrow occupation. This scenario provides a subtle counterpart to more commonly reported tidal ichnological signatures where intensive rhythmites are preserved within traces and provide evidence for the duration of infilling of open burrow systems (Rodríguez-Tovar *et al.*, 2019).

In the tidalite, the shortest (4 mm) burrows penetrate four or five heterolithic laminae, while the longest (30 mm) burrows penetrate up to 25 heterolithic laminae. On a semi-diurnal rhythm, the former would be equivalent to approximately one day of accrued sediment, and the latter to five days. These values provide inflated estimates for the maximum 'lifespan' of the active burrows because at least some of the laminae that they penetrate must already have been in place prior to the initial burrow registration. On the other hand, evidence suggests that some of the burrows could remain active over more than one tidal cycle because the sediment rims to the burrow tops (Fig. 7) can be interpreted as signatures of aperture reactivation following blanketing by new sediment (e.g. Sundberg, 1983). If the shortest burrows are estimated to reflect the minimum penetrative depth at the instant of burrow initiation, then the longest examples would record burrows that remained active during the iterative accrual of 20 successive laminae (four days).

The tidal rhythmites are robust empirical evidence for short duration sedimentary timescales which prove that the colonization and occupation of the substrates by the *Skolithos* tracemakers was rapid and transient. Irrespective of the actual tracemaker, phoronids offer an analogy for the type of viable ontogenies that would have emerged amongst a multitude of unknown (and unknowable) tracemakers in geological history and demonstrate that unexpectedly expeditious registration of ichnological signatures can happen. Planktonic phoronid larvae swim in open seawater for approximately seven days, before sinking to the seabed and then undergoing a catastrophic 15 to 30 minute metamorphosis in which they transform into juveniles with an elongate vermiform trunk (Emig, 2010; Santagata, 2015). Once a phoronid has developed this form, it can burrow downwards into soft-sediment from its posterior by utilizing hydrostatic pressure changes to coelomic fluid and metasomal muscle contractions, achieving full burial (apart from the lophophore) in as little as eight hours (Emig, 1982). The transition from a planktonic larva to an organism with a fully developed burrow can thus be achieved in less than nine hours.

From this perspective, the fact that the burrows share common horizons within a continuously deposited succession is unsurprising because the colonization of the substrate could be instantaneously instigated relative to the timeframe of the deposition of a tidal laminae couplet. However, the persistence of the active burrows for less than a week after initial registration appears unusually short, particularly as, once buried, modern phoronids are thought to have a life span of approximately one year (Emig & de Mittelwihr, 1999).

The lithology of the burrow infills can be used to explain this disconnect between known sedimentary and ecological timescales. The burrow infills invariably comprise siltstone, indicating that it is unlikely they were filled in during any iteration of the dominant tidal current, when a sand infill would be expected. Likewise, none of the burrows exhibit signatures of heterolithic 'tubular tidalites' (e.g. Gingras & Zonneveld, 2015; Rodríguez-Tovar *et al.*, 2019), that record rhythmic infill of burrows that remained open over multiple tidal cycles after abandonment. Instead, burrow abandonment appears to have unilaterally occurred during slackwater or neap tide sedimentation episodes. This suggests that these intervals were more likely to be terminal for the burrow occupants and that they may have been associated with hostile conditions for the tracemakers (for example, insufficient water depth).

The apparently short lifespan of the burrow tracemakers may also be reflective of the locally high rates of sedimentation (see section *Interpretation of tidal rhythmites*), if they were able to

withstand, and re-adjust after, only a finite number of episodes of sediment blanketing. If substrate colonization is rapid then ambient ecological conditions such as salinity, oxygen levels, or water temperature may appear favourable to waterborne larvae, even when longer-term sedimentation rates may be inimical. If the waters of the Alston Formation depositional environment were replete with larvae of phoronid-like organisms, opportunistic substrate colonization should be expected to have occurred throughout shallow waters, irrespective of whether local accommodation space was underfilled. In this scenario we should expect a preservational bias towards ichnological signatures of relatively juvenile 'doomed pioneers', within the tidal rhythmite facies. Elsewhere in the depositional environment, where local sedimentation rates were lower, tracemakers could achieve their full one year lifespans, but this scenario would rarely (or cryptically) be archived in the rock record due to the necessarily limited sediment accrual.

DISCUSSION: ICHNOFABRICS AND THE SPATIO-TEMPORAL SCALE OF OUTCROP

Key to understanding the significance and preservation of the Alston Formation ichnofabrics is a recognition of the spatio-temporal scale of their archive at outcrop. The tidal rhythmites provide a highly resolved temporal record of a few weeks, but only at a scale of <2 vertical metres, along a generally two-dimensional 11 m horizontal transect (Fig. 3). In modern ecological or neoichnological studies, the monitoring of such a diminutive field of view for several weeks is uncommon, and there is limited modern analogue for how signals are registered at this unorthodox spatio-temporal scale (counterintuitively short in timescale, compared to the longevity of the host strata, and limited in spatial extent, compared to surveys of modern analogues). Figure 4 shows 80 cm of rhythmite consisting of 289 sandstone and siltstone laminae, where only 15 of these laminae have been colonized by burrowers, at the scale of field of view, and none are overprinted. Because the substrates recorded in the tidal rhythmites were clearly amenable for colonization, the most viable explanation for this stochastic vertical distribution of burrowed surfaces is that burrows were concentrated in patches, with a random horizontal distribution within the wider depositional environment (Ronan, 1978; Dashtgard, 2011). Such patches were only captured for present-day observation when they overlapped with the diminutive spatial fragment of the wider environment that was destined to be archived and exposed at outcrop (cf. Marenco & Hagadorn, 2018).

The recognition that present day outcrop has only sampled a fraction of the wider environment also provides an explanation for the non-palimpsested nature of the crowded ichnofabrics.

Whether or not ichnofabrics are non-palimpsested, time-averaged or overprinted is dependent on a combination of variables of sedimentation rate, burrow penetration depth, patch recurrence, and sedimentary stasis duration (Fig. 10). In the case of the Alston Formation: (i) the aggradation of the lithic surface was so rapid that iterative substrates persisted in sedimentary stasis only long enough for one generation of burrowers to colonize them (avoiding time-averaging); and (ii) during the time it took for a new burrow patch to recur in the same (future outcrop) location as an antecedent patch, the thickness of sediment accrued was more than the vertical penetration of burrows (avoiding overprinting).

The controlling factors illustrated in Fig. 10 are primarily governed by local sedimentological and ecological heterogeneities that are not necessarily dependent on higher order controls, but which can be influential on the character of ichnological archives at small spatio-temporal scales. Archives with a tightly focussed temporal (high sedimentation rate) and spatial (limited outcrop extent) scale are informative on ecological heterogeneity in the depositional environment (Dashtgard, 2011), but interrogation of phenomena on a larger spatio-temporal scale (regional environment, macroevolutionary trends) requires equivalently scaled archives. Delineating the spatio-temporal context of outcrop samples should thus be a primary concern in ichnofabric analyses. The significance of the Alston Formation ichnofabrics is apparent because they are fortuitously preserved within a sedimentary chronometer, but recent advances in our understanding of stratigraphic time at outcrop suggest that similar-duration packages (potentially lacking chronostratigraphic indicators) can be expected to be encountered often. The hierarchical assembly of the sedimentary stratigraphic record means that pockets of underfilled accommodation space are frequently generated, inevitably archiving some packages of sediment that were deposited on counterintuitively 'human' timescales (Miall, 2015; Paola *et al.*, 2018; Holbrook & Miall, 2020; Ganti *et al.*, 2020), at spatial scales that are captured within natural rock outcrops (Davies *et al.*, 2019; Davies & Shillito, 2021). The possibility that these may have been under-recognized in the past has implications for future ichnofabric studies because: (i) equifinal ichnofabric signatures can be generated through several mechanisms (Fig. 10) that may be impossible to differentiate without understanding the spatio-temporal scale of the studied package; (ii) non-palimpsested ichnofabrics (and true substrates of burrow tops) have preservation potential within underfilled accommodation space, so *prima facie* assumption of time-averaging or overprinting should be avoided without direct evidence (e.g. McIlroy & Garton, 2010); and (iii) as

individual outcrops may sample only very small spatio-temporal scales, extreme caution should be exercised when interpreting their ichnofabrics in a macroevolutionary context (e.g. Tarhan *et al.*, 2015). In compensation of these limitations, small spatio-temporal scale samples instead provide high-fidelity windows into ancient environments, where observations such as population density, recurrence frequency at site, and burrow morphology (and thus, interpreted tracemakers) can be trusted as faithful palaeoecological archives.

CONCLUSIONS

Heterolithic tidal rhythmite facies are newly reported from the Brigantian Alston Formation of the Northumberland Basin. This rare example of a British Carboniferous tidalite suggests that Serpukhovian tidal range on the Northwest European Seaway was not wholly negligible, and that deposition may pre-date the closure of the Rheic Ocean. The rhythmite is additionally remarkable for hosting discrete crowded *Skolithos* ichnofabrics, which can be interpreted as faithful records of opportunistic colonization by patchy communities of short-lived vermiform tracemakers in a deltaic setting. The fact that the ichnofabrics are not palimpsested can be explained with reference to the short timescale (high sedimentation rate) and limited spatial scale of the outcrop. Extrapolating from the ichnological signatures of the tidalite, this study emphasizes that the spatio-temporal scale of trace fossil archives must be addressed in future ichnofabric analyses to understand the likely spatio-temporal scale of their controls (local, regional or global). In the case of the crowded *Skolithos* ichnofabrics of the Alston Formation, regional environmental information is limited, but the ichnofauna provides a faithfully rendered and high-definition glimpse into life over a few weeks in an interdistributary bay from *ca* 330 million years ago.

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FIGURE CAPTIONS

Figure 1 – Geological context of the tidalite locality. (A) Location within the Tweed Sub-Basin. (B) Geological map of the locality. (C) Stratigraphy of the Yoredale Group, coloured coded to map, showing stratigraphic position of the tidalite (star) immediately above the late Brigantian Eelwell Limestone in the Alston Formation. International and regional stratigraphy after Richards (2013) and Cózar & Somerville (2021): I – global subperiod; II – global stage; III – regional subsystem/stage; IV – regional substage; V – local lithostratigraphic units. (D) Satellite images from 2006 and 2018 showing how recent coastal retreat has exposed the tidalite outcrop, at the south end of the cliffs shown. (2006 image © Infoterra Limited & Bluesky, © Google Earth. 2018 image © CNES / Airbus, © Google Earth).

Figure 2 – Sedimentary log and photographs showing context of tidal bundles. Note that log is simplified to show dominant grain-size as section is heterolithic on many scales. (A) Horizontal *Planolites* burrows in overlying strata. (B) Wave ripple lamination and sub-horizontal *Teichichnus* burrows (arrowed) in overlying sandstones. (C) Acre Coal marker unit (top arrowed) below tidalite section. (D) Seat-earth at top of sandstone below the Acre Coal, exhibiting horizontal stigmarian root casts (white arrow) with root hairs preserved as ferrous iron-rich sediment (red arrows). Scale in each image is 10 cm.

Figure 3 – Tidalite at outcrop at a variety of scales. (A) View of the tidalite-bearing outcrop. Tidal bundles occur throughout the heterolithic strata below the labelled sandstone, but subtle changes in the dip of laminae (for example, see white box) indicate that there are likely to be cryptic disconformities throughout. Package highlighted in red contains bundles that can be traced laterally across the outcrop without discontinuity. Yellow area is enlarged in Fig. 4. Green lines I to IV mark selected areas where laminae counts were undertaken. Measuring stick is 2 m long for scale. (B) Typical view of bundles of sandstone (interpreted as spring tide deposits) punctuated by thicker horizons of siltstone (interpreted as neap tide deposits). At least eight packages (numbered), can be recognized with confidence. Visible part of measuring stick is 32 cm. (C) Close-up view of two individual bundles with sandstone laminae numbered. Reasons for variability in number of sandstone laminae discussed in the text. Visible part of measuring stick is 6 cm. (D) Detail of upper part of package showing subtle irregularities within the rhythmite. Package shown at white bracket has slightly different dip to same package along strike (yellow bracket), where sandstone laminae have become amalgamated. Other sets of sandstone laminae

exhibit thickness variation through pinching (red arrow) and swelling (blue arrow), and minor erosional discontinuities (purple arrow) bound the package. Visible part of ruler is 25 cm.

Figure 4 – Photomontage of vertical section through tidal bundles (location highlighted in Fig. 3), with graphic log showing 269 sandstone laminae in 80 cm of section. Note that number of sandstone laminae was counted at a vertical line in the centre of the photograph – even within this spatial range counts of sandstone laminae can be variable (see Fig. 5). Laminae are arranged into bundles that are interpreted as deposits of spring–neap tidal cycles, with estimated duration of packages shown. Bundles B1 to B6 are traceable across the outcrop and are those used for lamina thickness counts in Fig. 6. Erosional and discordant contacts (highlighted red) of unknown duration interrupt these packages of consistent sediment accrual. Figure also shows frequency of burrow top horizons and depth of penetration of burrows.

Figure 5 – Lateral discontinuity of individual sandstone laminae. (A) Discontinuity due to bundled laminae having lenticular form (arrowed), likely due to limited sand supply during deposition. (B) Discontinuity due to some sand laminae having erosive bases (arrowed). (C) Secondary discontinuity due to post-depositional compression, resulting in small thrust fractures (white arrows) that have led to stratigraphic duplication of some laminae (highlighted in yellow). Scale bar in each image is 1 cm.

Figure 6 – Patterns of thickness variation and number of laminae in bundles. (A) Frequency of occurrence different numbers of sandstone laminae in bundles, showing a mean number of 14.1 and median of 14. (B) and (C) Thickness of sandstone laminae in the top six bundles (B1 to B6) of the package highlighted in Fig. 3 (note that B6 can be erosionally truncated): (B) shows three vertical counts spaced 5 cm apart at Line I in Fig. 3; (C) shows individual examples of counts at lines II to IV in Fig. 3. Note that although individual thicknesses and number of discernible laminae are variable, there is consistency in the overall thickness of bundles and that internal laminae tend to exhibit thickest values towards the middle of each bundle.

Figure 7 – Ichnological characteristics of the tidal bundles. (A) True substrate bedding plane exposure showing mutual avoidance of burrows with sand rims (yellow box). Ruler is 20 cm. (B) Eroded surface cutting through layers and showing pervasive nature of equally spaced burrows through multiple laminae. Ruler is 1 m. (C) Close up of burrow aperture on true substrate showing siltstone-filled inner burrow, lined with dark clay (blue arrow) and surrounded by a raised sand

rim on bedding surface (yellow arrow). Scale bar is 1 cm. (D) Multiple burrows on mud substrate with sand rims. Scale bar is 1 cm. (E) Vertical profile immediately below true substrate showing inclined mud-lined burrows extending down through multiple laminae. Scale bar is 1 cm. (F) Vertical expression of inclined burrows, oblique to cut of outcrop, showing mud-lined burrows at multiple horizons without overprinting (Note that while some of these burrows appear to potentially contain a meniscate infill, this is an illusion in some examples where the soft infill of the burrow has been eroded away, and the apparent lamination is the bedding behind the burrow. None of the burrows have a meniscate infill.) Scale bar is 1 cm.

Figure 8 – Pair correlation functions (PCFs) for samples T1 to T4. The x-axis is the distance between burrows in millimetres. The y-axis is the PCF value, whereby PCF = 1 indicated complete spatial randomness (black line on plots), PCF < 1 indicates segregation/spacing out of burrows and PCF > 1 indicates aggregation of burrows. The grey area is the Monte Carlo simulation envelope (999 simulations with 5% minimum and maximum values taken as the envelope). The green lines are the observed data for; (A) T1, (B) T2, (C) T3 and (D) T4. Note that for T2 the observed slope of segregation is shallower than for T1, T3 and T4, indicating weaker avoidance behaviour.

Figure 9 – Escape traces (fugichnia) attesting to locally rapid deposition, from the sandstone underlying the Acre Coal. (A) Downturning of laminae around fugichnia (fu) within climbing wave-ripple laminated sandstone. (B) Fugichnia at different iterations of the lithic surface (highlighted), suggesting pulsed rapid input of sediment. Scale bar in both images is 5 cm.

Figure 10 – Conceptual model showing how different combinations of sedimentation rate, patch recurrence, sedimentary stasis duration, and burrow depth can impart variable ichnofabric motifs at outcrop. (A) Burrowed horizons may be non-palimpsested [single generation of burrowers (red)], time-averaged [multiple generations of burrows (red and blue) re-using same substrate], or overprinted [second generation of burrows (blue) extends down into an antecedent burrowed surface (red) from overlying sediment package]. (B) Variables across a wider area (shown by multiple horizontal squares), in which sediment is accruing over time from interval t1 to tn, punctuated by intervals of sedimentary stasis (even t-numbers). Sedimentation rate refers to the rate at which individual laminae/beds accrue during a state of deposition. Patch recurrence refers to the time taken for a patch to revisit the same spatial location. Stasis duration refers to the length of time the system is not in a state of deposition (or erosion) between the deposition of successive
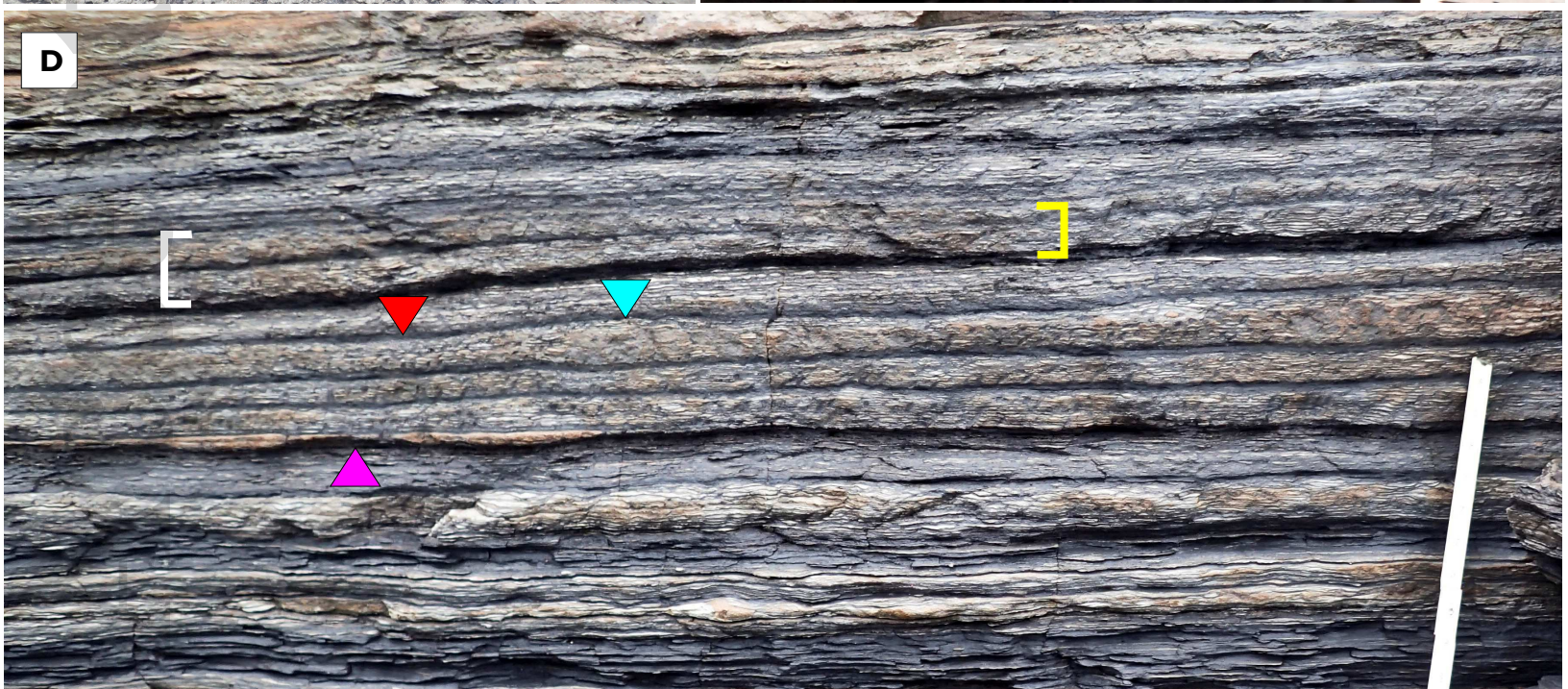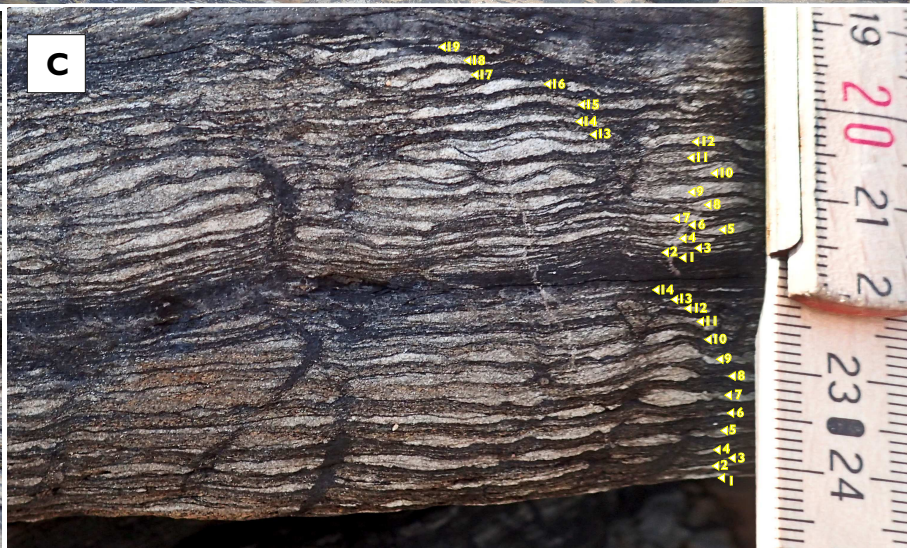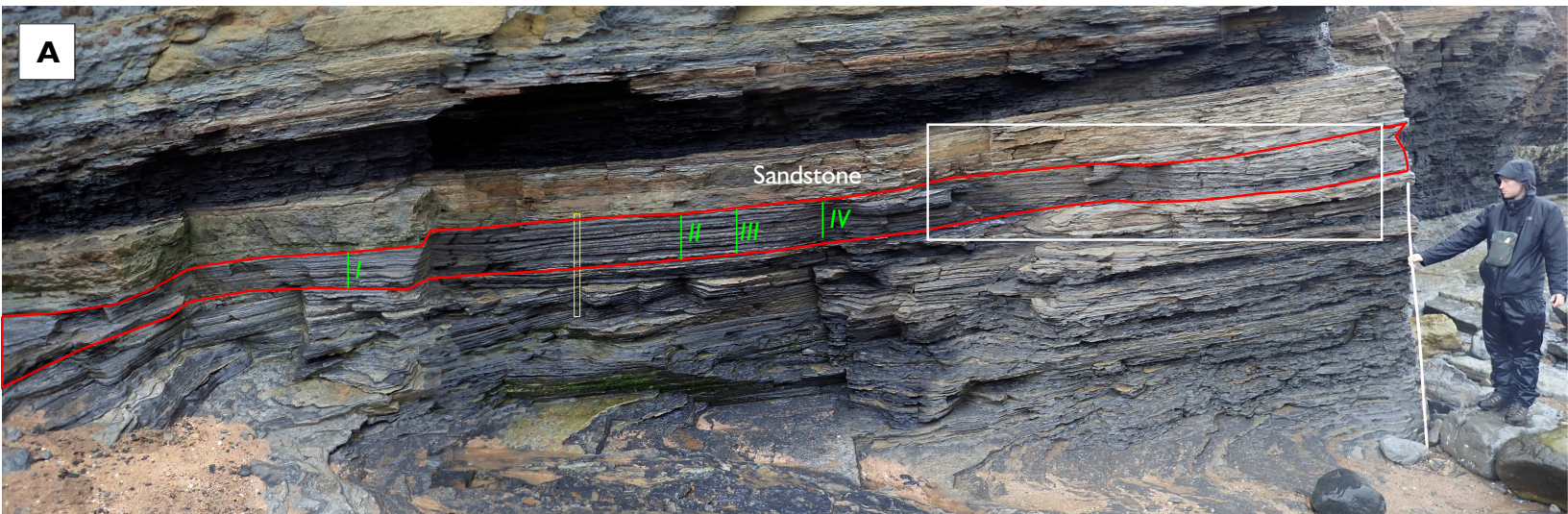
laminae/beds. Burrow depth refers to the maximum downward penetration of burrows within an ichnocoenosis. (C) Sixteen alternative combinations of the variables in (B), and the resultant ichnological signatures that are archived in the accrued sediment (combinations of non-palimpsested, time-averaged and overprinted are shown as likely end results in real world examples, where different signatures would occur on different parts of the same surface due to local heterogeneities). Red rectangle marks a potential random sampling of the wider area at outcrop. Alston Formation rhythmites fall under scenario *I,* as low burrow depth and high sedimentation rate can be directly ascertained. Lack of regularity to burrow horizons (for example, scenario *II*) attests to patchiness of burrows in depositional environment.
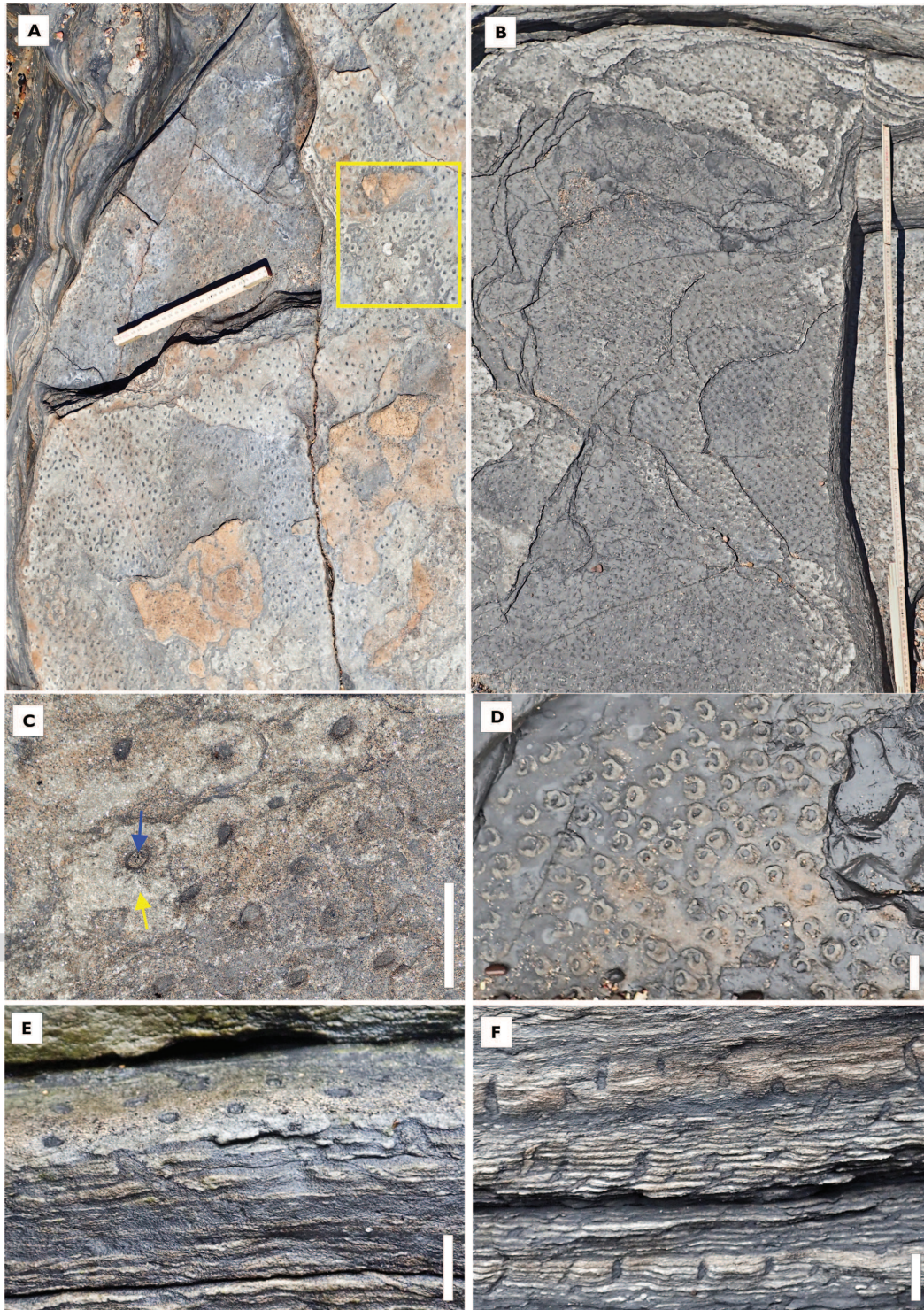
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Burrows	Bundles	Likely Duration

80 cm

S?

c. 14 days

70 cm — N

N

S?

N

B6 (S)

N

60 cm — B5 (S) c. 84-105 days

B4 (S)

N

B3 (S)

N

50 cm — B2 (S)

N

B1 (S)

N

S?

N

40 cm — S?

N c. 56 days

S?

N

S?

30 cm — N

S?

c. 21-28 days

N

S?

20 cm — S?

N

S?

> 28 days

10 cm —

0 cm —
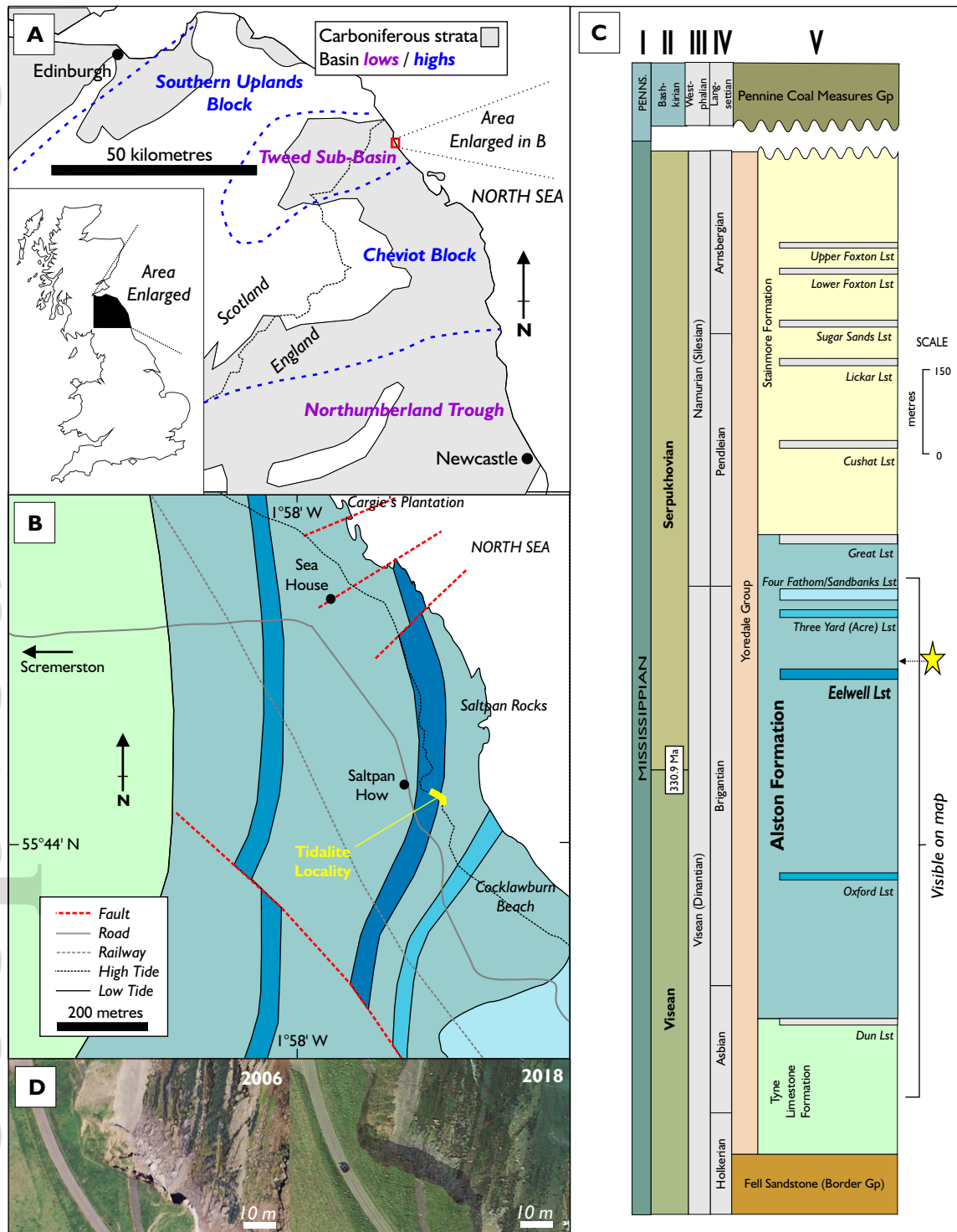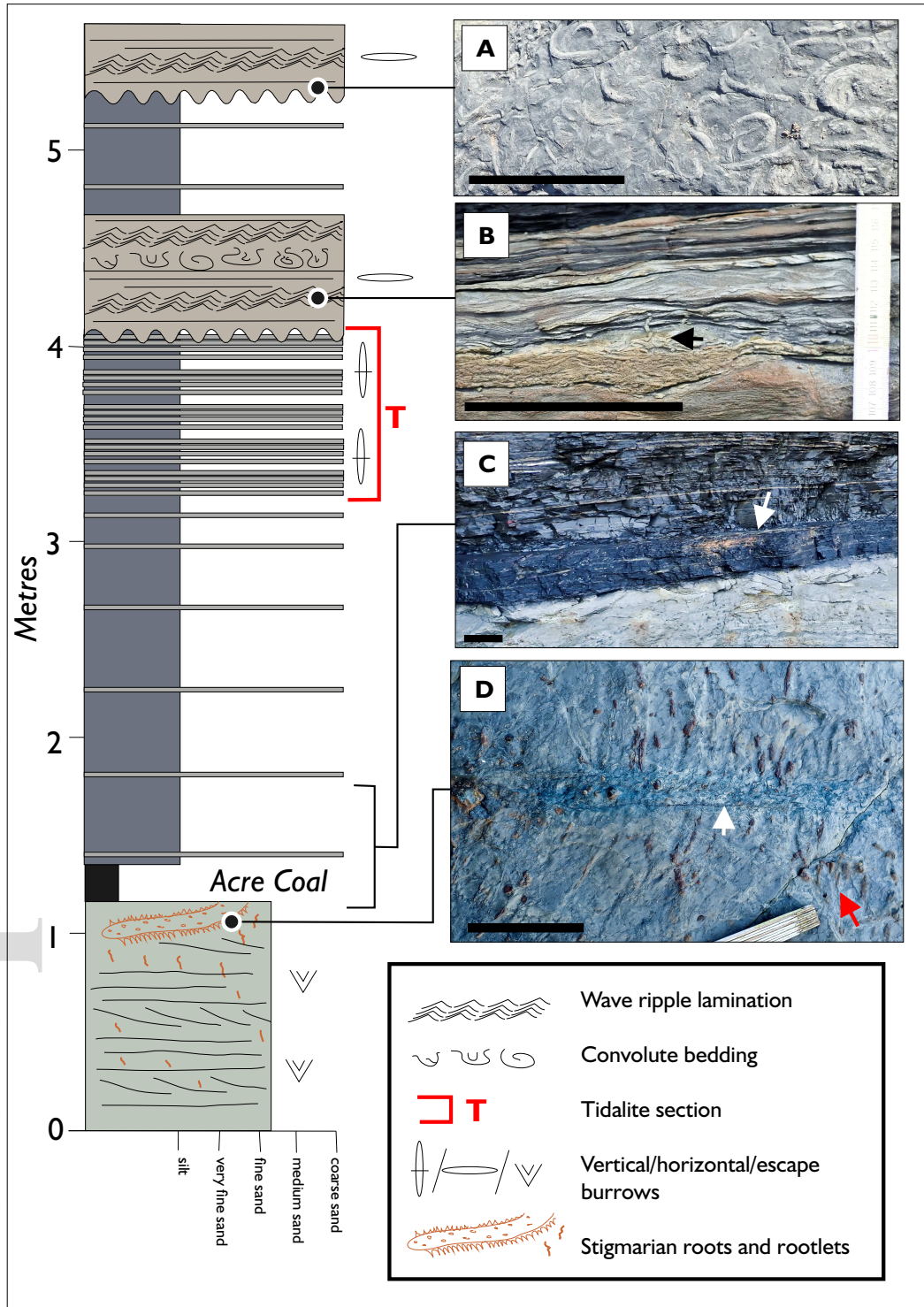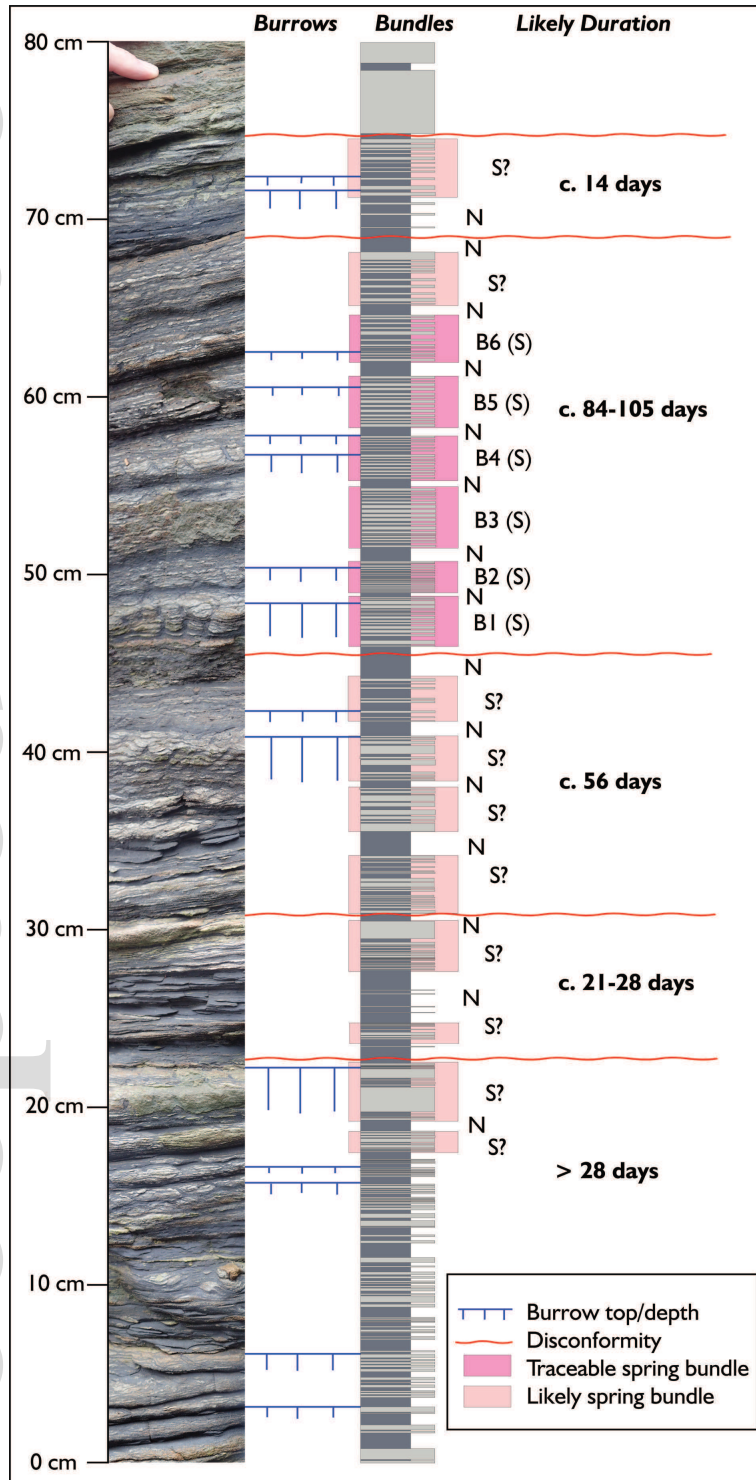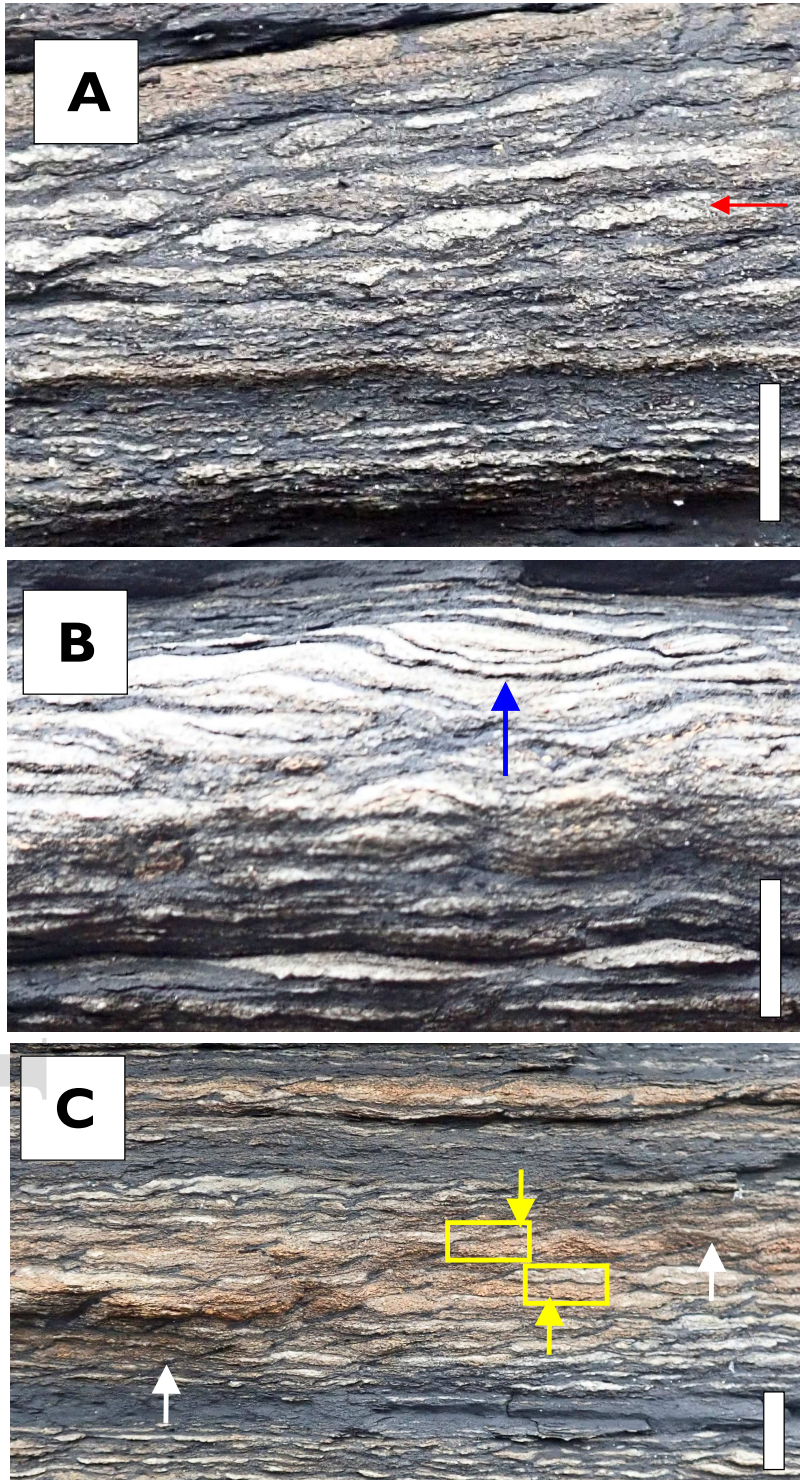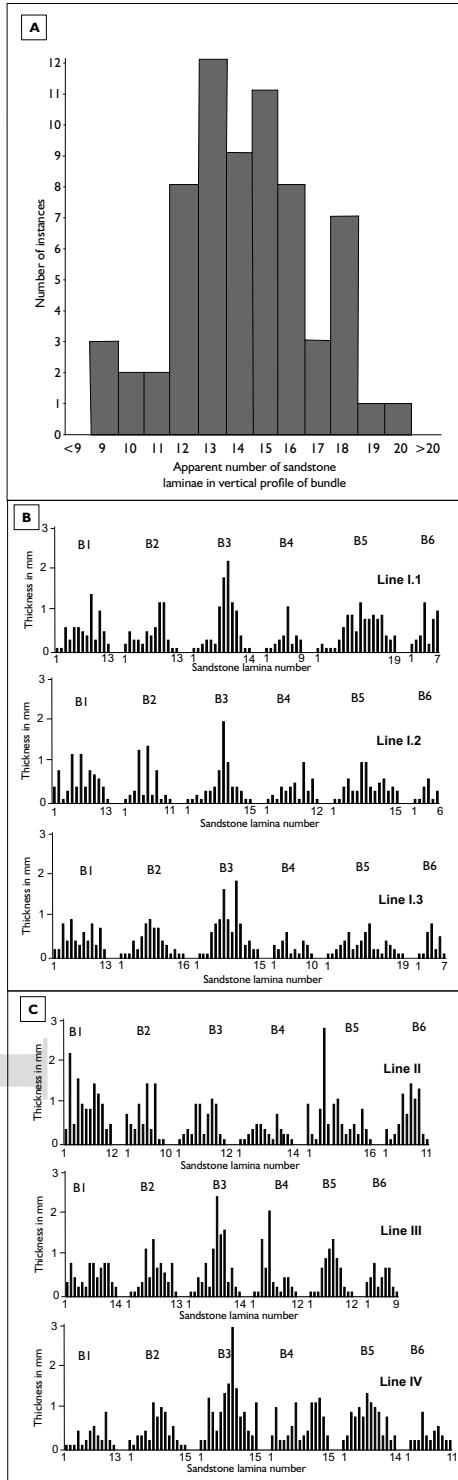
⊔⊔⊓ Burrow top/depth
〜 Disconformity
▦ Traceable spring bundle
▦ Likely spring bundle
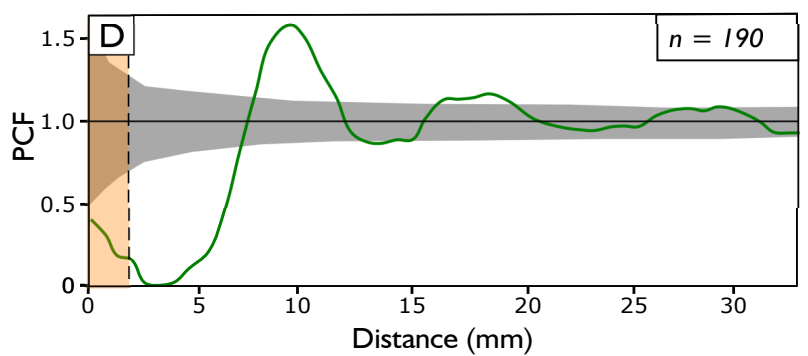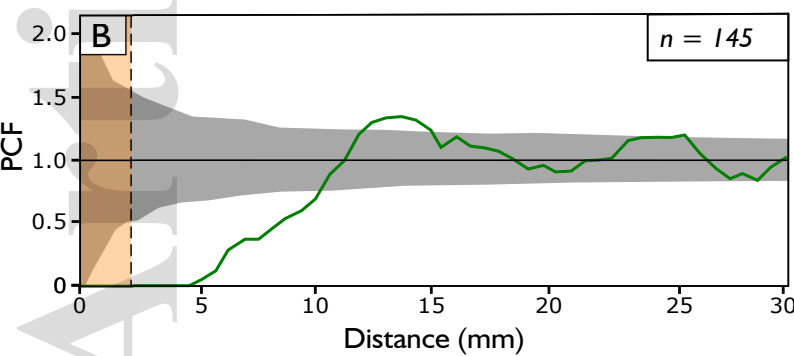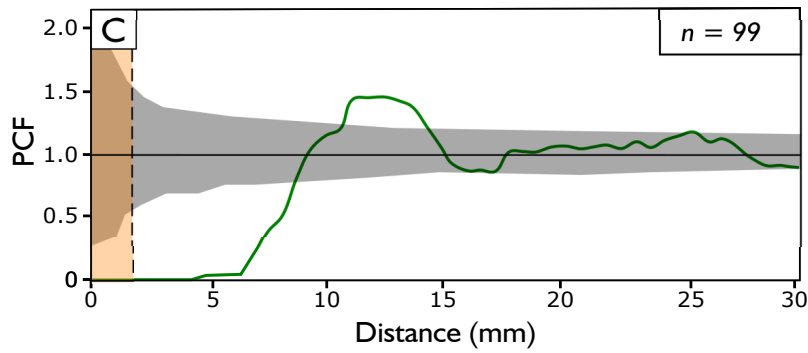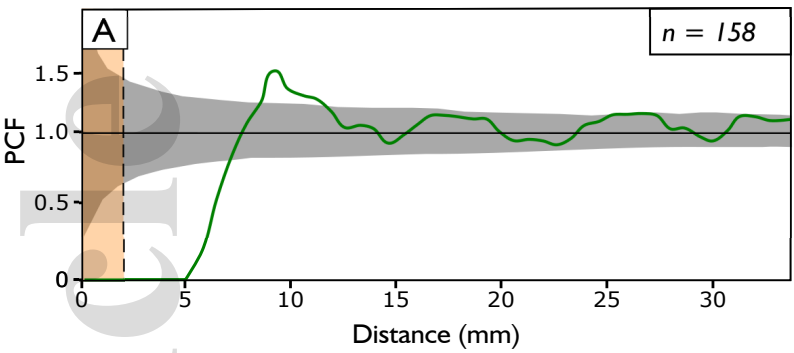
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