Short-stasis signatures in Cambrian and Ordovician shallow-marine sandstones: implications for the ichnological record and time preserved at outcrop

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Abstract: Shallow-marine sandstones are an archetypal facies in the stratigraphic record of the Cambrian Explosion and the Ordovician Radiation but have been considered uninformative owing to erosional signatures, time incompleteness and unfossiliferous outcrops. New analyses of the Carnedd-y-Filliast Grits (Furongian, Wales) and littoral sandstone successions from Baltica and Laurentia reveal that, besides erosion, bedding planes in such outcrops commonly register sedimentary stasis. Most stasis intervals were brief, reflecting (1) a high sedimentation frequency, (2) post-depositional substrate resculpting by wave action during 'active-layer stasis', inhibiting infaunal colonization and rendering the surface representative of only the interval immediately preceding burial, and (3) the low preservation potential of longer-stasis surfaces, which mainly occur within heterolithic packages that, in low-subsidence settings, are commonly eroded and replaced by amalgamation surfaces between sandstones. The short-stasis signature of littoral sandstones renders metre-scale architectural elements relatively time-complete but biases their fossil record at outcrop. Short-stasis surfaces are high-resolution snapshots but form incomplete representations of ancient ecosystems compared with surfaces that capture longer intervals. As such, the predominance of short-stasis surfaces contributed to the low ichnodiversity and sparse fossil content of littoral sandstones, implying that early Paleozoic littoral ecosystems were more biodiverse than their known record suggests.

Littoral sandstones deposited above the wave base form an important component of the rock record of two intervals of marine biodiversification: the Cambrian Explosion and the Ordovician Radiation (Miller 1997; Conway Morris 2006; Marshall 2006; Mángano *et al.* 2016; Mángano and Buatois 2016, 2017; Buatois *et al.* 2020; Harper *et al.* 2021; Zhang and Shu 2021). The sandstones in many instances represent low-subsidence settings or form basal strata overlying unconformities (e.g. Swett *et al.* 1971; Hereford 1977; Wright *et al.* 1993; Jensen 1997; Long and Yip 2009; Ghienne *et al.* 2013; Molyneux *et al.* 2023; Woo *et al.* 2023; see also Ager 1973), meaning that they often represent intervals of which the contemporaneous regional rock record is relatively sparse.

The comparative abundance of lower Paleozoic littoral sandstones (LPLS), deposited above wave base, renders this facies a crucial target as an archive of Earth-historic information. Yet with rare exceptions (Slater 2024), many LPLS successions are unfossiliferous at outcrop, causing its body fossil record to be relatively poor (Peters 2007; Slater 2024). Consequently, the fossil record of this facies relies on bio-sedimentary structures imparted on substrates, which include impressions of body fossils (e.g. Jensen *et al.* 1998; Hagadorn *et al.* 2002; Hagadorn and Belt 2008) and, more abundantly, trace fossils (e.g. Crimes 1968; Hereford 1977; Jensen 1997; Desjardins *et al.* 2010; 2012; Davies *et al.* 2011; Mángano *et al.* 2013; Jensen *et al.* 2016; Marenco and Hagadorn 2019). Despite the relative richness of the trace fossil record compared with the body fossil record, ichnodiversity above the fairweather wave base is low compared with more offshore shallow-water settings (Buatois *et al.* 2020). It is necessary to evaluate this low ichnodiversity in the context of the sedimentology of LPLS: owing to the scarcity of body fossils and the stratigraphic abundance of LPLS, their functioning as sedimentary archives of ichnological data has an outsized impact on the fossil record of littoral ecosystems.

One complication when using LPLS for Earth-historic purposes is that those deposited in low-subsidence cratonic settings have been considered exceptionally incomplete records of time (Sloss 1996; Holland and Patzkowsky 2002). This facies conveys rapid rates of deposition, but net vertical sedimentation rates are among the lowest in the rock record (Miall 2015). This apparent

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time-incompleteness in individual outcrops is in part explained by the vast spatial extent of LPLS, which gave rise to early ideas about these strata being spatially diachronous (e.g. Walcott 1891; Shaw 1964), implying that individual outcrops only record a fraction of the total time recorded by the larger unit (Runkel *et al.* 2008; see also Paola *et al.* 2018; Davies *et al.* 2019).

Within individual outcrops, most elapsed time is represented by bedding planes (Ager 1973; Sadler 1981; Dott 1983; Miall 2016), which are therefore essential for reconstructions of sedimentary systems and the ecosystems they hosted. Many bedding planes may be expected to be erosional, as the facies belt of LPLS has been considered to be dominated by sediment reworking (Went 2013), commonly resulting in condensed sections of amalgamated sandstone (Swift *et al.* 1991). Yet there is increasing recognition of the prevalence of stasis in sedimentary systems (Tipper 2015; Paola *et al.* 2018; Straub *et al.* 2020; Davies and Shillito 2021) and of the fact that depositional events are not necessarily preceded by erosion (Peakall *et al.* 2020; Davies and Shillito 2021). This means that depositional events can follow intervals of stasis, resulting in the morphology of the sediment–water interface being faithfully cast as ‘synoptic topography’ on bedding planes (Paola *et al.* 2018). Such bedding planes are referred to as ‘true substrates’ when the synoptic surface is exposed in outcrop (Davies and Shillito 2018).

Bedding planes can represent a range of time intervals (Miall 2016), and the physical, biological and geochemical processes that were active during this time determine their preserved characteristics (Wheatcroft *et al.* 2007; McLaughlin *et al.* 2008). For instance, trace fossils originating from bedding planes are an informative indicator of stasis, because their construction requires sufficient quiescence for fauna to colonize the substrate (Pollard *et al.* 1993; Díez-Canseco *et al.* 2023). As longer colonization windows enable the overprinting by successive generations of trace makers on the same substrate (e.g. Wheatcroft 1990; Gingras *et al.* 2011; Savrda 2014), the approximate duration of colonization windows can be reflected by the preserved trace fossil assemblage (Allport *et al.* 2022). Characterizing the ichnology and morphology of LPLS bedding planes provides insight into the sedimentary controls on bio-sedimentary features imparted during stasis and preserved on true substrates.

The degree of amalgamation and textural homogeneity often encountered in LPLS can obscure their internal architecture and limit the exposure of their sedimentary surfaces. For that reason, we here compare selected examples of LPLS from Baltica and Laurentia with a case study of the Carnedd-y-Filliast Grits, a Furongian shallow-marine sandstone unit that crops out in North Wales, UK. Its depositional setting in the Arfon Basin provided sufficient subsidence to limit the degree of amalgamation compared with lower-subsidence settings, enabling the recognition of discrete architectural elements in outcrop. In addition, large ripple marks are a common sedimentary structure in the unit, which owing to their size aid the reliable identification of true substrates.

Although signatures of deposition and erosion are prevalent in LPLS, results show that intervals of sedimentary stasis are also commonly preserved on bedding planes. These bedding planes typically reflect substrates in brief stasis or in ‘active-layer stasis’, when the substrate was subject to physical processes that continuously resculpted the sediment–water interface (see also Davies *et al.* this volume, in press). This stasis signature suppressed infaunal colonization of the substrate, even though trace fossils and other bio-sedimentary structures imparted during stasis account for most of the fossil record of LPLS. Therefore, we propose that the predominance of short-term stasis exerted an outsized control on the palaeobiological diversity archived in this facies.

The Carnedd-y-Filliast Grits

The Carnedd-y-Filliast Grits, known formally as the Carnedd-y-Filliast Member of the Marchlyn Formation, consist of light-grey weathering coarse-grained sandstones that are distinct from the finer-grained and thinner-bedded mudstones and sandstones of the rest of the formation. The Carnedd-y-Filliast Grits have been biostratigraphically dated to the Furongian and form the coarsest stratigraphic unit of this age in North Wales (Rushton and Molyneux 2011). Its deposition represents a shallowing following deeper-water slate and greywacke deposition in the Arfon Basin. The unit forms prominent exposures in the landscape throughout its outcrop area in the county of Gwynedd that have previously been described by Williams (1930) and Crimes (1970*a*). Figured examples presented here are from outcrops at Cwm Graianog on the eastern flank of Carnedd-y-Filliast mountain (3.14739 N, −4.05636 E; Fig. 1), on the lower slopes of Gyrn Wigau, east of Gerlan (53.18040 N, −4.03807 E) and in the Nantlle Valley, west of Rhyd-Ddu (53.05763 N, −4.17166 E). The unit has an exposed thickness of ~120 m on Carnedd-y-Filliast mountain and can broadly be subdivided into alternating thick-bedded sandstone-dominated and thin-bedded heterolithic facies associations, each forming packages around 5–15 m in thickness (Fig. 1). These facies associations have distinct sedimentary and ichnological characteristics, which are discussed below.

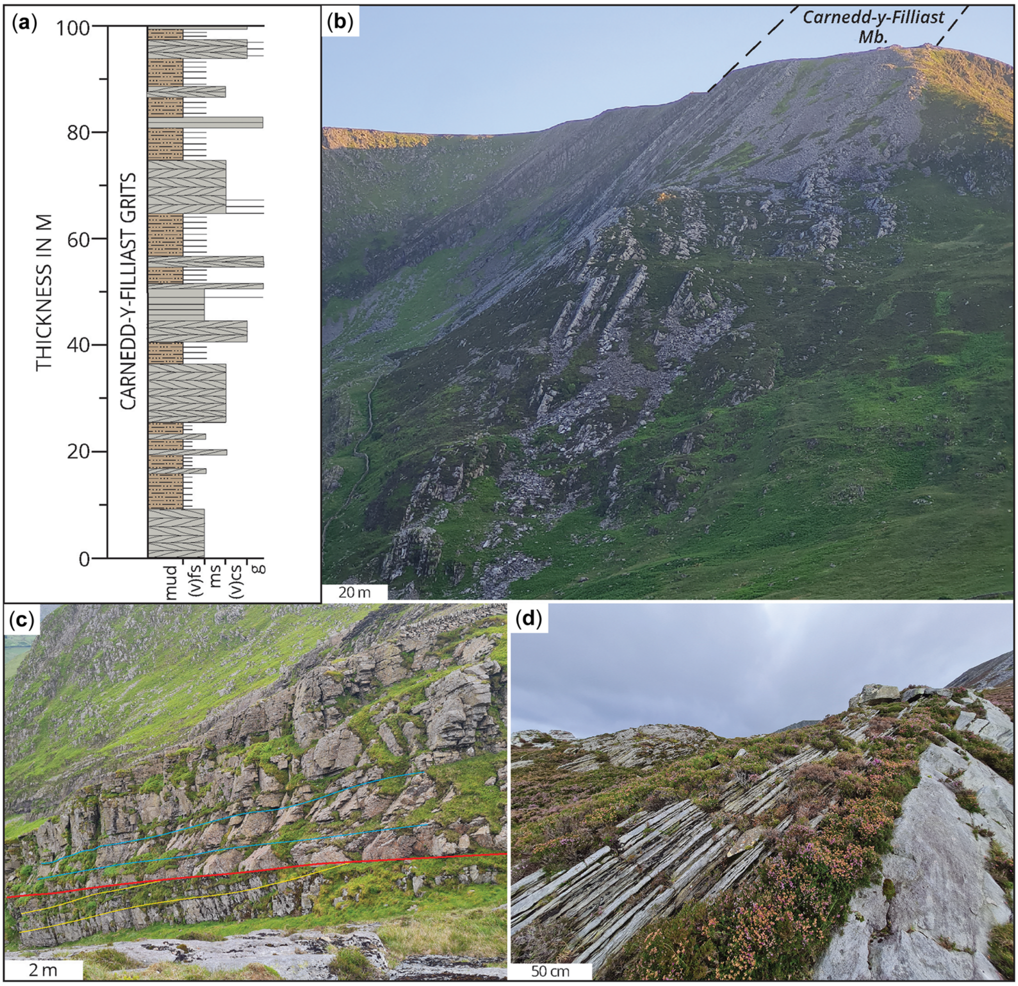

Fig. 1. Representative stratigraphy and outcrop of the Carnedd-y-Filliast Grits at its type section (Gwynedd, Wales) at Cwm Graianog. (**a**) Stratigraphic log of the northern limb of Cwm Graianog, showing alternations between the thick-bedded sandstone-dominated facies associations (grey) and the thin-bedded heterolithic facies associations (brown). (**b**) The outcrop belt of the Carnedd-y-Filliast Grits forms prominent ridges across Gwynedd. The coarser packages are well exposed, whereas finer strata are more recessive in the landscape. (**c**) Locally the upper boundary of the unit is marked by an angular unconformity overlain by basal Arenig strata. (**d**) Impression of a contact between a sandstone-dominated (right) and a heterolithic package (left).

Sandstone-dominated facies association

In the sandstone-dominated facies association, modal grain sizes range from fine sand to granules, and packages exhibit an approximate coarsening-upward trend at the scale of the unit. The facies association internally consists of ungraded trough cross-stratified sets of which measured thicknesses range from 4 to 130 cm, with a median thickness of 12 cm. In individual exposures, superposed cross-sets sometimes exhibit opposing dip directions, forming herringbone cross-stratified fabrics. The sum of recorded dip directions in the area reflects this in a bimodal distribution (see fig. 26C in Crimes 1970*a*).

Bedding planes in the sandstone-dominated facies association in several instances exhibit synoptic topography or true substrate morphologies (Figs 2–4), which occur either at coset boundaries within the sandstone packages or at the boundaries between the sandstone and heterolithic facies associations. The most common sedimentary structures on these surfaces are large wave ripple marks, which are in many instances draped with continuous or flaser-

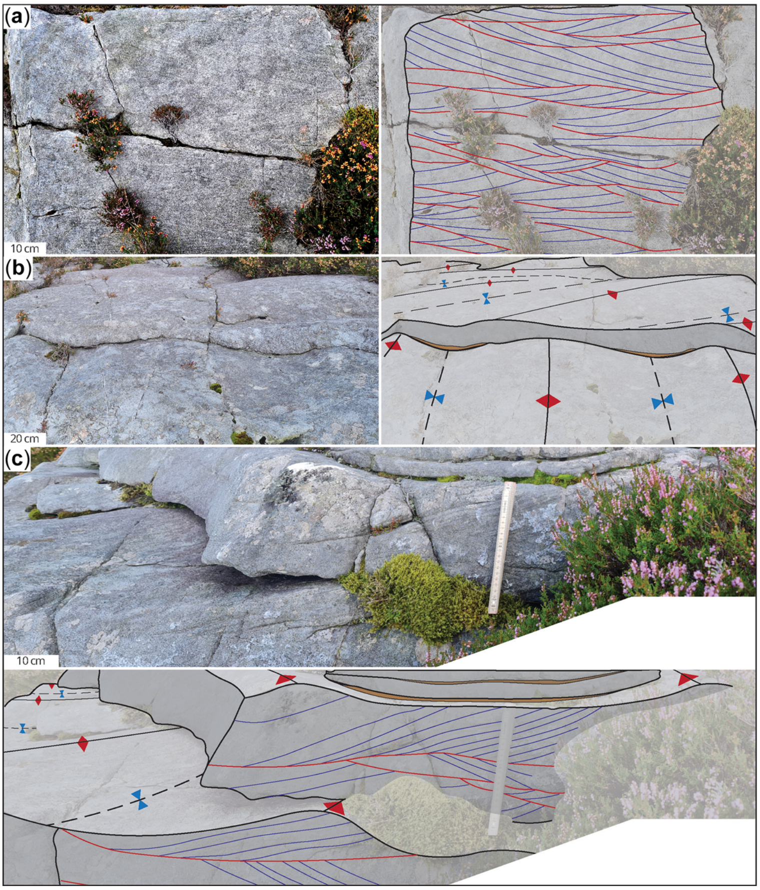

Fig. 2. The sandstone-dominated facies association. (**a**) Sandstone-dominated packages consist of trough cross-stratified cosets with erosive internal set boundaries. (**b**) Bedding planes commonly display large wave ripples overlain by flaser-bedded mudstone, indicating sedimentary stasis followed by non-erosive sedimentation. Red arrows mark crests and blue arrows mark troughs. Such surfaces reflect sedimentary stasis followed by non-erosive sedimentation. (**c**) Large wave ripples commonly occur at coset boundaries, marking intervals of oscillatory wave sculpting of the sediment–water interface during breaks in net deposition.

bedded mud drapes. The exposure at Cwm Graianog displays the broad spatial dimensions of one of the surfaces on which the ripple marks occur (Fig. 3a). The ripple marks have amplitudes ranging between 5 and 13 cm and wavelengths ranging between 60 and 100 cm. The profile of these ripples is symmetrical to sub-symmetrical, with the length of stoss sides rarely being more than 2.5 times as long as the lee side. The internal stratification of the ripple marks can in various places be observed to be unidirectionally cross-stratified and therefore discordant with the symmetrical external shape of the ripple mark.

Some ripples have sharp crests, but most are flat-topped, most commonly reflecting the true bedform morphology (although in several specific outcrops, marked with glacial striations, Quaternary glacial scouring may have diminished original signatures). Ripple crests are straight and mostly continuous (Fig. 3b), but also show morphological defects such as crest terminations and dislocations (Fig. 3c) or secondary crests within the primary troughs (Fig. 3d), corresponding to shorter wavelengths between 40 and 60 cm. Secondary crests are sometimes positioned closer to the primary crests, resulting in double-crest morphologies (Fig. 3e). Other surficial sedimentary structures are scarce in this facies association, although current ripples are occasionally observed and interference ripples and mud-cracked float blocks have previously been reported (Crimes 1970*a*).

Trace fossils are rare in this facies association and mostly limited to vertical structures recognized

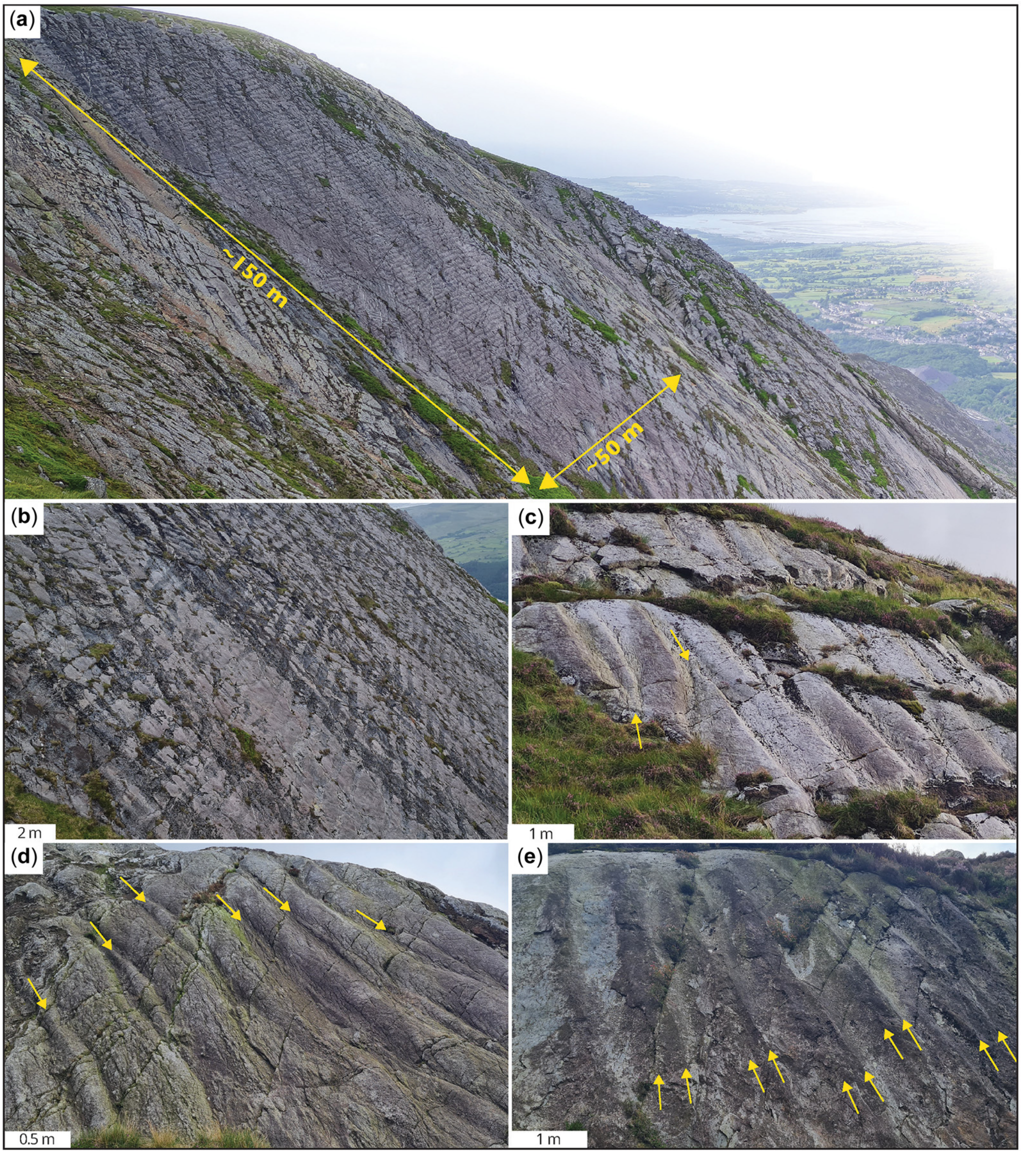

Fig. 3. Large wave ripples on bedding planes of the sandstone-dominated facies association. (**a**) Large bedding plane showing the broadness of true substrate preservation, Cwm Graianog. (**b**) Close-up of the upper part of the exposure of (a), showing the straightness and continuity of ripple crests. (**c**–**e**) Yellow arrows mark morphological defects typical of wave-formed ripples, including crest terminations and dislocations (c) and structures reflecting wave shortening over time, namely secondary crest development (d) and split-crest morphologies (e).

in plan-view on epirelief. Traces may represent burrow tops or horizontal cross-sections, when the traces are top-truncated following minor erosion. It is, however, improbable that many of the observed traces originated from higher surfaces, as the burrow patches in which they occur reflect the morphology of the surface on which they are found, being preferentially situated in and aligned with ripple troughs (Fig. 4). Most traces are identified as *Skolithos* (lined vertical burrows; Fig. 4b), and more rarely, as *Diplocraterion* (U-shaped burrows with spreiten; Fig. 4b, c), when paired burrows are horizontally connected to form a dumbbell shape, or *Arenicolites* (U-shaped vertical burrows without

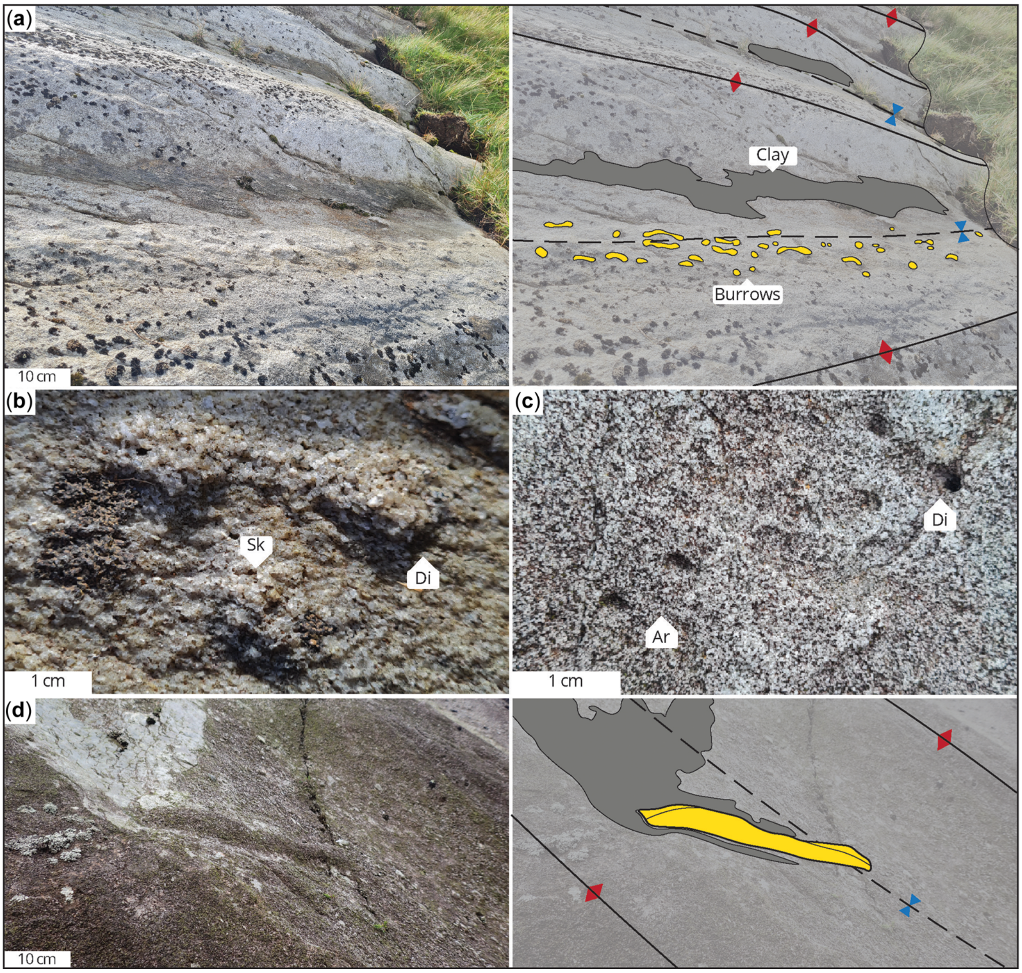

Fig. 4. Trace fossils of the sandstone-dominated facies association. (**a**) Rippled bedding plane preserving a partial mud flaser and a patch of burrows. Although some burrows exhibit minor erosional truncation, they are confined to and aligned with ripple troughs, showing that the bedding plane approximates the colonized surface. (**b**) Vertical burrows of (a) consist of isolated burrows (*Skolithos*; Sk) and paired burrows connected by a stem, representing a spreiten-bearing U-shaped burrow (*Diplocraterion*; Di), Clogwynygarreg (Nantlle Valley). (**c**) Paired vertical burrows also occur without stem, indicating U-shaped burrows without spreiten (*Arenicolites*; Ar), Cwm Graianog. (**d**) Very rarely, horizontal tubular burrows can be recognized in ripple troughs as positive relief on bedding planes.

spreiten; Fig. 4c), when burrows are paired but not visibly connected in plan-view. Very rarely, undetermined horizontal traces about 5 cm in diameter can be observed in positive epirelief on bedding planes (Fig. 4d).

Heterolithic facies association

Packages of the heterolithic facies association separate the sandstone-dominated packages and are best exposed in the sections at Cwm Graianog and Gyrn Wigau. This facies association consists of 2–15 cm-thick sandstone beds that are interbedded with millimetre- to centimetre-scale mudstone beds and partings (Fig. 5). Most sandstones are very fine to fine grained, but outliers with up to granular grain sizes occur. Surficial sedimentary structures are rare compared with the sandstone-dominated facies association, although ripple marks can occasionally be observed in profile or on bedding planes (Fig. 5b). Cross-lamination can occasionally be recognized in the sandstone beds (Fig. 5c, d).

The facies association is comparable with the fine-grained strata in the lower part of the Marchlyn

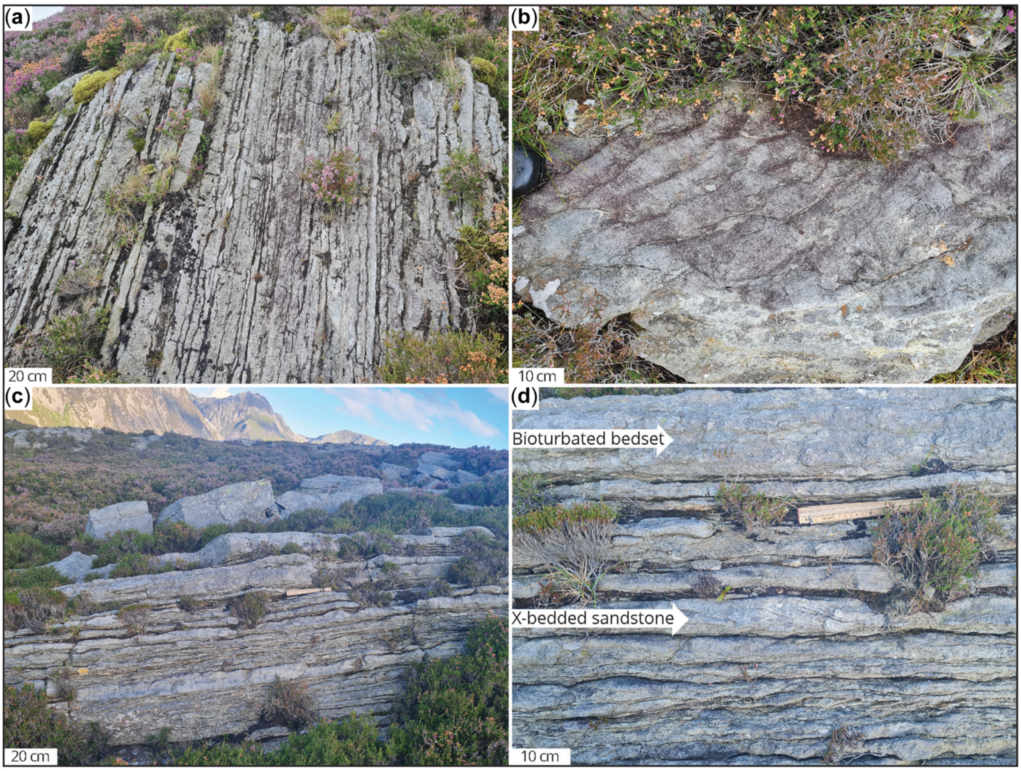

Fig. 5. The heterolithic facies association. (**a**) Heterolithic strata are characterized by thin-bedded sandstones and mudstones, often forming recessive gulleys in the landscape between sandstone ridges, but occasionally exposed at Cwm Graianog and the lower slopes of Gyrn Wigau. (**b**) True substrates can occasionally be recognized, in this instance as a surface with ripple marks. (**c**) Thicker beds occasionally occur in the heterolithic packages. (**d**) Closeup of (c), showing cross-bedded sandstone and bedsets moderately homogenized by bioturbation, recognizable from the uneven, mottled texture in side view.

Formation but can be distinguished by a higher contribution of sandstone beds and by a high abundance of trace fossils (Fig. 6). Bioturbation intensities are variable but bedsets up to 20 cm thick are in several instances observed to be moderately homogenized (Fig. 5d). Most determinable trace fossils are recognized in positive hyporelief on the lower bedding planes of the sandstones. The most common trace fossils include passively filled tubular burrows (*Palaeophycus*; Fig. 6) and bilobed traces with scratch marks (*Cruziana semiplicata*; Fig. 6a). The Cwm Graianog outcrop serves as the type locality for *Cruziana semiplicata* (Salter 1865), and this and other arthropod-related trace fossils, including *Diplichnites*, *Dimorphichnus*, *Monomorphichnus* (Fig. 6b) and *Rusophycus* (Fig. 6c), have extensively been described from the Carnedd-y-Filliast Grits and coeval strata in North Wales by Crimes (1968, 1969, 1970*b*). Less abundant trace fossils include *Treptichnus pedum* (Fig. 6d), *Phycodes palmatus* forming large palmate branching patterns (Fig. 6e), and horizontal trails of *Helminthoidichnites* and *Helminthopsis* (Fig. 6h). One specimen of *Asterichnus* was observed, characterized by a radial arrangement of branches that is about 5 cm in diameter (Fig. 6g).

Depositional Environment

The Carnedd-y-Filliast Grits were deposited in a shallow-marine setting above wave base, as is apparent from the abundant wave-formed ripple marks and supported by the abundance of thick-bedded ungraded quartzose sandstones. The stratigraphic association of sandstone-dominated and heterolithic packages reflects a spatially segregated depositional environment of dynamic sandy morphological elements such as sand waves, bars or dunes, and more quiescent environments situated between these elements. The heterolithic facies association reflects episodic sand sedimentation alternating with finer-grained background sedimentation, indicating a

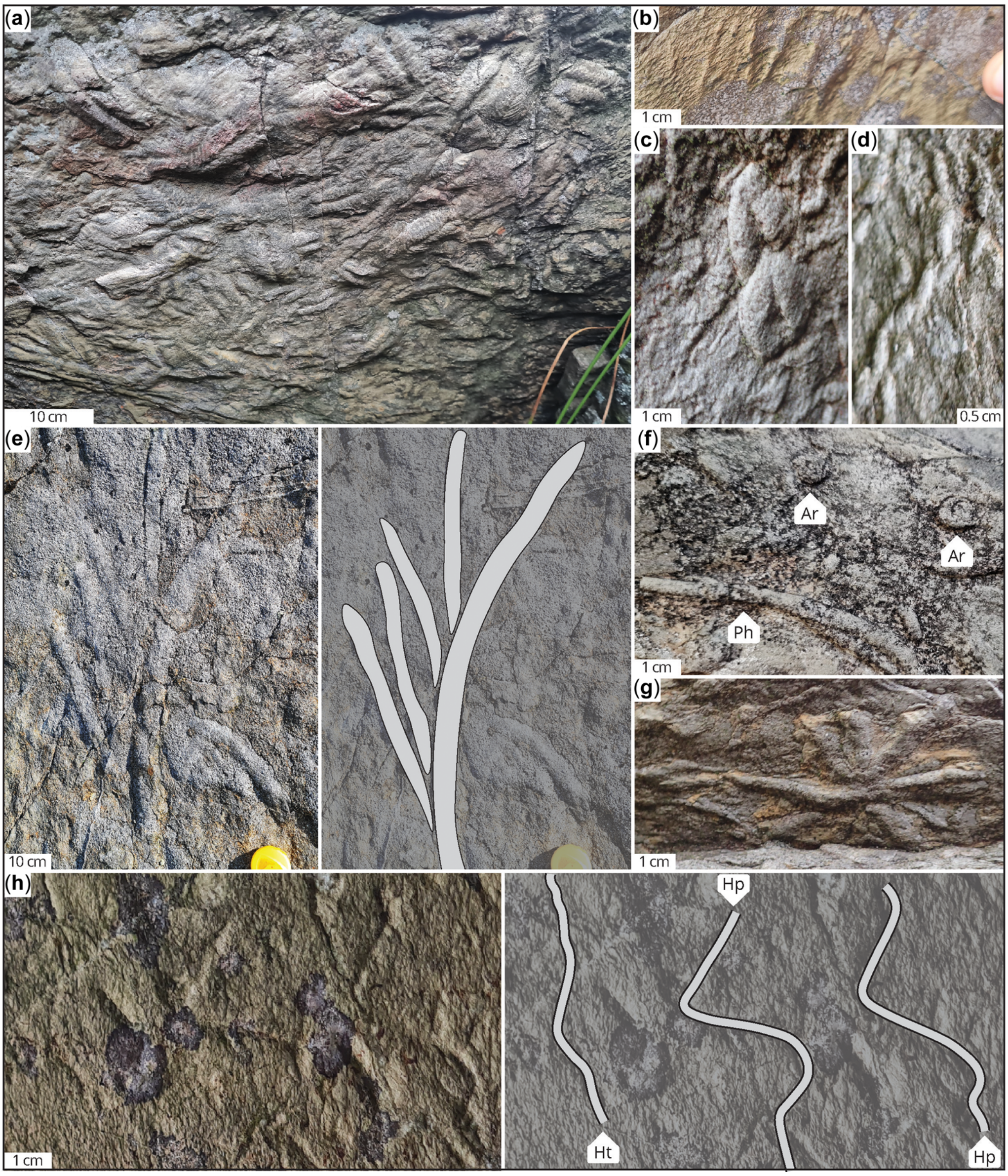

Fig. 6. Trace fossils of the heterolithic facies association. (**a**) The unit often shows dense assemblages of *Cruziana semiplicata* and other traces attributed to arthropod trace makers, such as *Monomorphichnus, Dimorphichnus, Rusophycus,* and *Diplichnites* (see also Crimes 1970*b*), Gyrn Wigau; (**b**) *Monomorphichnus,* Gyrn Wigau; (**c**) Serial *Rusophycus*, Cwm Graianog; (**d**) *Treptichnus pedum*, Cwm Graianog*;* (**e**) *Phycodes palmatus*, Cwm Graianog*;* (**f**) *Arenicolites* (Ar) and *Palaeophycus* (Ph), Cwm Graianog; (**g**) *Asterichnus*, Cwm Graianog; and (**h**) *Helminthoidichnites* (Ht) and *Helminthopsis* (Hp), Gyrn Wigau.

more sporadic and less voluminous supply of sand. The upper bounding surfaces of the sandstone-dominated packages thus reflect the abandonment or migration of sand-dominated morphological elements, marking a locally reduced sediment supply.

The processes involved in the deposition of the sandstone-dominated facies association differ from those that sculpted the ripple marks observed on the bedding planes. Internally, the sandstones are thick, ungraded and trough cross-stratified, and reflect transport and deposition on current ripples and dunes under unidirectional currents. The bimodal palaeocurrent distribution observed at unit scale (Fig. 26C in Crimes 1970*a*) suggests the influence of two opposing, possibly tidal, unidirectional currents on the depositional environment. In contrast, the ripple marks commonly observed on bedding planes in these sandstones reflect oscillatory wave action. The size of the ripple marks merits classification as large wave ripples, consistent with wave action on coarse substrates (the 'LWRs' of Cummings *et al.* 2009). The ripple marks show a high degree of symmetry, straight crests, lateral continuity and occasional morphological defects, all of which are indicative of the sculpting of the sediment surface by wave-induced oscillation (De Raaf *et al.* 1977; Myrow *et al.* 2018; Perron *et al.* 2018; Collinson and Mountney 2019). The discordance between the relatively symmetrical shape in profile and the internal fabrics of the ripples, which frequently display unidirectional cross-strata, is also common in wave ripples (De Raaf *et al.* 1977) and may indicate a slight asymmetry to the oscillation leading to lateral ripple migration (Inman and Bowen 1963). The wavelengths and amplitudes of the ripples further rule out formation by unidirectional currents, because their values often fall between the mostly discrete ranges associated with current ripples and dunes (Allen 1968). The secondary crests of the wave ripples are disequilibrium patterns, indicative of wavelength shortening in response to changing hydrodynamic conditions over time (Myrow *et al.* 2018; Perron *et al.* 2018).

Surfaces and sedimentation states

The spatio-temporal significance of the bedding planes of the Carnedd-y-Filliast Grits can be interpreted by deconstructing the unit into the sum of its sedimentation states (deposition, erosion and stasis) based on the signatures of each sedimentation state in outcrop. Deposition is reflected by the sediment itself, whereas erosion and stasis are represented by the intervening surfaces. The effects of erosion are reflected by truncation patterns and scoured topographies. Indicators for stasis include trace fossils, which required a colonization window to be constructed, and true substrates, which may be evidenced by surficial trace fossils or sedimentary structures.

The distribution of evidence for each sedimentation state in the facies associations of the Carnedd-y-Filliast Grits is discussed below. Sedimentary surfaces are characterized based on the combination of sedimentation states that they represent, using abbreviations for deposition (D), erosion (E) and stasis (S). A scoured surface, for example, might be a D–E–D surface (deposition, followed by erosion, followed by deposition).

Sandstone-dominated facies association

The sandstone-dominated facies association consists of cosets that are internally dominated by signatures of deposition and erosion, indicating dune migration without evidence for intermittent stasis. Dune foresets formed continuously (D–D surfaces; Fig. 2a, c), as is evident from the lack of trace fossils, mud drapes and discordant parasitic bedforms associated with the cross-stratification, which would have indicated breaks in dune migration. The dunes had a subcritical angle of climb, meaning that sets rarely exhibit climbing or sigmoidal morphologies and are in almost all cases top-truncated (D–E–D surfaces; Fig. 7a).

The upper bounding surfaces of cosets are less consistently erosive (Fig. 2b, c) and more commonly reflect intervals of sedimentary stasis followed by a non-erosive sedimentation event (D–S–D or D–E–S–D surfaces; Fig. 7b). The progression from stasis to deposition without intervening erosion enabled the preservation of the wave-rippled morphology that the sediment–water interface attained during the preceding interval of stasis (i.e. true substrates; Fig. 7b). The duration of the colonization window was limited, as reflected by fact that trace fossils are rare on the ripple-marked surfaces as well as in the internal fabric of the underlying beds, where vertical burrows could have been preserved even if their surficial expression would have been destroyed.

Several observed true substrates in the sand packages have undergone partial erosion of ripple crests. In these cases, the ripple crests are bound by amalgamation surfaces (D–S–E–D surfaces), whereas the ripple troughs still preserve a record of stasis (D–S–D or D–E–S–D surfaces). The large size of the wave ripples would have required relatively strong or prolonged erosion to completely rework them. If the ripples had been smaller, it is possible that the true substrate would have been destroyed entirely.

Heterolithic facies association

The stratigraphic alternation between mudstones and sandstones within the heterolithic facies association (Fig. 5) represents a lower frequency of sand deposition and longer durations of intervening stasis compared with the sedimentary conditions recorded in the sandstone packages. These more prolonged intervals of stasis were commonly preserved on surfaces (D–S–D or D–E–S–D surfaces) and facilitated prolonged colonization windows, increasing the probability that one or multiple

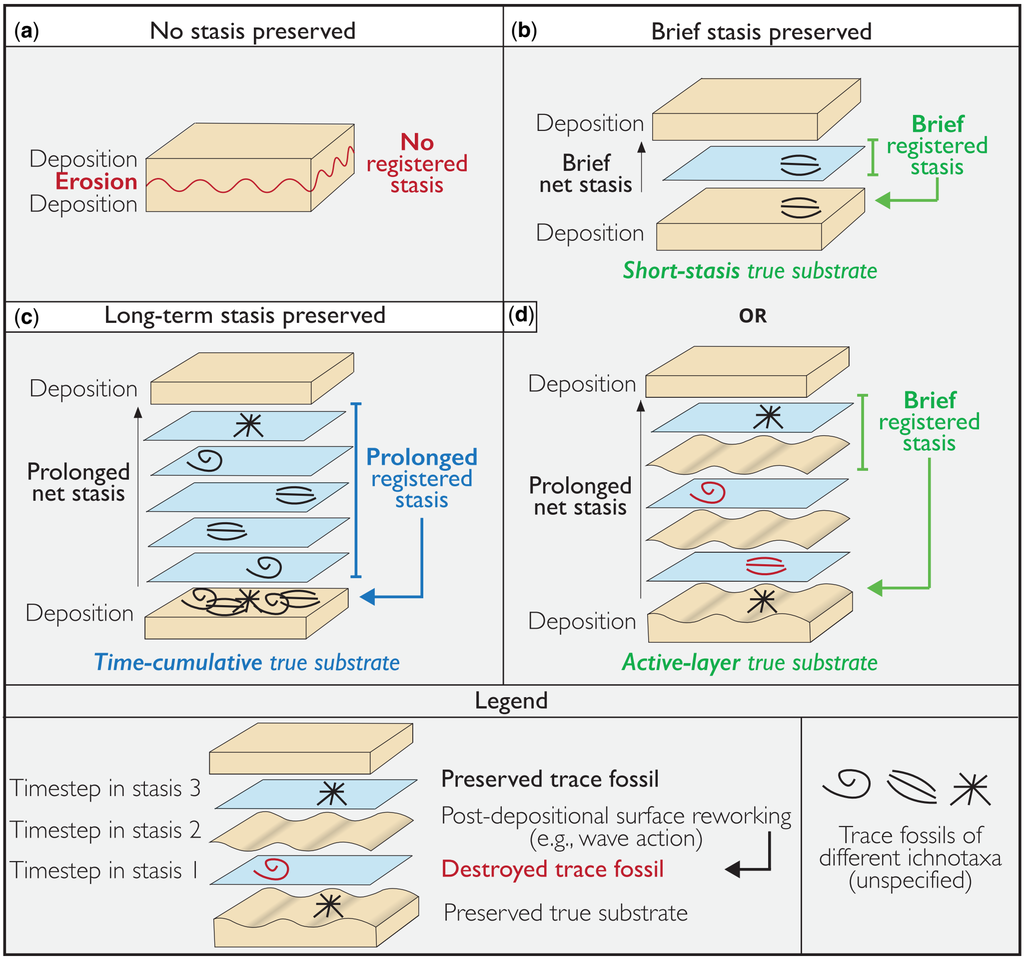

Fig. 7. Categorization of bedding planes based on the duration of net stasis and registered stasis. Net stasis is the time without net substrate aggradation or erosion. Registered stasis is the time required to construct the preserved ichnology and morphology of the substrate. Overprinting of trace fossils originating from higher-up surfaces can occur but is not depicted. (**a**) Erosional contacts result in bed amalgamation. (**b**) When stasis is followed by deposition without intervening erosion, the stasis-morphology of the sediment-water interface is preserved. Surfaces registering brief stasis intervals are short-term snapshots, lacking time-averaged ichnological signals. (**c**) Longer net stasis intervals enable a higher abundance and diversity of trace fossils to be cumulatively registered. (**d**) An active surface-layer can repeatedly reset the morphology of the sediment-water interface, shortening colonization windows and destroying previously produced trace fossils (shown in red). This way, ‘active-layer stasis’ shortens registered stasis relative to net stasis.

successive generations of tracemakers interacted with the part of the surface that was preserved and presently exposed in outcrop (Fig. 7c). Consequently, true substrates in this facies association are more likely to host trace fossils and to be densely and diversely populated (Fig. 6).

It is worth noting that trace fossils are to various degrees three-dimensional and may thus correspond to intervals of stasis that post-dated the burial of the surface on which they are found. Without recognizable traces that are demonstrably surficial, it can therefore be difficult to discern whether a trace fossil-bearing surface is an original surface of colonization. Nevertheless, the duration of the colonization window and stasis recorded in a facies association can control the extent to which the ichnological potential of an ecosystem is translated into its stratigraphic record. Spatial variability in modal stasis durations therefore formed a primary mechanism behind the varying trace fossil abundance and diversity between the heterolithic and the sandstone-dominated facies associations.

Stasis in lower Paleozoic littoral sandstones

The record of stasis in the Carnedd-y-Filliast Grits can serve as a case study for the record of stasis in sandstones that were ubiquitously deposited in shallow-marine environments during the Cambrian and Ordovician. However, these Lower Paleozoic littoral sandstones, as referred to here, encompass a wide range of successions. For instance, LPLS include basal quartzites, which have been considered 'persistent facies' of the Cambrian and Ordovician (Ager 1973), but not all LPLS are basal or strictly quartzites ('a metamorphosed rock composed of quartz so tightly cemented that it will break across constituent grains'; Ireland 1974). Within this broad spectrum of LPLS, the sandstone-dominated facies association of the Carnedd-y-Filliast Grits is a representative example, whereas its heterolithic facies associations are less characteristic. Using examples from the Carnedd-y-Filliast Grits and additional successions deposited on Baltica and Laurentia, this section examines (1) the predominance of short-term and active-layer stasis registered in sandstone packages and (2) the scarcity of heterolithic packages, recording longer intervals of stasis, in low-subsidence settings.

Short-term and active-layer stasis

The true substrates observed in the sandstone packages of the Carnedd-y-Filliast Grits, compared with those in its heterolithic packages, are characterized by signatures of brief stasis (Fig. 7b), hosting rapidly constructed bedforms and non-palimpsested, low-density and low-ichnodiversity trace fossil assemblages (Figs 2–4). This brevity of stasis reflects the high-frequency sedimentation that is characteristic of marine environments situated above the fair-weather wave base.

In many instances, the breaks in sedimentation recorded in the sandstone packages were probably longer than the time taken to construct the preserved morphology and ichnology of the true substrate. In these cases, intervals of stasis consisted of two distinct phases: active-layer stasis and colonization windows. During active-layer stasis (Fig. 7d; see also Davies *et al.*, this volume, in press), substrates are susceptible to semi-continuous hydrodynamic agitation, creating an active surface layer at the sediment–water interface. During such post-depositional activity (see also Wheatcroft *et al.* 2007), the surface is still in stasis because it is not associated with net aggradation or erosion of the substrate (Davies and Shillito 2021). During colonization windows, the substrate was more quiescent, enabling the colonization of the sediment surface by the producers of trace fossils. However, a recurrent active sediment layer can repeatedly destroy pre-existing sedimentary structures and trace fossils, continuously resetting the morphology of the sediment–water interface. The resulting 'active-layer true substrates' thus only register the brief moments immediately before burial and represent a significant disconnect between longer durations of 'net stasis' (the total time without net aggradation or net erosion) and shorter durations of 'registered stasis' (the time required to construct the preserved morphology and ichnology) (Fig. 7d).

An active surface-layer restricts opportunities for fauna to colonize the substrate and prevents the cumulative preservation of shallow and surficial trace fossils over time. However, burrows that extend into the substrate beyond the active layer are not affected by surface reworking and are more likely to be preserved. The limited number of trace fossils observed in cross-section in the Carnedd-y-Filliast Grits therefore indicates that burrows with such a penetration depth were uncommonly produced. One explanation for this is that the active layer would have been relatively thick, as indicated by the high amplitude of the wave ripples. In addition, as burrows below the active surface-layer would have been preserved cumulatively over time, their scarcity supports the interpretation that colonization windows were brief. This brevity of colonization windows would have resulted in more burrows that may have been destroyed at the surface but would still have been preserved at depth. The brevity of the colonization windows is consistent with frequent sedimentation events and with pervasive wave action during active-layer stasis.

Sedimentary indications for active-layer stasis in the Carnedd-y-Filliast Grits are occasionally preserved, illustrating that the duration of net stasis represented by bedding planes exceeded the duration of registered stasis. In these instances, the hydrodynamic properties of the oscillatory wave action changed during an interval of net stasis, resulting in disequilibrium patterns in the ripple marks. Examples include the secondary crests (Fig. 3d) and double-crest morphologies (Fig. 3e), which are both indicative of wavelength shortening (Myrow *et al.* 2018; Perron *et al.* 2018). This shows that the duration of net stasis was longer than the minimum time taken to construct the individual bedforms: it must have been prolonged enough for initial long-wavelength ripples to be constructed and to subsequently readjust to different conditions, as registered on the true substrate.

Evidence for similar morphological readjustment during active-layer stasis can be recognized in the

LPLS of the Hardeberga Sandstone of the lower Cambrian of Baltica, which exhibits subaqueous structures that have been overprinted by subaerial structures. Examples include large wave ripples juxtaposed with adhesion marks (Fig. 8a, b), drainage channels developing around subaqueously constructed sedimentary relief (Fig. 8c), ladder ripples (Fig. 8d) and wave ripples juxtaposed with the imprints of stranded jellyfish (Fig. 8e; see also Clemmensen *et al.* 2017). Whereas these structures might individually only take seconds to minutes to construct, the juxtaposition of subaqueous and subaerial features requires net stasis of at least several hours to accommodate the retreat of the tide.

Allen and Friend (1976) provided a modern example of active-layer stasis from a tidal sand bank in the North Sea, where most net sedimentation occurred during specific moments, namely spring tides, whereas the net sedimentary impact during the rest of the tidal cycle was minimal. Yet during this interval without net sedimentation, the sediment surface still had an active layer that was susceptible to surficial ripple migration resulting from everyday hydrodynamic activity.

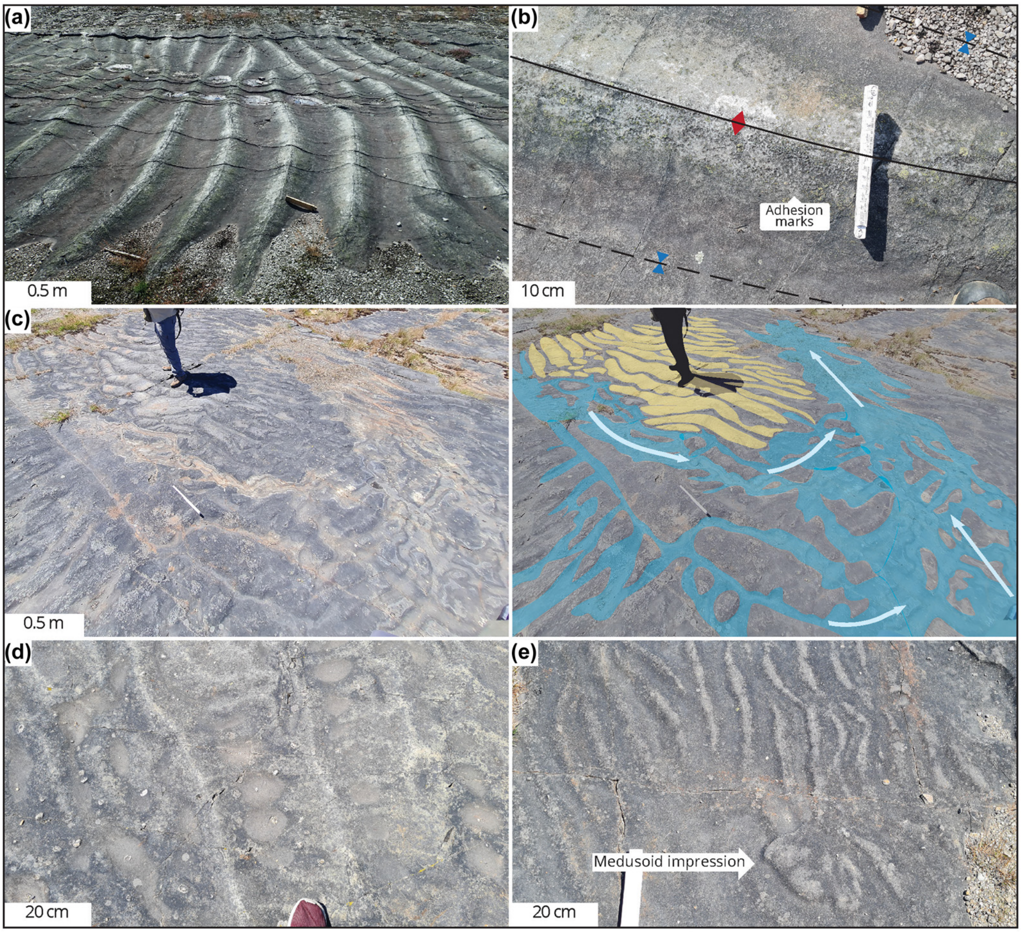

Fig. 8. Evidence for active-layer stasis from the Hardeberga Sandstone (lower Cambrian, Baltica), where net stasis (the time without net aggradation or erosion) exceeded registered stasis (the minimum time required to construct the preserved morphology). Examples show subaqueous structures juxtaposed with subaerial structures, indicating a morphologically active surface-layer that changed as the tide retreated. (**a**, **b**) Large wave ripples with adhesion marks on their crests, indicating subaerial exposure following subaqueous ripple formation. Tobisborg (Sweden); (**c**–**e**) True substrate showing beach morphologies (Strøby Quarry, Denmark; see also Clemmensen *et al.* 2017). (c) A low-water drainage channel being deflected around a subaqueously formed, wave-rippled mound; (**d**) ladder ripples, indicating low-water drainage following subaqeous ripple formation; and (**e**) impression of a jellyfish (medusoid) that stranded during low-water, on top of wave ripples that formed during high-water.

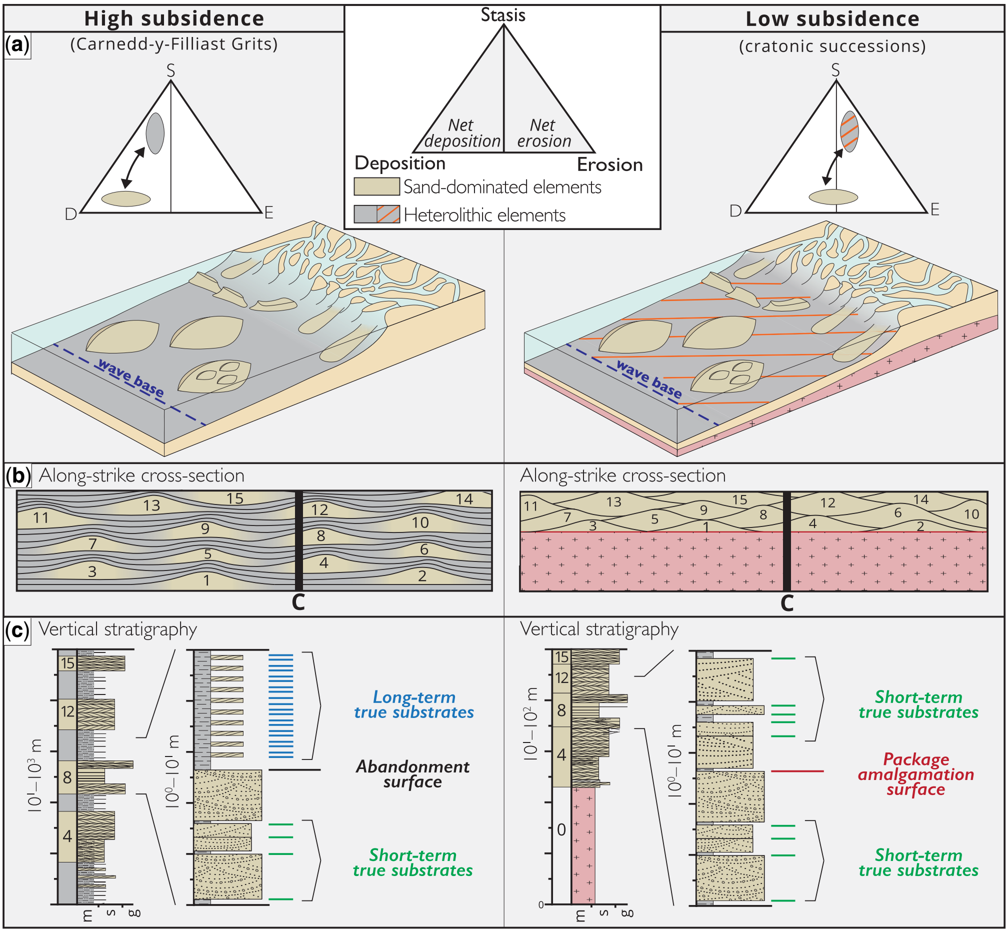

Fig. 9. Conceptual model for stasis durations registered in littoral sandstones under different subsidence regimes. (**a**) The relative importance of deposition, erosion and stasis determines the short-term characteristics and long-term preservation potential of sand-dominated and heterolithic elements. Erosional propensity is higher in low-subsidence settings, primarily reducing the preservation of heterolithics. (**b**) Along-strike sections of (a). Numbers mark arbitrary timesteps. In low-subsidence settings, the scarcity of preserved heterolithics results in amalgamation of sand-dominated architectural elements. (**c**) Vertical logs through (b). Surfaces registering longer-term stasis occur mainly in heterolithic packages. In high-subsidence settings, the local arrival and abandonment of sand elements results in alternating packages of sandstones and heterolithics. Yet in low-subsidence settings, heterolithic packages are mostly absent, resulting in a predominance of short-stasis signatures in the resulting record.

Prolonged stasis and the scarcity of heterolithic strata

The bedding planes of the heterolithic facies association of the Carnedd-y-Filliast Grits register more prolonged intervals of stasis and a higher abundance and diversity of trace fossils (Fig. 6). The relative stratigraphic contribution of such a finer-grained facies association in shallow-marine successions depends on the specific depositional environment (Swift *et al.* 1991), but has been noted to be particularly low in LPLS deposited in low-subsidence settings, giving rise to the characteristic connectivity of these sandstones (Fig. 9; e.g. Dalrymple *et al.* 1985; Dott *et al.* 1986; Runkel *et al.* 2007). The scarcity of heterolithic strata requires their more quiescent depositional environments to have covered smaller portions of the shallow-marine realm or their preservation potential to have been reduced. Reduced long-term preservation potential in low-subsidence settings would also have affected sand-sized sediment but might have had an outsized impact on the preservation of finer-grained deposits (Runkel *et al.* 1998, 2007), which are associated with lower sedimentation rates and more susceptible to post-depositional winnowing (Fig. 9a).

The scarcity of heterolithic facies associations, containing most prolonged-stasis surfaces (Fig. 9b), contributes to the general brevity of stasis recorded in LPLS successions (Fig. 9c). In low-subsidence settings, heterolithic packages have equivalents that are non-depositional (i.e. reflecting erosion or stasis), which are discussed below.

Package amalgamation surfaces and basal unconformities

The stratigraphic alternation between sandstone-dominated and heterolithic packages in high-subsidence settings can reflect allogenic forcing or an autogenic dynamic whereby sand-dominated morphological elements migrate away from the spatial window captured in outcrop and reappear later (Fig. 9a, b). In low-subsidence settings, this temporary absence of sand-dominated morphological elements is not associated with heterolithic deposition but with non-deposition. As a result, these intervals are expressed as surfaces, which may separate amalgamated sand packages or coincide with a basal unconformity (Fig. 9c).

Package amalgamation surfaces represent the abandonment and reappearance of sand-dominated morphological elements and thus represent temporal gaps that equate to their recurrence time. The temporal gap may also be longer if the surface is associated with significant erosion. Individual outcrops of LPLS might only capture a single sand-dominated package representing a coherent architectural element but may also consist of several amalgamated packages. In this case, the sandstone packages are temporally distinct, and the surfaces separating them mark a significant portion of the total time interval represented by the outcrop (Fig. 9c). The preserved morphology of the amalgamation surfaces may reflect erosion, stasis or both. If the surface is preserved as a true substrate, it is probable that it will have been affected by erosion (Fig. 7a) or active-layer stasis (Fig. 7d) and may consequently be difficult to discern from other, less temporally significant surfaces.

The basal unconformities of LPLS successions mark the establishment of a littoral depositional environment, but as sand sedimentation is not spatially consistent, there is a chance that the initial sedimentation state in any given location is either stasis or erosion. For example, when the basal surface of an LPLS succession is a subaerial unconformity, it may represent a stasis interval that followed subaerial erosion and flooding but preceded initial shallow-marine deposition (Fig. 9c). However, outcrop evidence for such 'pre-depositional stasis' is rare, as basal sandstones in many instances overlie rigid bedrock that is impenetrable for trace makers.

Pockets: sediment preservation in non-depositional settings

Bathymetric depressions on the seafloor can provide shelter from erosion during the temporary absence of sand-dominated morphological elements in low-subsidence settings. Such 'pockets of accommodation space' enable the preservation of sediment

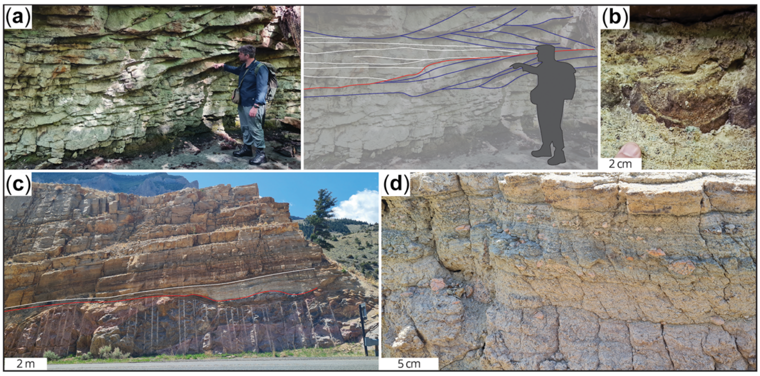

Fig. 10. Outcrop expressions of 'pockets of accommodation space' that sheltered sediment from erosion in the depositional environment of lower Paleozoic littoral sandstones, enabling sediment preservation during intervals that otherwise would have no preserved record. (**a**, **b**) Bathymetry created by deposition (blue) and erosion (red) formed a depression that was filled with trace fossil-bearing heterolithic strata (white; b). The heterolithic strata pinchout into an amalgamation surface. File Haidar Formation (Västergötland, Sweden). (**c**, **d**) The 'Great Unconformity' and the Flathead Sandstone (Wyoming, USA), showing a depression in the bedrock filled with immature paraconglomerates underneath more mature overlying strata. The depression enabled the preservation of a time interval that elsewhere was lost in the unconformity.

that correlates to package amalgamation surfaces or basal unconformities of adjacent strata. In this way, these pockets provide a stratigraphic record of time intervals that are elsewhere unrecorded.

An example of a pocket associated with a package amalgamation surface is shown from the lower Cambrian File Haidar Formation of Västergötland, Sweden (Fig. 10a, b), where trace fossiliferous heterolithic strata were deposited and preserved in the hollow created by the depositional and partially erosional relief of the underlying sandstone. The heterolithic package is also overlain by thick cross-stratified sandstones and pinches out laterally into a package amalgamation surface. The heterolithic strata represent an interval of time between two intervals of sand deposition that was only archived within the pocket created by the bathymetric depression.

An example of a pocket associated with a basal unconformity is shown from the basal Flathead Sandstone of Wyoming, USA (Fig. 10c), where a depression in the bedrock is filled with immature arkosic paraconglomerates (Fig. 10d). This facies potentially represents non-marine sediment deposited before the flooding or early marine palimpsest sediment (see Swift *et al.* 1971) and is in sharp textural contrast with the more mature overlying sandstones. The immature paraconglomerates being absent outside of this pocket demonstrates that the bathymetric depression protected its infill from potential subaqueous erosion. The impact of large-scale antecedent topography on Cambrian transgression patterns is widely known (e.g. Nielsen and Schovsbo 2011; Myrow *et al.* 2023; Woo *et al.* 2023), but outcrop-scale bathymetric relief also impacted sedimentation, enabling the preservation of records of time that elsewhere are lost in the unconformity.

Discussion

True substrates in lower Paleozoic littoral sandstones serve as indicators of sedimentary stasis and as archives of Earth-historic information in strata that are commonly considered to be unfossiliferous, time incomplete and dominated by signatures of erosion. The recognition of true substrates in outcrop has implications for various aspects of the early Paleozoic shallow-marine realm and its rock record.

Short stasis and the ichnological record

The true substrates within the sandstone facies of the Carnedd-y-Filliast Grits and other examples of LPLS can be characterized as either short-term (Fig. 7b) or active-layer true substrates (Fig. 7d), meaning that their preserved morphology and ichnology predominantly reflect brief intervals of registered stasis. This brevity prevented the accumulation of chemical or biological signals over time (Fig. 7c) and thereby controlled the Earth-historic information that these surfaces host.

Short-stasis true substrates: incomplete but uniquely accurate

The duration of stasis that is registered on a bedding surface determines the spatio-temporal significance of the information that the surface captured (Fig. 11). Long-term true substrates can register relatively complete samples of the original ecosystem,

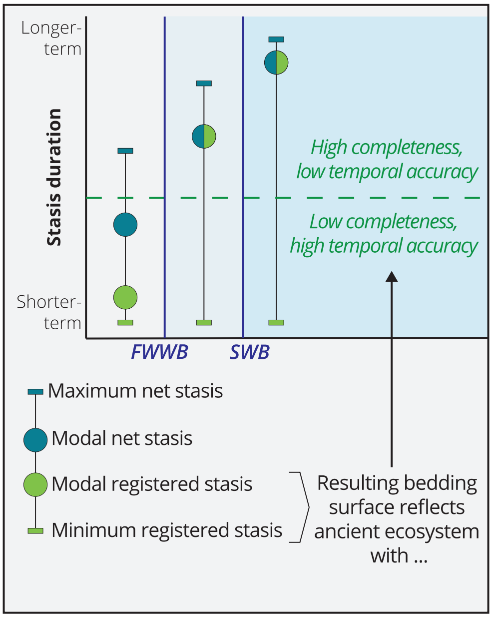

Fig. 11. Simplified model illustrating the typical spatio-temporal significance of sedimentary surfaces relative to fairweather and storm wave base (FWWB and SWB). Registered stasis can be equal to net stasis or lower, when the surface gets 'reset' by post-depositional processes (e.g. wave action). Maximum and modal net stasis durations increase offshore as the frequency of sedimentation events decreases. Minimum registered stasis is always low owing to the possibility of surface activity just prior to subsequent deposition. Above FWWB, modal registered stasis durations are lowest, reflecting a high sedimentation frequency, and often lower than net stasis, owing to pervasive wave action. Surfaces with longer registered stasis are more spatio-temporally complete, as data can accummulate over time. Surface registering shorter stasis are less complete, but more accurate, as registered data are more likely to be coeval. Therefore, the short-stasis signature of the littoral zone suppressed the registered trace fossil record.

as there is sufficient time for different trace fossils to colonize and overprint on the spatial plot of the substrate that is captured in outcrop (Fig. 7c). Yet such time-cumulative true substrates have reduced spatiotemporal veracity, as trace fossils are unlikely to have been formed at the same time as part of one coeval small-scale community, even if they are found on the same bedding plane. In contrast, short-stasis bedding planes represent shorter colonization windows and are therefore less likely to host trace fossils (Fig. 7b, d), and when trace fossils are present, the preserved ichnoassemblage represents a smaller sample of the original ecosystem. However, any information hosted on short-term true substrates is likely to be coeval. Longer-term true substrates (Fig. 7c) can thus host more spatially complete representations of an ecosystem, but short-term true substrates (Fig. 7b, d) host more temporally accurate representations of an ecosystem.

An example of how the duration of sedimentary stasis can impact the spatio-temporal significance of ichnological data can be found in reconstructions of bioturbation (see also Marenco and Hagadorn 2019). On the short-term surfaces in the sandstones of the Carnedd-y-Filliast Grits, trace fossils are limited to rare patches occurring in ripple troughs (Fig. 4). This patchiness is analogous to modern tidal flat settings, where Dashtgard (2011) showed that bioturbators rarely occupy more than 3% of the substrate and that significant temporal overprinting is required to achieve high bioturbation intensities. Similar ichnological patchiness has been recognized in other successions in the rock record (e.g. Mangano *et al.* 2002; McIlroy 2007; Marenco and Hagadorn 2019). When short-term true substrates record patchy bioturbation, they accurately represent the spatial distribution and short-term functioning of this process. However, a patchy ichnoassemblage may also be considered an unfinished work-in-progress that underrepresents the maximum potential impact of a bioturbating community on sedimentary fabrics. When long-term true substrates record highly bioturbated ichnofabrics, this reflects the true potential of a bioturbating community, but any information related to the temporal continuity and spatial heterogeneity of this process is lost.

Implications for Cambro-Ordovician shallow-marine biodiversity

The registered duration of sedimentary stasis exerts a control on the trace fossil record (Fig. 7), but this is not a constant variable across the marine realm (Fig. 11). The lower Paleozoic littoral rock record predominantly recorded brief intervals of stasis, resulting from: (1) a relatively high sedimentation frequency, resulting in relatively brief intervals of net stasis; (2) relatively pervasive post-depositional agitation of an active surface layer by oscillatory wave action and tidal currents; and (3) reduced preservation potential of fine-grained shallow-marine strata, yielding longer-stasis surfaces, in low-subsidence settings (Fig. 9). This brevity of registered stasis (Fig. 11) primarily affects the ichnological record at small spatio-temporal scales, causing individual beds and outcrops to host less dense and less diverse trace fossil assemblages. However, owing to the persistence of littoral sandstones in the early Paleozoic shallow-marine rock record, the outcrop-scale propensity to register brief stasis would have been widespread and thereby sufficiently amplified to also affect regional and global trace fossil records. In this way, the short-stasis signature contributed to the low ichnodiversity above fairweather wave base compared with coeval environments situated between the storm- and fairweather wave base (Buatois *et al.* 2020).

The unfossiliferous nature of strata deposited in early Paleozoic littoral settings has previously been attributed to limited biological activity owing to unfavourable environmental conditions in epeiric seas (e.g. Peters 2007). Yet owing to the scarcity of body fossils, trace fossils have formed the main source of palaeobiological information. As these trace fossils were predominantly imparted during intervals of stasis that are best characterized as ‘snapshots’ rather than as ‘timelapses’ (Fig. 11), it appears likely that early Paleozoic littoral environments hosted more diverse ecosystems than the data collected thus far would suggest.

Implications for time completeness at outcrop

True substrates can be difficult to identify in texturally homogenous successions but are shown to be relatively common in the sandstones of the Carnedd-y-Filliast Grits, where the reliable identification of true substrates was aided by the large dimensions of the ripple marks (Figs 2–4). The demonstrable commonness of short-term true substrates and short-term depositional signatures implies that metre-scale packages of LPLS can represent short time intervals (days to years) with only minor time gaps, meaning that the rock record is relatively time complete at this scale. Lower Paleozoic littoral sandstones have been considered exceptionally incomplete records of time (Sloss 1996; Holland and Patzkowsky 2002), but their record of true substrates underscores that temporal completeness depends on how it is defined: individual outcrops can be largely time complete while also representing merely a fraction of the total time represented by a diachronous larger unit (see also Runkel *et al.*

2008; Paola *et al.* 2018; Davies *et al.* 2019; Davies *et al.*, 2024, this issue).

When considering outcrops as representative samples of short-term dynamics across the broader system (Paola *et al.* 2018; Davies *et al.* 2019; Davies *et al.*, 2024, this issue), it becomes apparent that the short-term sedimentary dynamics captured in LPLS commonly involved stasis and non-erosive sedimentation. At the same time, the early Paleozoic shallow-marine realm is also associated with pervasive erosion and sediment reworking, as reflected by the high textural maturity of many LPLS successions (see Went 2013; Lorentzen *et al.* 2020). These seemingly contradictory aspects can be reconciled through consideration of their different spatio-temporal hierarchies: most sedimentary surfaces in outcrop are lower-order surfaces reflecting brief intervals of missing time. However, most missing time is reflected by the less numerous higher-order surfaces that separate larger architectural elements (i.e. package amalgamation surfaces; see also Miall 2016; Miall *et al.* 2021). These higher-order surfaces represent relatively prolonged intervals of non-deposition during which sediment can be reworked many times before its ultimate deposition, resulting in textural maturation over time.

Non-uniformitarian controls on true substrate preservation

True substrate preservation is not a time-specific phenomenon but a widespread attribute of sedimentary systems (Davies and Shillito 2021). However, we can speculate that the conditions required for true substrate preservation – sedimentary stasis and non-erosive flows – might have changed in prevalence in the shallow-marine realm throughout the geological past. Lower Paleozoic littoral sandstones have previously been interpreted in the context of their pre-vegetation age: prior to the landscape-stabilizing effects of land plants from the mid-Paleozoic onwards (Davies and Gibling 2010, 2011; McMahon and Davies 2018; Davies *et al.* 2021; Ielpi *et al.* 2022; Veenma *et al.* 2023), enhanced erosion and aeolian winnowing of unvegetated hinterlands have been suggested to have resulted in a more voluminous supply of sand to the early Paleozoic marine realm (Dalrymple *et al.* 1985; Runkel *et al.* 1998, 2007; Dott 2003; Went 2013).

Runkel *et al.* (2007) argued that LPLS are in many respects similar to syn-vegetation equivalents (e.g. in terms of facies and depositional processes involved), but that potential non-uniformitarian signatures may be found in (1) anomalously extensive shoreline migration across vast, gently sloping, low-subsidence cratons and (2) a higher connectivity of strata deposited during such migrations resulting from the higher pre-vegetation sand supply, leading to horizontal ‘stretching’ of stratal elements.

These stretched stratal elements are diachronous and their extensiveness therefore does not necessarily imply that individual sand-dominated morphological elements at any given moment were also of larger scale. However, it is probable that larger shallow-marine areas were affected by fluvial discharge, resulting from sediment delivery via the expansive braid deltas that were prevalent before land plants evolved (MacNaughton *et al.* 1997; Muhlbauer and Fedo 2020). Directly downflow of these vast and spatially volatile systems, successive sedimentation events would have had a lower chance of reaching the same location twice in quick succession, leading to longer stasis intervals than those occurring downflow of more fixed and confined sediment conduits.

The subsequent marine dispersal of a greater amount of sediment across seas with limited vertical accommodation space probably meant that sand-dominated morphological elements were more widespread within the shallow-marine realm. Considering their characteristically short durations of sedimentary stasis compared with other sub-environments, this probably contributed to the predominance of short-stasis signatures in the rock record of early Paleozoic littoral settings. The enhanced spatial breadth of sand sedimentation, combined with the fact that flows with higher sediment concentrations are more likely to be aggradational, could also have resulted in true substrates being more common and extensive in the rock record.

Conclusions

The record of sedimentary stasis on the bedding planes of Cambrian and Ordovician littoral sandstones enhances our understanding of these strata as sedimentary and fossil archives of the early Paleozoic shallow-marine realm. Modal intervals of stasis registered in this facies were brief, reflecting frequent sedimentation events in littoral settings, frequent post-depositional agitation of the sediment surface layer by wave action and reduced long-term preservation potential of heterolithic strata, which record the majority of longer stasis intervals, in low-subsidence settings. The brevity reflected by most bedding planes demonstrates that despite having been considered time incomplete, limited time is missing from outcrop-scale architectural elements.

Bio-sedimentary structures registered on short-stasis bedding planes (e.g. trace fossils) can be sparse but when present are likely to be coeval. Longer-stasis bedding planes record such data cumulatively over longer periods and are consequently more complete representations of the original ecosystem. The predominance of brief stasis registered in lower Paleozoic littoral sandstones therefore suppressed the abundance and diversity of fossils in outcrop, contributing to relatively low ichnodiversity reported from littoral successions. Considering that trace fossils are the most abundant palaeobiological proxy in these strata, early Paleozoic ecosystems situated in littoral settings were probably more diverse than their known fossil record would suggest.

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