A Late Silurian crisis in the Welsh Basin

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Abstract. The Ludfordian stage of the Ludlow series, records the terminal phase in the history of the Welsh early Palaeozoic marine basin. Later Ludfordian facies became uniformly shallow marine, with event deposits and ubiquitous hummocky cross stratification suggesting storm-influenced accumulation between fair-weather and storm-wave base. The terminal shallowing trend was accompanied by a developing ecological crisis signalled by an impoverishment of the marine macro-fauna and a marked reduction in bioturbation of the sediments accumulated between the storm events. Of increasing importance in these latter sediments are often greenish, non-bioturbated, shaly siltstones showing minutely-wrinkled partings. The wrinkle structures are thought to signify increasingly extreme conditions, since they record the presence of microbial mats: sea bed colonisations that today typically develop in ecologically harsh environments. The subsequent passage from these ecologically stressed open-marine conditions to marine-influenced brackish waters of the Downton Castle Sandstone Formation – highlighted on the shelf at Ludlow by the famous bone bed – is signalled in basinal areas to the west only by the rapid replacement of the later Ludfordian marine shelly fauna by brackish water forms. A major positive carbon isotope excursion associated with the Ludlow Bone Bed, suggests that there may have been global, climatic, as well as local, influences on the Ludfordian ecological crisis and on the abrupt faunal changes at the level of the Bone Bed.

The Silurian-Devonian boundary, as originally conceived by Murchison in the Welsh Borderlands, was conventionally equated with the famous Ludlow Bone Bed. Above, were the increasingly non-marine facies of the Devonian Old Red Sandstone; below were the fossiliferous grey marine strata of the Silurian Ludlow epoch. The boundary stratotype has since been re-located to a wholly marine section at Klonk in the Czech Republic. There, a further Silurian series, the Pridoli, is now interposed between the Ludlow series and the Devonian. As a consequence, the Ludlow Bone Bed is now taken as the local base of the Pridoli series (Basset et al., 1992). Despite this reduction in the Bone Bed's global stratigraphic status, there is still interest in this classic transition from marine to continental facies. Was this locally driven, for example, pressaging the increasing restriction and gradual structural inversion of the Welsh Lower Palaeozoic Basin (Bailey & Rees, 1973; Allen, 1985; Woodcock, 1990)? Or were there external factors at work, as is suggested by aspects of the developing ecological crisis in the marine basin?

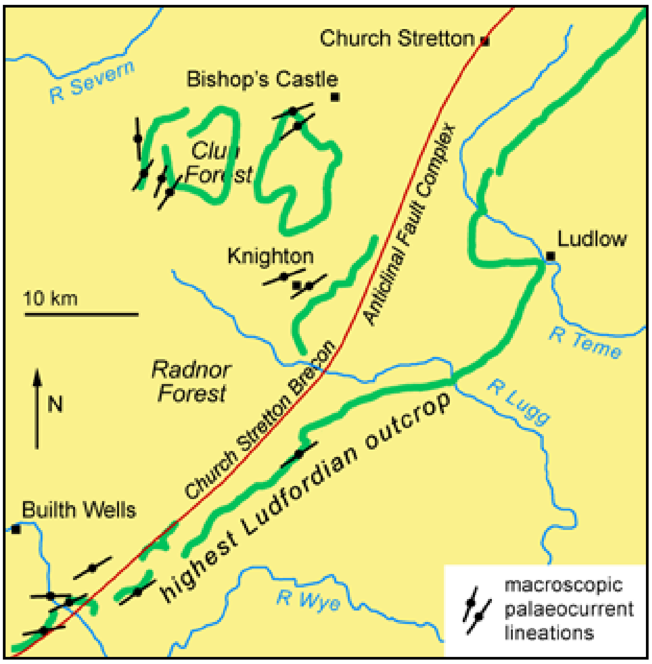

***Figure 1**. Approximate main outcrops of the highest marine Ludfordian, these following the base of the Downton Castle Sandstone Formation of the Old Red Sandstone magnafacies (palaeocurrent data after Bailey and Rees 1973).*

Original regional fieldwork in south Central Wales and the Borderlands used extant maps as the basis for a study of Ludlovian facies (Bailey, 1969; Bailey & Rees, 1973). This work has lately been updated by field visits that focused on the highest marine Ludfordian and the facies associations of the wrinkle structures developed at this level, structures that provide key evidence for an ecological crisis during the latter, Ludfordian, stage of the Welsh Ludlovian.

Ludfordian facies

The Ludfordian of the Welsh Basin sees hemipelagic facies of the previous Gorstian stage, characterised by laminated siltstones, shelly silt-turbidites and widespread slumping, giving way to progressively shallower marine facies, culminating in a transition to the brackish-water deposits of the Downton Castle Sandstone Formation (previously, the 'Downtonian'). The tough, thin-bedded, pale-laminated siltstones comprising earliest Ludfordian facies in the Builth Wells area (uppermost Wilsonia Shales of Straw, 1937; laminated siltstone facies of, Bailey, 1969; 'Striped Flags' of Kirk, 1951 and Woodcock & Tyler, 1993) show abundant evidence of intermittent bottom current action and few indications of bioturbation. The palaeocurrent evidence suggests that the deep water currents followed the trend of the Church Stretton-Brecon Anticlinal fault complex, the deep-seated structure that defined the palaeoslope between the Midland Shelf Sea and the Welsh Basin (Fig. 1).

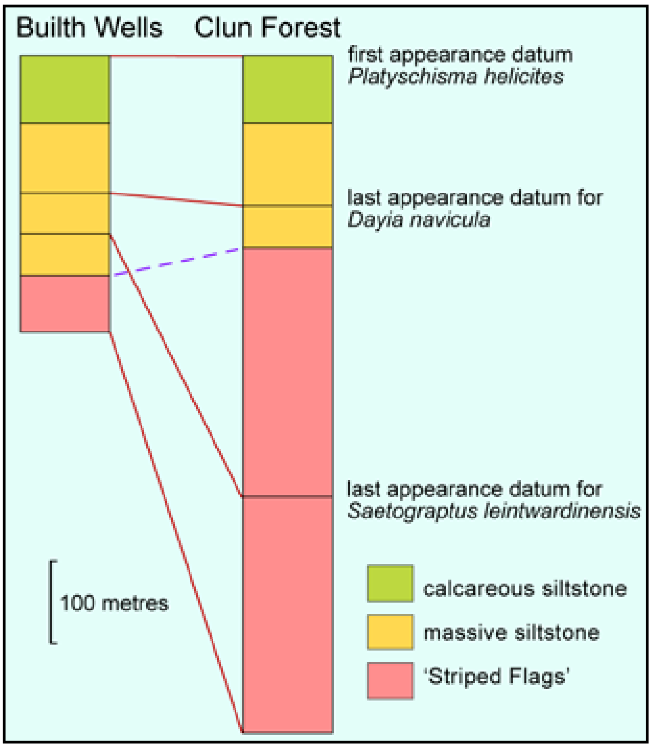

***Figure 2**. Ludfordian facies relationships between the Builth Wells and Clun Forest areas, showing the key biostratigraphic datums. The first appearance datum of P. helycites, a form not found in the Builth area, is conventionally taken as the top Ludfordian, i.e. top Ludlow series, corresponding to the Ludlow Bone Bed of the type area.*

First appearance of *Saetograptus leintwardinensis* defines the base of the succeeding Ludfordian stage. In the Builth area, within this graptolite biozone (Fig. 2), there is a rapid upward transition from the hemipelagic Striped Flags to massive, homogeneous, shelly siltstones (Orthonota Mudstones of Straw, 1937; massive siltstone facies of Bailey, 1969). These are thought to owe their unlaminated, crudely layered, rubbly-weathering character (Fig. 3) and the scattered, often fragmentary and disarticulated, nature of their shelly fauna, to pervasive bioturbation by a deep-burrowing benthic macro-fauna. The facies change strongly suggests an early Ludfordian transition from hemipelagic to shallower-water shelf facies; and this is evident at the same stratigraphic level along the basin margin as far north as Radnor Forest.

Moving north into the Clun Forest area, a diachronicity in Ludfordian facies becomes apparent. The accumulation of the 'Striped Flag'/laminated siltstone facies (Bailey, 1969), locally represented by the *Dayia navicula* Beds (Earp, 1938), persisted long after the local last appearance of *S. leintwardinensis* (Fig. 2). This younger development of the facies retains its hemipelagic character, but is less regularly bedded than its Builth counterpart, a feature that relates to the reduced evidence of scouring bottom currents and the increased signs of the activities of small benthic burrowers. The upward transition to the shallower water, pervasively bioturbated, massive siltstone facies (upper Dayia navicula Beds of Earp, 1938; Wern Quarry Beds of Holland, 1959, and Woodcock & Tyler, 1993) is abrupt, as in the Builth area, but, as indicated by its relationship with the *S. leintwardinensis* zone, significantly delayed (Fig. 2). The marked contrast in the post *leintwardinensis* facies and thicknesses in the two areas implies that the early Ludfordian saw the onset differential subsidence, whereby hemipelagic conditions were maintained in the Clun Forest (notably in the Knighton area, Holland, 1959), while the shallower-water massive siltstone facies prograded basinwards from the more marginal and more slowly subsiding Builth Wells – Radnor Forest area (Fig. 1). The spread of this facies continued until the entire basin in south Central Wales was accumulating the pervasively bioturbated shelly massive siltstones, but the later developments of the facies (Chonetes striatella Beds of Straw, 1937; Dalmanella lunata Beds of Earp, 1938; Llanwen Hill Beds of Holland, 1959) feature increasingly frequent 'event' deposits, in the form of laterally extensive, decimetre-thick, laminated calcareous siltstone beds, lacking bioturbation (Fig. 3). Basin-wide, the increase in the frequency of these event deposits sees the massive siltstones pass transitionally upwards into c.70 m developments of the highest marine Ludfordian calcareous siltstone facies (Bailey, 1969) distinguished in the Builth Wells area as the Holopella Grits and Shales (Straw, 1937) and in the Clun Forest area as the uppermost Dalmanella lunata Beds (Earp, 1938) and the Llan Wen Hill Beds (Holland, 1959; Woodcock & Tyler, 1993). The growing frequency of the well-defined calcareous siltstone beds sees a

***Figure 3**. Ludfordian massive siltstone facies, with rubbly-weathering character that is typical of these massively-bedded, heavily bioturbated somewhat shelly siltstones. The interbedded calcareous siltstone event deposit (below the scale) has non-bioturbated lamination with hummocky cross stratification. Llanbedr-Painscastle, Builth Wells [SO146449].*

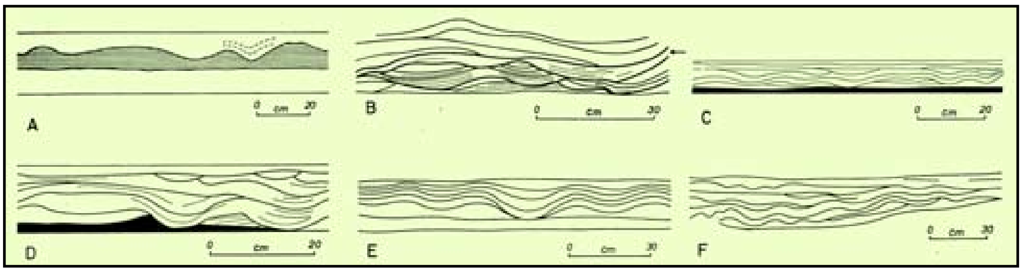

Figure 4. *Line drawings of the anisotropic 'scour and drape' form of hummocky cross-stratification developed in calcareous siltstone beds within massive siltstone facies, Llanbedr-Painscastle, Builth Wells [SO149447]*

concomitant increase in the numbers of lensoid beds and thin seams packed with disarticulated and broken marine shells, evidently washed-in death assemblages. The sedimentary background to the increasingly frequent event deposits also shows a progressive change, with the rubbly-weathering massive bioturbated siltstones (Fig. 3) giving way to thinly bedded, or shaly, bioturbation-free, often grey-green and micaceous, siltstones (Figs. 6, 8A).

In the Builth Wells area the highest Ludfordian marine strata are followed, after a possible hiatus, by a thin basal 'quartzite' and poorly fossiliferous green marls assigned to the 'Downtonian' (Straw, 1937), but in the Clun Forest area (Fig. 1), the base Downtonian is not marked by a facies change and there is no representative of the Ludlow Bone Bed. The well-bedded calcareous siltstones and intercalated greenish, shaly, micaceous, siltstones persist, and passage into the 10m-thick Platyschisma Beds of the lowest 'Downtonian' (Earp, 1938; Holland, 1959) is signalled only by replacement of the largely washed-in Ludfordian marine brachiopod faunas (*Protochonetes ludloviensis [formerly Chonetes striatellus]* assemblage) by largely washed-in assemblages of brackish water gastropods (*Platyschisma helicites*), bivalves, fish remains and lingulid brachiopods (Earp, 1938; Holland, 1959; Miller et al., 1997). Fossils in the following 70m local development of Earp's 'Green Downtonian' suggest brackish waters with an intermittent marine influence.

Environments and bed forms

The diachronous transition from the 'striped flags' to massive siltstone facies suggests northward-migrating shallowing that eventually allowed the colonisation of the entire Welsh Basin by a benthic macro-fauna including active deep burrowers. Thereafter, as outlined above, the basin saw a gradual diminution in the importance of this latter facies, involving the increasing frequency of non-bioturbated strata, both well-bedded calcareous siltstones and thin-bedded, often shaly-splitting and green-tinged, micaceous siltstones. Evidently, conditions became inimical to the benthic burrowers and grazers; but, otherwise, what does the increasing development of the new lithosomes imply?

The calcareous siltstones' bedforms suggest that they are rapidly accumulated 'event' deposits. Massive or planar laminated beds may show a basal layer of shell debris that suggests grading. Others show hummocky cross-stratification (HCS) (Figs. 4–6). The latter beds typically show internal, or upper-bedding-plane, erosion surfaces with broad centimeter-scale, or larger, undulating relief. The isotropic or often anisotropic (elongate) 'hummocks' are concordantly draped by convex-upward laminae (Figs. 4–6). Within individual calcareous siltstone beds, each denoting a depositional event, there may be several, mutually discordant, erosion surfaces, each with concordantly draping laminae (arrowed, Fig. 4B). Such relationships

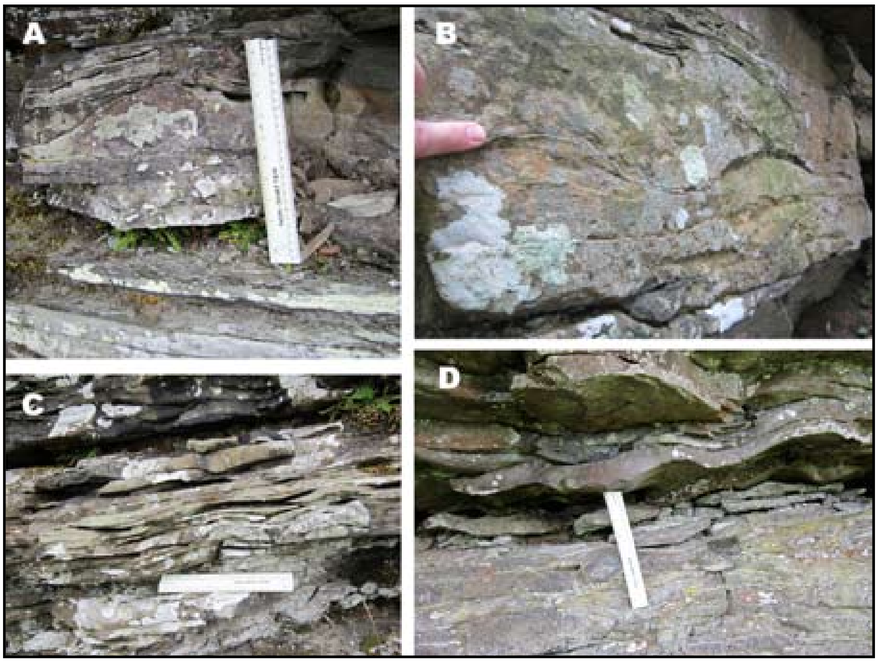

Figure 5. *Later Ludfordian hummocky-cross-stratified storm deposits in the Builth Wells area.* ***A****: Calcareous siltstone bed with upper surface eroded into prominent hummocks; note shaley layering below the base of the 25 cm scale. Old quarry, Llanstephan [SO116418].* ***B****: Calcareous siltstone beds with draped hummocky surfaces (finger for scale), with truncated laminae to the right of the prominent lichen patch. Old quarry, Llanstephan [SO116418].* ***C****: Calcareous siltstones with 'scour and drape' hummocky cross stratification, Llanbedr-Painscastle [SO149447].* ***D****: Calcareous siltstones with prominently hummocked upper surface (at base of 25cm scale) and with 'rippled' layer configuration (above scale) following the hummocky basal relief of a shallow scour feature (see Figure 3F). Llanbedr-Painscastle [SO149447].*

Figure 6. *Ludfordian storm-influenced deposits, Medwaledd Brook [SO147848], Clun Forest.* ***A****: An upward-thickening series of calcareous siltstone tempestites; hammer is 27cm long.* ***B****: Tempestites draping and filling a prominent scour in the hummocky surface visible behind the lower half of the 25 cm scale.* ***C****: Prominent hummocks on the upper surface of a calcareous siltstone bed, blanketed by shaly sediment (just above the 25 cm scale). The hummocky calcareous siltstone layer itself occupies a broad swale. Above is a prominent non-hummocky tempestite layer*

imply that these hummocks are not aggradational, but instead were sculpted by episodes of bottom erosion occurring during, or soon after, the accumulation of the individual calcareous silt layers. The bed-forms (termed 'scour ripples' by Bailey, 1966) thus belong to the 'scour and drape' class of HCS (Southard, 2006). The draping of the hummocks creates intervening areas of concave upwards 'swaley' cross-lamination, sometimes accentuated, with thickened infill (Figs. 4D, 4E). Closely associated with the HCS layers are larger-scale features, catenary in cross-profile, with cross-cutting basal relationships suggesting a few decimeters of seabed scour. Their draped basal erosion surfaces may be hummocky (Figs. 4F, 5D) or smooth (Fig. 6B), and in the latter instance the feature could represent an accentuated scour between widely-spaced hummocks, to the left and right.

The laterally-extensive, graded calcareous siltstone event deposits are regarded as 'tempestites' – products of storm-induced sediment gravity flows (SGFs; Fig.6A) that spread across the shallow basin floor. These beds rarely show sole-markings, but a regional study of the anisotropies in their magnetic grain fabrics (Bailey and Rees 1973) suggested that the SGFs flowed northwards along what continued to be the axial bathymetric trend of the Welsh basin (Fig. 9). Those calcareous siltstones and shell layers with the anisotropic scour-and-drape HCS (Figs. 4, 5, 6) are considered to be another manifestation of SGF activity, since the pronounced bottom scour occurred repeatedly *during* the accumulation of these event deposits, re-suspending the newly deposited coarse silts. The rapid accumulation of the HCS layers occurred under 'combined flow' conditions that involved the episodic interaction between silt-depositing, unidirectional, SGFs and storm-wave-generated, oscillatory bottom currents (Duke, 1999; Southard, 2006; Quin, 2011; Leeder, 2011).

The graded tempestites and the HCS calcareous siltstone layers (Figs. 6, 8) thus, respectively, suggest deposition below and above the depth of contemporaneous storm-wave stirring. However, the close association of these two bedforms and larger erosional features (Figs. 6, 8), suggests fluctuating storm-intensities, rather than changes in sea level. Storm surge set-up from the north of the basin (Fig. 9) could account for the northward SGF underflows, though the relatively small scale and enclosed nature of the Welsh-Cumbrian Basin in the Ludfordian (Bassett et al., 1992; Turner et al., 2017) seem to preclude the unrestricted open-water conditions thought necessary for such an HCS-generating storm-wave set-up (Leeder, 2011). Perhaps the limitations imposed by the restricted nature of the shallow basin were off-set by the increasing frequency and severity of the storms, a Ludfordian climatic trend that continued during the accumulation of the 'Downtonian' Platyschisma Beds.

Ludfordian wrinkle structures

In the Welsh basin, the later Ludfordian empoverishment of the shelly macro-faunas and the diminishing role of the benthic deep burrowers of the massive siltstone facies broadly suggest a developing ecological crisis. This may have been climate related, with the increasing frequency of the depositional storm events inhibiting the activities of the sub-littoral benthic macro-faunas. But, the intervals between the increasingly frequent storm events involved the growing importance of a green-tinged, micaceous, shaly facies with 'minutely-rippled' parting planes. These unusual and enigmatic micro-bedforms (Straw, 1937; Earp, 1938; Bailey, 1969), which also occur on the upper surfaces of the laminated siltstone beds, can now be recognised as the *wrinkle structures* (Fig. 7 A-C).

These, minutely-wrinkled sediment surfaces and bed-forms are currently thought to have environmental stress connotations, since modern examples are commonly found to occur in harsh marine environments, where burrowing and grazing benthic macro-faunas are largely excluded (Noffke, 2008, 2009; Noffke & Awramik, 2013). They record the effects of sediment-accreting microbial mats, growing at the sediment-water interface. The mats are formed by generations of biofilms consisting of communities of trillions of

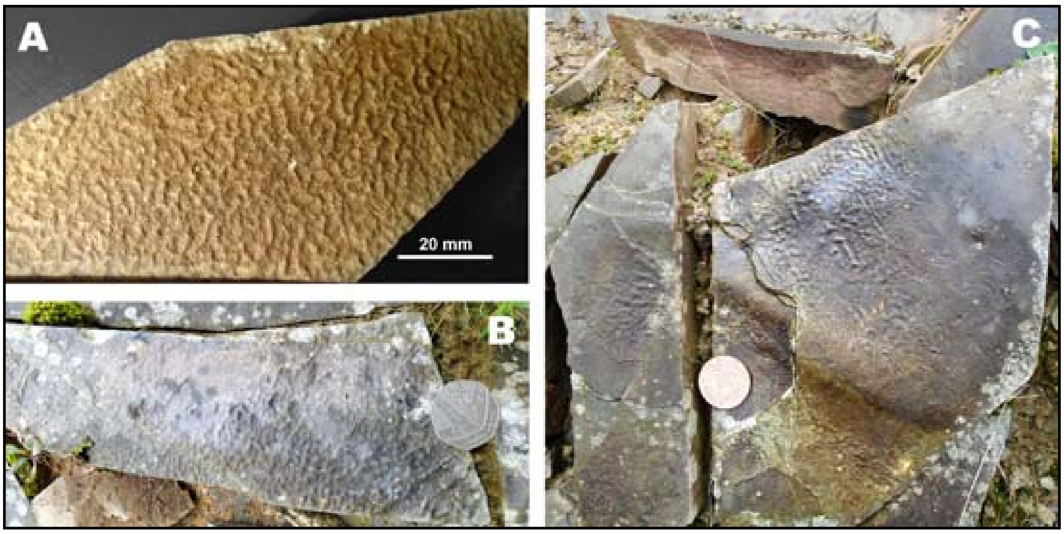

***Figure** 7. Later Ludfordian wrinkled bedding surfaces, representing microbial mats; Medwaledd Brook, Clun Forest [SO147848].*

***A**: Isotropic wrinkling of the upper bedding surface of a laminated calcareous siltstone tempestite.*

***B**: Wrinkled surface with prominent grazing trail (diameter of coin 27 mm).*

***C**: Patchy wrinkling on a smoothly hummocked surface (diameter of coin 24 mm).*

cells, mostly photosynthesising cyanobacteria, with a supporting inter-cellular, polymeric mucilage. This responds to sudden fluid shear stress by changing its molecular structure, a visco-elastic response that braces the films against erosion (Noffke & Awramik, 2013) and may help to generate and preserve the surface wrinkling as a sedimentary trace (Herminghaus et al., 2016). Preservation is further assisted by filamentous elements extending from the surfaces of the biofilms which trap and accrete suspended sediment particles, notably micas (Noffke & Awramik, 2013; Herminghaus et al., 2016). Laboratory experiments with water flowing over synthetic visco-elastic films, coated with fine-sand-sized particles, generated the irregular, isotropic, patterns of surface wrinkling found in the later Ludfordian (Fig. 7 A-C), whereas the parallel, anisotropic 'Kinneyia', traces were found to be a response to more vigorous water flow (Herminghaus et al., 2016).

Wrinkle structures, thought to record microbial mat development, featured widely in Proterozoic marine environments where microbes were the sole life forms (Noffke, 2008; Noffke & Awramik, 2013; Herminghaus et al., 2016). In the Phanerozoic, however, such microbially-induced sedimentary structures (also known as microbialites) are rarer and seem to be associated with intervals of environmental stress that caused the local collapse of marine ecosystems, or even global mass extinctions (Pruss et al., 2004; Mata & Bottjer, 2009, 2011). In effect, whatever the stresses, they eliminated the benthic burrowers and grazers that had inhibited benthic microbial mat development since Cambrian times (Mascord, 2019).

Significantly, at various stages in the Phanerozoic there is also a marked association of wrinkle structures with very fine grained quartz sandstone/siltstone beds showing HCS (Mata & Bottjer, 2009). This is taken to indicate microbial colonisation of occasionally storm-churned sub-littoral environments, at depths between fair-weather and deepest storm wave base. It is supposed that the storm-generated SGFs imported the microbial forms, while the clean, quartzose, 'event' deposits provided a favourable substrate for the initial colonisation (Noffke & Awramik, 2013).

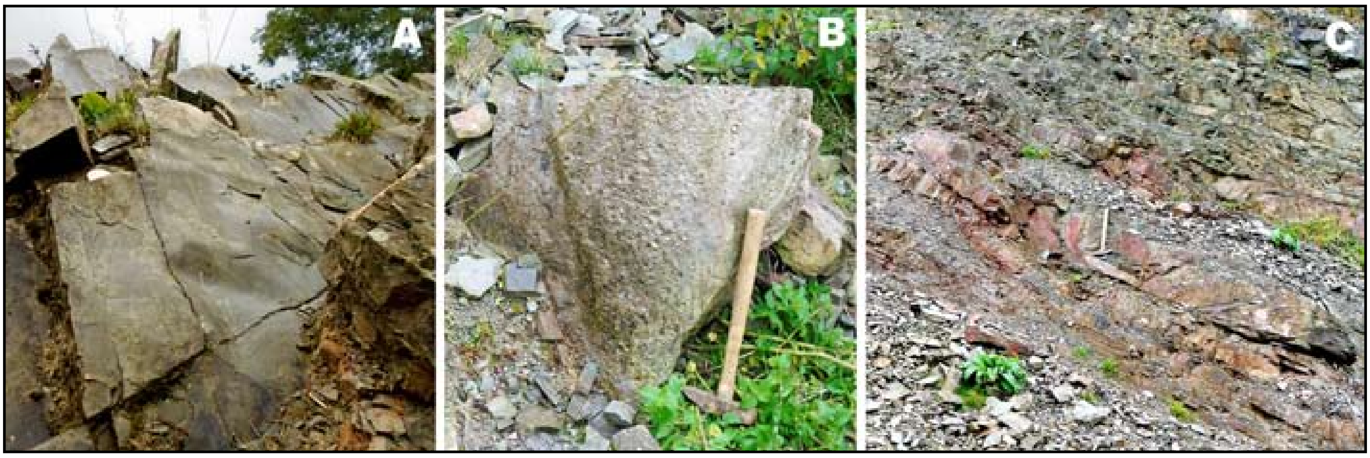

***Figure 8.** Sedimentary structures closely associated with the wrinkled horizons shown in Figure 7; on Clun Forest [SO147848]. **A**: Subtly hummocked micaceous siltstones (diameter of coin 24 mm). **B**: loose block with a shell-filled erosional gutter (hammer is 30 cm long). **C:** Strata immediately overlying the wrinkled horizons shown in Figure 7, with a shallow, metres-wide, tempestite-infilled, scour feature (left and above the 30-cm hammer), and parallel-bedded tempestites towards the top of the section.*

Thus, the Ludfordian wrinkle structures of the Welsh basin appear to conform to a globally-repeated Phanerozoic pattern of occurrence. A key question is whether the microbial mats were exploiting, or helping to maintain, the basin-wide ecological stresses that had largely excluded the burrowing and grazing benthic metazoans. In other words, were they the 'permitted', adventitious, colonisers of sub-littoral environments that had become inimical to benthic metazoans, or agents in creating this adverse ecology?

The wrinkle structures' particular association with the grey-green, micaceous, shaly siltstones at first sight suggests that the microbial mats particularly thrived in the tranquil, but ecologically hostile, conditions of accumulation between the storm events. But, alternatively, the microbial mats may have been *agents* in the shaly lithosome's development. For example, after the initial colonisation of a new tempestite substrate by an imported microbial biome, each subsequent micaceous shale lamina could represent the suspended sediment 'captured' and bound by the filamentous elements of an individual sea bed biofilm (Noffke & Awramick, 2013). This accretionary model could allow microbial films to be developed without the distinctively wrinkled bedding surfaces, the patchiness of the wrinkle structures (Fig. 7) perhaps being a function of the thickness and/or varying visco-elasticity, of the biofilms. The 'lamina-by-lamina' accretion of the characteristic micaceous shales, would make this Ludfordian lithosome a benthic, siliciclastic, counterpart of the microbially-mediated stromatolitic layer structures in carbonate environments (Noffke & Awramick, 2013). The greenish colouration of the captured sediment, signifying mildly reducing conditions, could be a micro-environmental effect of the biofilms.

Global influences?

The Ludfordian stage sees the Welsh basin evolve from hemi-pelagic arm of the global ocean to a shallow, marine-influenced 'Downtonian' lake (Bassett et al., 1992). The shallowing ('silting-up') of the still-differentially-subsiding basin and the empoverishment of its marine macro-faunas can be attributed to progressive tectonic inversion that both created new peripheral sediment provenance areas (Fig. 9) (Allen, 1985; Woodcock, 1990; Bassett et al., 1992) and increasingly restricted the connection with the global ocean, with consequent effects on water depths and temperatures, salinities and primary productivities. However, some of the basin's historic changes in facies and faunas suggest global, possibly climatic, influences.

For example, the early Ludfordian extinction of the pelagic *S. leintwardinensis* and the subsequent absence of graptolite faunas could be attributed to the developing restriction of the Welsh Basin; but a *leintwardinensis* extinction event, with impacts on graptolites and other taxa, is recognised in the more open marine hemipelagic Ludfordian of the Prague Basin of the Czech Republic, hinting at a global influence on the Welsh extinction (Storch et al., 2014).

The increasing frequency of storm-related event deposits in the later Ludfordian suggests a climatic trend, possibly global in origin, that persisted into the earliest 'Downtonian'. Repeated depositional blanketing of the sub-littoral seafloor may have been a factor in the elimination of the benthic deep burrowers of the massive siltstone facies, already stressed by more general ecological factors. A climatic trend may thus have been a factor in the successful invasion of the basin by microbial mats.

The marked reduction in the salinity of the storm-churned 'Downtonian' waters of the Clun Forest area again suggests a global climatic influence in the sense that a eustatic fall could account for the basin's sudden isolation from free exchange with the world ocean. Continuing fluvial inputs from uplands already rising to the northwest and southwest, coupled with storm mixing of the basin's waters would then created the brackish 'Downtonian' lake (Sutherland 1994). The condensed, centimetres-thick, Ludlow Bone Bed records a contemporaneous short-term regression, affecting the less rapidly subsiding Midland Platform, and locally followed by the accumulation of several metres of 'Downtonian' siltstones with *Platyschisma* and HCS (Smith & Ainsworth, 1989).

The most striking evidence for a global influence on the Ludfordian environmental changes affecting the Welsh Basin and Midland Platform comes from the marine isotopic record. In the fully marine platformal limestone and basinal shale sequences of Bohemia and the Baltic region there is an important mid-Ludfordian, graptolite/conodont extinction event, occurring significantly higher in these sections than the biozone

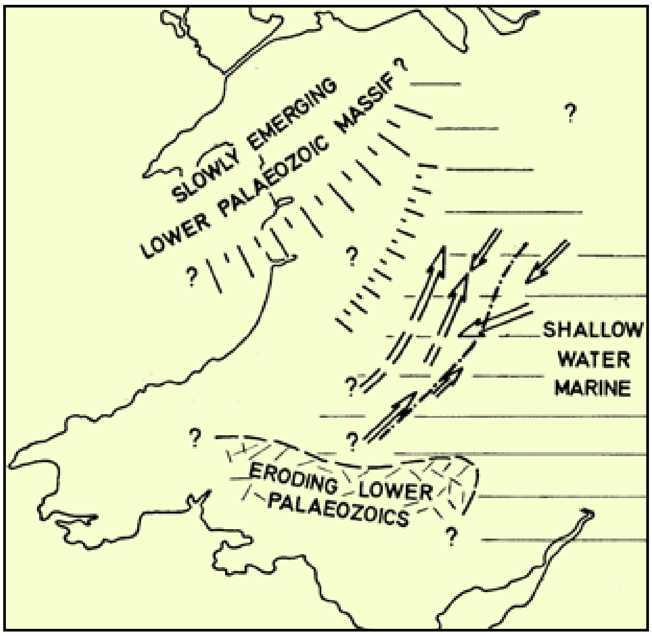

***Figure 9**. Latest Ludfordia palaeogeography of the Welsh Basin (after Bailey & Rees, 1973).*

of *S.leintwardinensis*. This *Lau* extinction event is associated with regressive carbonate facies, microbial mat development (Calner 2008) and a positive carbon isotope (C-13) excursion (CIE) lasting as much as 1 myr (Cramer et al., 2015). The positive CIE proves to be a global event and is the largest such excursion so far encountered in the Phanerozoic (Calner 2008; Barrick et al. 2010; Loydell & Fryda, 2011). Its global association with evidence of a short-lived marine regression, has suggested an as yet undetected glaciation of polar Gondwana continents, implying climatic cooling (Calner, 2008). This accords with the conventional interpretation of positive CIEs which invokes high marine phytoplankton productivities and consequent burial sequestration of the more abundant Carbon-12 isotope, which brings about a global relative enrichment in organic and carbonate Carbon-13 and a reduction in atmospheric CO_2, coupled with extinctions and climatic cooling.

The global character of the Lau-related mid-Ludfordian positive CIE suggested a search for its presence in the Ludfordian of the Welsh Borders. Loydell and Fryda (2011) argue that having failed to establish a CIE at the most obvious candidate level *within* the Ludfordian succession at Ludlow (base Whitcliffe Formation), the clear alternative is the regression associated with the Ludlow Bone Bed. Detailed sampling of a 3.5m section through this horizon in Weir Quarry, west of Ludlow, established the continuously rising limb of a positive CIE, commencing just below the Bone Bed. This excursion is sufficiently pronounced to be correlated with the global mid-Ludfordian Lau CIE (Loydell & Fryda, 2011).

The correlation of the Ludlow Bone Bed with the mid-Ludfordian Lau extinction event, though supported by the unusual magnitude of the Bone Bed CIE and some reinterpretation of the palaeontological evidence (Loydell & Fryda, 2011), is disputed (Turner et al., 2017), since it means that 'Downtonian' strata must, at least in part, belong to the Ludfordian stage of the Ludlow series, rather than to the following Pridoli series, as is presently thought. This entails a reduction in the stratigraphic range of the Pridoli in the Welsh Borderlands (Turner et al., 2017). However, independent isotopic evidence supports the older, mid-Ludfordian, date for the Bone Bed CIE, in the sense that there is, as yet, no record of a marked positive CIE at the well-established Ludlow-Pridoli series boundary in the marine type sequences of Baltica (Calner, 2008; Cramer et al., 2011; Kaljo et al., 2012, 2015).

The steadily rising C-13 values in the sample series from Weir Quarry section, beginning in storm-influenced wholly marine strata just below the Ludlow Bone Bed and ending in the brackish water, but still storm-influenced, Platyschisma Shales 1.8m above it, suggest that the regressive/transgressive lag deposit forming the Bone Bed involves no significant hiatus in accumulation. Also, unless there is a small misalignment in the carbon isotope sample series with respect to the Bone Bed, the relationships indicate that the beginning of the global positive CIE marginally pre-dates the rapid local transition from marine to brackish waters and the palynological evidence of an associated change from dominantly marine to overwhelmingly terrestrial floras (Richardson & Rasul, 1990; Loydell & Fryda, 2011). Even so, it seems plausible that the global climatic changes that culminated with the mid Ludfordian Lau CIE were an influence on the developing ecological crisis in the Welsh Basin, perhaps accounting for the increasing storm influence on sedimentation, and reinforcing the local environmental stresses that resulted from the increasing restriction and silting-up of the marine basin.

Synopsis

The classic Ludfordian sections of the Welsh Basin indicate progressive shallowing and show that this latter trend was accompanied by a developing ecological crisis involving:

- a general decline in the richness of the marine shelly faunas;
- the increasing tendency for these to occur mainly in the form of washed-in death assemblages;
- the ultimate basin-wide extinction of the benthic deep-burrowers of the massive siltstone facies; and
- the widespread, late-stage colonisation of the basin floor by microbial biomes.

Shallowing and restriction alone may explain the faunal crisis. The accompanying now-cryptic changes in water temperature, chemistry and primary productivity, for example, could account for the early extinction of *Seitograptus leintwardinensis* and the loss of the long-lived Ludlovian brachiopod *Dayia navicula* (Straw, 1937), neither of which appears to be sedimentary-facies-related. But the ecological effects of shallowing and restriction may have been reinforced by climatic influences, the most obvious of which is the increasing frequency of storm-driven depositional events, affecting the survival of the basin's benthic burrowers and shelly epifaunas. Also, confirmation of the contentious correlation of the Ludlow Bone Bed CIE with the mid-Ludfordian Lau CIE and extinction event of Baltic regions (Loydell & Fryda, 2011) will mean that the Welsh Basin's transformation from a marine to a continental depocentre can be tied to a short-lived (glaciogenic?) global regression (Calner, 2008)

Whether or not the correlation stands, the highest 70m of the marine Ludfordian, recording the run-up to the Bone Bed CIE, suggest an increasingly storm-influenced, sub-littoral, ecological 'desert' environment where the exclusion of benthic burrowers and grazers allowed microbial colonisation, generating wrinkle structures. Storm-generated SGFs may have both imported the microbial biomes and deposited a substrate suitable for them to colonise. Once established, the mat-forming microbial biomes may have become accretionary agents in the accumulation of latest marine Ludfordian's characteristic greenish, micaceous, shales, perhaps helping to sustain a between-storms benthic realm hostile to shallow marine macro-faunas that were still being washed in from the basin's margins.

The Ludfordian development of the Welsh basin thus presents the inverse of the Cambrian Substrate Revolution (Mascord, 2019), during which the microbial biomes that had flourished during the Proterozoic were overwhelmed by newly-evolved burrowing and grazing metazoans. As outlined above, the reasons for the microbial 'counter-revolution' in the Welsh Basin's Ludfordian remain conjectural, though clearly it was a response to a local ecological crisis, which, like others in the Phanerozoic (Pruss et al., 2004) was at least in part a response to a long-term global climatic trend.

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