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SYMPOSIUM

How far did feedback between biodiversity and early diagenesis affect the nature of early Palaeozoic sea floors?

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Abstract: Latest Precambrian to Early Palaeozoic biosphere evolution triggered changes in early diagenesis and carbonate precipitation which fed back to biodiversity through colonisation of hard substrates. Progressive increase in the depth and intensity of bioturbation and bio-irrigation lowered the zone of early carbonate cementation in the uppermost sediment column. This firstly led to a decline in the abundance of the flat pebble conglomerates which had been a common feature of Cambrian to Early Ordovician successions, replaced by the peak and subsequent decline in the Palaeozoic abundance of submarine hardgrounds. The availability of very widespread lithified sea floors in shallow subtidal settings during the Ordovician promoted a rapid expansion in sclerobiont diversity and contributed to the Great Ordovician Biodiversification Event (GOBE).

Key words: biotic feedback, biodiversity, early diagenesis, Early Palaeozoic, GOBE

EARLY Palaeozoic changes in biotic diversity both of skeletal and soft bodied organisms impacted upon carbonate production, sea floor substrates and early diagenesis on and just below the sea floor. Brasier *et al.* (2011, p. 523) proposed that for the Ediacaran–early Cambrian the evolution of active burrowers, grazers and scavengers expanded the mixed layer (Ekdale *et al.* 1984), and this along with biomineralization "led to an increase in the average depth at which lithogenesis was taking place in the sediment". During the Cambrian–Ordovician both the depth and intensity of bioturbation increased (e.g. Cambrian Substrate Revolution; Bottjer *et al.* 2000). Bioturbation traces are preserved in the 'transition layer' rather than the surficial, homogenized mixed layer, which is rarely preserved (Ekdale *et al.* 1984) but which stayed very thin (0.2-1.5 cm) through the Early Palaeozoic (Tarhan *et al.* 2015). From the Early Cambrian to Mid-Ordovician, bioturbation traces increased in size but remained very shallow (less than 6 cm), with burrow traces typically preserved as casts along bed junctions, and with sediment mixing low (ichnofabric index mean < 2.4 on a scale from 0-6 (homogenized sediment); Droser & Bottjer 1986; Tarhan *et al.* 2015, fig 3). From the Late Ordovician, size, density and complexity of burrows increased, although the mean ichnofabric intensity for Ordovician-Silurian remained low at 2.8 (Tarhan *et al.* 2015, fig 3). However, in the Late Ordovician, 3D *Thalassinoides* traces become common, penetrating to depths < 30 cm (Droser & Bottjer 1989). We (Wright & Cherns 2016*a*) proposed a diagenetic model that, as the depth and degree of bioturbation increased during this interval, systematic changes in the depth of the redox boundary and the thickening of the mixed layer and the Taphonomically Active Zone (TAZ) lowered the depth of early calcite cementation in the sediment. This is turn reduced the frequency of physical scouring of the cemented zone by such processes as storms. Here we elaborate on the model, discuss the impact on sclerobiont biodiversity (Taylor & Wilson 2003), which contributes to the Great Ordovician Biodiversification Event (GOBE; Webby *et al.* 2004), and investigate the wider implications of changes in the nature of sea-floor carbonates and early Palaeozoic biodiversity.

FLAT PEBBLE CONGLOMERATES

Flat-pebble conglomerates and breccias (FPC) are intraformational limestone conglomerates with rounded, thin tabular limestone intraclasts (Myrow *et al.* 2014; Fig. 1A, 2A, B). Our data focus on the most studied examples, from mid–outer shelf/ramp settings and exclude the flat-pebble deposits from peritidal successions that are common from the Precambrian to the present-day and which represent reworked desiccation cracks and supratidal crusts (Wright & Cherns 2016*b*). The more enigmatic subtidal FPC have generally been interpreted as shallow cemented limestone beds reworked by storm events or even tsunamis (Mount & Kidder 1993; Pratt 2002; Myrow *et al.*2004; Pratt & Bordonaro 2007). The distinctive lithofacies of subtidal FPC formed in shallow marine carbonate successions from Late Proterozoic to Early Ordovician, when it effectively disappeared from the stratigraphical record (Sepkoski 1982; Sepkoski *et al.* 1991; Liu & Zhan 2009; Wright & Cherns 2016*a*; Fig 1A). The accepted explanation (e.g. Sepkoski *et al.* 1991) has been that increased bioturbation in sediments of this age resulted in the prevention of cementation by physical mixing of the sediment.

HARDGROUNDS

Hardgrounds are cemented layers exhumed from cementation zones at or just below the sea floor, which when exposed at the sea floor become sites of colonisation by sclerobionts, including encrusters and borers (Taylor & Wilson 2003). Such cemented layers can be extensive or more discontinuous and nodular, and may be reworked as discrete clasts or hiatus concretions (Voigt 1968). The Phanerozoic peak of abundance is in the Ordovician (Fig 1A; Taylor & Wilson 2003; Palmer & Wilson 2004; Harper 2006; Taylor 2008; Christ *et al.* 2015 fig. 2). This abundance of hardgrounds has been linked to prevailing seawater geochemistry, with the suggestion that “calcite seas” were undersaturated with respect to aragonite so sea-floor dissolution released carbonate for local cementation (Wilson *et al.* 1992; Taylor & Wilson 2003; Palmer & Wilson 2004; Harper 2006). However, hardgrounds also declined in abundance towards the end of the Ordovician and into the Silurian, in spite of continuing "calcite seas" (Fig. 1A). A simple link between hardground abundance and "calcite sea" intervals seems unlikely since hardgrounds are not common in other Palaeozoic "calcite sea" intervals through to the Early Carboniferous (Mississippian; Fig. 1A and Christ *et al.* 2015), when Mg/Ca was very similar (e.g. Dickson 2004; Ries 2006).

Kenyon-Roberts (1995) was unable to find evidence of sea floor dissolution associated with Ordovician hardgrounds in the classic sections in North America. His material came mainly from the Upper Ordovician (early Katian; Trentonian/Caradoc) Simcoe Group of southern Ontario and the laterally equivalent Trenton and Black River Groups in northern and central New York State, and the Middle Ordovician (late Arenig, Dapingian–Darriwilian; Vecoli *et al.* 2015) Kanosh Formation of southwest Utah. He noted a low diversity of early cementation styles in the hardgrounds found in storm-influenced facies, and hardgrounds were effectively absent from shoal settings (cf. Mesozoic hardgrounds, see below).The Ordovician hardgrounds exhibit equant, columnar drusy spar to microspar mosaics of non-ferroan to weakly ferroan, manganoan low Mg-calcites. Kenyon-Roberts interpreted these as the products of syn-sedimentary cementation by sub-oxic bacterially mediated oxidation of organic matter in marine-derived pore waters of probable elevated salinity. The cements were originally low Mg-calcite.

Furthermore if higher frequency of hardgrounds during some "calcite seas" reflected a greater propensity for the dissolution of aragonitic skeletal components, this should be reflected in the biota with a decline in the preservation of the aragonitic component. Comparison of skeletal Lagerstätten from Palaeozoic "calcite seas" (Mississippian) and "aragonite seas" (Pennsylvanian) show no discernible preferential removal of the aragonite component during the former (Cherns & Wright 2011).

Early, large scale diagenetic dissolution of aragonite is particularly well known from Recent and Cenozoic cool-water settings, even in seawater oversaturated in respect to aragonite and calcite (e.g. Nelson *et al.* 2003; James *et al.* 2005). Many studies have now established that early aragonite dissolution takes place in the TAZ where undersaturation is generated largely by oxidation of H_2S, and calcite is precipitated below the TAZ (see Feedback Model below).

In the early Darriwilian Kanosh Formation of Utah, hardground intraclasts are common, constituting up to 30% of the succession and identical to diagenetic nodules found in the surrounding shales (Wilson *et al.* 1992; Kenyon Roberts 1995; Fig 2B). Whereas more continuous, as well as reworked, hardgrounds characterise younger Ordovician units, the Kanosh hardgrounds show evidence of multiple phases of cementation, exhumation, encrustation and reburial (Wilson *et al.* 1992; Palmer & Wilson 2004).

HARDGROUND FAUNAS

The earliest hardground faunas were cryptic, cavity-dwelling encrusting faunas (coelobionts) and cylindrical *Trypanites* boreholes described from Lower Cambrian archaeocyathid reefs and hardgrounds on Labrador (James *et al.* 1977; Kobluk *et al*. 1978; Kobluk & James 1979; Fig. 1B). From then through to the Mid Ordovician, macroborings of *Trypanites* are uncommon (Chow & James 2002; Taylor and Wilson 2003) although larger *Gastrochaenolites* in Lower Ordovician FPC and hardgrounds, and Lower-Middle Ordovician (Arenig) hardgrounds (Ekdale *et al.* 2002; Benner *et al.* 2004) confirm this behavioural niche on inorganic substrates. On organic substrates, microborings (< 1 mm) in Cambrian skeletons (brachiopods, echinoderms, tommotiids) provide evidence of predatory behaviour (Conway-Morris & Bengtson 1994). Simple pelmatozoan holdfasts of eocrinoids dominate in a low diversity encrusting assemblage on Upper Cambrian FPC (Brett *et al.* 1983); a similar fauna is reported from the Upper Cambrian of Greenland (Palmer 1982, fig.1). Pelmatozoan holdfasts also dominate in low diversity encrusting faunas on Lower-Middle Ordovician hardgrounds such as the Kanosh and on demosponges in the San Juan Formation of Argentina (Carrera 2000), with limited bryozoans and few macroborings by comparison with younger hardgrounds. By the Mid-Ordovician, the diversity of encrusting organisms had greatly increased, largely reflecting rapid evolutionary radiation within echinoderms and bryozoans (Sprinkle & Guensburg 2004; Taylor & Ernst 2004; Taylor 2016; Fig. 1B), part of the GOBE (Webby *et al.* 2004; Servais *et al.* 2010). Palmer (1982) recorded Middle Ordovician hardground faunas dominated by echinoderms (crinoids, edrioasteroids) and a diversity of bryozoans, with cornulitids and abundant worm borings. Similar diverse assemblages are found on Upper Ordovician hardgrounds (Fig. 2D). From Late Cambrian to Mid Ordovician, the surfaces affected by bioerosion changed from cemented FPC utilised by the early encrusting hardground faunas through reworked, encrusted limestone nodules and skeletons, to beds with complex hummocky and undercut surfaces with diverse encrusting and boring biotas (Brett & Liddell 1978; Brett & Brookfield 1984; Wilson *et al.* 1992; Fig. 3). Taylor & Wilson (2003, p. 44) suggested that the "Ordovician was a golden age for epizoans on hard substrate" owing in part to increased hard substrate availability. How far evolutionary diversification can be ascribed to the 'trigger' of those new habitats and ecological niches is naturally debatable. However, the GOBE also encompassed parallel evolutionary trends in several other major sessile suspension feeding groups characteristic of the Palaeozoic Fauna, and that utilised hard substrates, such as brachiopods, sponges and metazoan reef-builders such as corals and stromatoporoids (Servais *et al.* 2010).

Encrusting and boring faunas mimic the record of submarine hardgrounds through the Palaeozoic (Fig. 1B). Early (Late Cambrian) encrusters settled on fragmented cemented layers represented by FPC, but their temporal replacement by more continuous hardgrounds by early-mid Ordovician increased the availability of stable surfaces to both encrusters and borers. Hardgrounds are recognised from the preserved sclerobiont encrusters and borings, and are more easily recognised after the early Ordovician (Brett & Liddell 1978) but are also increasingly common.

The establishment of stable hard seafloor substrates correlates also with the evolution of reef communities in the GOBE (Harper 2006). Cambrian–Ordovician sponge-microbial mounds were replaced by metazoan reefs in the late Middle Ordovician (late Darriwilian). The earliest skeletal-dominated reefs are Early Ordovician (Late Tremadocian/Ibexian) bryozoan-sponge and bryozoan-pelmatozoan reefs that occur alongside sponge-microbial mounds, where bryozoans encrusted a sponge or pelmatozoan framework (Adechi *et al.* 2011). In the Mid Ordovician labechiid stromatoporoids and tabulate corals formed the skeletal frame builders, associated with encrusting bryozoans, solenoporacean algae and sponges (Carrera & Rigby 2004; Webby 2002). Heavily calcified skeletons characterise these metazoan reef builders, while microbial carbonate abundance declined (Riding 2006; Liu & Zhan 2009). Mid-Late Ordovician reef evolution correlates with the period of most abundant and widespread hard substrates in Palaeozoic shallow carbonate platforms (Fig. 1A-B).

A FEEDBACK MODEL

Changes identified in the geochemical zonation of shallow sea floor sediments from the Ediacaran to Cambrian (Brasier *et al.* 2011) can be extended and refined to provide a holistic explanation for the decline in FPC, the peak in abundance of hardgrounds and their subsequent decline during the late Ordovician-Silurian (Wright & Cherns 2016*a*). Syndepositional, microbially-mediated diagenetic processes trigger the mobilization of calcium carbonate during shallow burial affecting shell preservation and leading to calcite cementation (e.g. Sanders 2003; Berkeley *et al.* 2007; Cherns *et al.* 2011). These decay processes are most effective where organic matter accumulates, typically in finer grained sediment (e.g. Walter & Burton 1990; Hendry 1993; Walter *et al.* 1993). Calcium carbonate dissolution, preferentially of the more soluble aragonite, takes place in the uppermost sediment layer largely as a result of acidity caused by the aerobic oxidation of H_2S. While much of this dissolved calcium carbonate back-fluxes from pore waters to the water column, some becomes re-precipitated as calcite in the sediment column, initially forming nodules in areas of increased alkalinity such as the sulphate reduction zone (e.g. Sanders 2003, 2004). The TAZ corresponds to the oxidized zone of dissolution, whose depth is controlled by oxygen diffusion from the overlying water column and by sediment mixing caused by burrowing organisms (bio-irrigation; e.g. Aller 1982; Aller & Aller 1998). Microbially mediated decay processes have been shown to skew significantly the marine invertebrate fossil record (Cherns & Wright 2009, 2011) but they also provide the basis for understanding the limestone–marl alternations that form a widely developed facies in Phanerozoic epeiric sea settings (Munnecke & Samtleben 1996; Westphal & Munnecke 2003*a*; Munnecke & Westphal 2005; Fig 1C).

Brasier *et al.* (2011) proposed that during the Ediacaran–Cambrian the redox boundary and pH were lowered, with deepening of the zone of lithification as a consequence of the progressive development of the mixed layer. Late Proterozoic precipitation of calcium carbonate took place at or very close (< 1 cm) to seafloors covered with microbial mats (Fig. 3). Early Cambrian transgression and continental weathering increased the extent of marine carbonate precipitation, still taking place direct from seawater and close to the sediment surface (Peters & Gaines 2012). Biomineralization meant that from the early Cambrian carbonate was also remobilized in the shallow sediment through microbial degradation of organic matter. Metazoan burrowing depressed the zone of cementation but it remained very shallow in subtidal areas through the Early–Mid Cambrian, typically millimetre scale and < 3 cm depth (Droser & Bottjer 1988; Tarhan *et al.* 2015). The mixed layer of homogenized, soft to soupy sediment resulting from intense and rapid bioturbation, which in modern seas is typically 8-10 cm thick, was much thinner at < 1.5 cm in the Cambrian-Ordovician (Tarhan *et al.* 2015; also Berger & Johnson 1978; Ekdale *et al.* 1984). Only burrow traces that penetrate the underlying, heterogeneous transition layer are recorded in the fossil record. Subtidal bioturbation was low intensity and shallow, and its depth – by inference also the depth of the zone of cementation - remained < 6 cm until the Mid Ordovician (Droser & Bottjer 1988, 1989; Tarhan *et al.* 2015). Droser & Bottjer (1989) noted significant increases in both bioturbation depth (< 30 cm) and intensity in Late Ordovician carbonate successions, although in siliciclastic successions, Late Ordovician-Silurian burrows are more complex and larger but still shallow, and increase in intensity is limited (Tarhan *et al.* 2015).

The diagenetic model proposed for Cambrian to Late Ordovician (Wright & Cherns 2016*a*) is extended here to include Late Proterozoic (Ediacaran) matgrounds (Fig. 3), when extensive microbial mats and a lack of metazoan burrowers meant that the TAZ was limited to the depth of oxygen diffusion through microbial mats and carbonate precipitation took place at or very close to the sediment surface (Brasier *et al.* 2011). The 'Cambrian substrate revolution' (Bottjer et al. 2000) effectively removed microbial mats from shallow marine settings largely through substrate disturbance by bioturbation. The early Palaeozoic evolution of burrowing organisms, and protracted increases in both the depth and intensity of burrowing, led to progressive thickening of the TAZ and increased the depth at which secondary carbonate re-precipitated (Fig. 3). Shallow subtidal FPC formed while the TAZ was very thin, the zone of cementation was very shallow, and the carbonate-cemented layer formed close enough to the sediment-water interface to be prone to erosional reworking caused by storm currents and wave scour. Thin platy limestone clasts are frequently close packed, even imbricated, in event beds (Fig. 2A, B). Frequent reworking of the shallow, thin cemented layers is also a likely mechanism to explain the abundance of peloids in early Palaeozoic limestones (Coniglio & James 1985). With continued thickening of the TAZ through the Ordovician the depth at which carbonate precipitated increased, and the resulting cemented horizons were less frequently reworked by scouring. Thus FPC declined and, as a result of being less frequently exhumed, the originally nodular cemented layers became more continuous and thicker. Ordovician diversification and faunal expansion increased the skeletal contribution to remobilized carbonate in the TAZ (Pruss *et al.* 2010). When exposed by scour these cemented layers formed reworked nodules and hardgrounds on which hard substrate biotas expanded (Mid–Late Ordovician; Figs 2 and 3). In more offshore settings where sea-floor erosion was uncommon, the secondary carbonate accumulated to produce the nodular, diagenetic bedding represented by limestone–marl alternations.

A possibility arising from this model is that there might be an intermediate phase between FPC and hardgrounds seen with the abundance of reworked thicker cemented zones as what might be called ‘fat’ flat pebbles or hiatus nodules (Fig. 2C). This would explain the high occurrence of hardground intraclasts as exhumed nodules in the Middle Ordovician Kanosh Formation (Kenyon-Roberts, 1995; Palmer & Wilson 2004), although this could reflect other factors such as reworking due to more frequent storms. We do not have quantitative data on the relative thicknesses of the Kanosh intraclasts compared to FPC clasts or to later Ordovician hardgrounds but the Kanosh represents a similar depositional setting to those younger Ordovician successions (C. E. Brett, pers. comm. 2015). Of course hardground intraclasts are not restricted to the Early–Mid Ordovician but we draw attention to what might be an explanation for at least one example where reworked hardgrounds were common.

Significant thickening of the TAZ in carbonate settings through the Late Ordovician further deepened the cementation zone, reducing the likelihood of exhumation and leading to the decline in hardground abundance and more widespread development of diagenetic bedding (Figs 1, 3; Westphal 2006, fig. 2). Assuming that shallower seafloors were more susceptible to periodic reworking than deeper ones (Peters and Loss 2012), Wright & Cherns (2016*a*) hypothesized that diagenetic bedding would then have been preserved in shallower areas than previously. Limestone-marl alternations are typical facies of carbonate shelves in low to temperate palaeolatitudes, and their temporal distribution largely parallels that of hardgrounds (Westphal & Munnecke 2003*a*; Fig. 1C).

DISCUSSION

Our proposal is that the protracted increases in the depth and intensity of bioturbation in response to the evolution of burrowing infauna in the early Palaeozoic, together with increasing skeletal carbonate input from the GOBE, also affected early diagenesis of carbonates and sea floor substrates. Our diagenetic model (Fig. 3) explains the sequence of well documented changes through this interval in the nature of shallow sea floor carbonates and carbonate facies, which then impacted on ecological diversity. Thus a complex feedback system existed between evolving biodiversity and sediment substrates. For example, increased abundance and diversification of skeletal faunas is apparent from the Mid Ordovician replacement by skeletal carbonates of the microbial/oolitic carbonates of the Cambrian to early-mid Ordovician commonly associated with FPC (Kiessling *et al.* 2003; Liu

& Zhan 2009; Pruss *et al.* 2010; Liu *et al.* 2011), and may explain the thicker limestone layers of exhumed hiatus nodules ('fat' flat pebbles) and hardgrounds. This led to major changes in skeletal biodiversity as hard bottom epifaunas expanded on exhumed carbonate substrates. In turn, hardgrounds declined as deeper and more intense bioturbation further depressed the zone of early carbonate cementation. The model provides an explanation for the problematic temporal distribution in abundance of distinctive carbonate features such as FPC and hardgrounds. Changes in ecological diversity and bioturbation have been invoked also to explain the decline in abundance of other, younger carbonate facies such as the decline in peritidal carbonates after the earliest Cainozoic (Wright & Azeredo 2006).

Increased abundance and diversification of skeletal faunas, the expansion of hard bottom encrusting and boring biotas, and the evolution of reef ecosystems are all features of the GOBE (e.g. Webby 2002; Servais *et al.* 2010). Large increase in the biodiversity of Ordovician sclerobionts (e.g. bryozoans, pelmatozoans and edrioasteroids) was attributed by Taylor and Wilson (2003) to the increase of substrate availability provided by submarine carbonate hardgrounds (Fig 1B). Hard substrate communities evolved various strategies for excavating and/or attaching to the surface, and competitive overgrowths are evident already in Ordovician sclerobionts (Taylor 2016). Macroborings diversify in the mid-late Ordovician (Wilson & Palmer 2006). The preservation *in situ* of borings and skeletons of encrusting fossil organisms aid in recognition of fossil hardgrounds.

The original thin cemented carbonate layers that became FPC in the Cambrian–Early Ordovician formed at very shallow depths, so scouring may frequently have produced areas of hard sea floor. Yet encrusting organisms are relatively infrequently reported from FPC, notably low diversity Upper Cambrian assemblages with pelmatozoan holdfasts (Brett *et al.* 1983), and it is not until the Mid Ordovician that more diverse and common sclerobionts characterize hardground faunas (e.g. Brett 1988). Was the FPC pebble substrate too unstable for sclerobionts, perhaps reburial too rapid, or why were these earlier hard substrates not exploited more? The ‘fat’ flat pebbles of the Early-Mid Ordovician Kanosh hardgrounds are encrusted and lightly bored. Arguably, the mid-Ordovician adaptive radiation of sclerobionts thrived only once thicker and more stable hardground substrates, their cementation boosted through increased skeletal input, were exhumed on shallow sea floors.

Potential sampling biases have to be explored in consideration of peaks of abundance of FPC, hardgrounds and the sclerobiont spike in diversity. Abundance data have been corrected for stratigraphical bias in Fig. 1 through using normalized data. Another question is whether any sampling bias relates to the area of carbonate deposition during the Cambrian–Ordovician. The Ordovician was an interval when major continents lay in low latitudes and shallow carbonate seas were at a maximum for the Palaeozoic (Kiessling *et al.* 2003; Christ *et al.* 2015). Large present outcrop areas represent the low latitude palaeocontinents of Laurentia, Baltica, Siberia and South China (Fig. 4). The distribution of both FPC and hardgrounds in the Cambrian–Ordovician is concentrated in low to temperate latitudes (Fig. 4). The intervals from which the Ordovician hardgrounds are described are commonly mixed shale-carbonate successions representing offshore marine settings (Westphal & Munnecke 2003*a*). Wall *et al.* (2009) have suggested that the peak in generic diversity in the Ordovician (i.e. the GOBE) correlates with a period of high outcrop area and may represent a sampling bias. However, both the Ordovician and Silurian are characterised by broadly similar palaeogeography, high outcrop area and generic diversity, so that if comparable sampling bias were to apply to records of hardgrounds and FPC, then while this could account for the relative abundance of Ordovician hardground papers it is contrary to their decline in the Silurian. Neither does it explain the very dramatic disappearance of FPC during the early Ordovician.

One test for the diagenetic model (Fig. 3; Wright & Cherns 2016) is whether or not it explains other examples in the Phanerozoic for both hardgrounds and FPC. From Figure 1A it is clear that FPC occurrences are rare after the early Palaeozoic. Those in the Silurian and early Triassic correspond to post-extinction events, when suppression of bioturbation would have led to shallowing of the TAZ ('anachronistic facies'; e.g. Wignall & Twitchett 1999; Calner 2005). The late Devonian example is of early Famennian age (Kazmierczak & Goldring 1978). The Jurassic example from Portugal (Kullberg *et al.* 2001) represents an unusual tectonically triggered debris flow deposit. Cambrian–Ordovician FPC and Ordovician hardgrounds appear to have developed in similar environmental settings (Fig. 4), with hardgrounds replacing FPC temporally in the early Ordovician; their relative changes in abundance cannot be simply explained by either changes in outcrop area and sampling or the extent of depositional settings.

The Jurassic–Cretaceous and Ordovician represent the periods with the highest reported hardground occurrences and the most widespread global carbonate systems (Fig. 1A; Kiessling *et al.* 2003, Christ *et al.* 2015). All are periods of 'calcite' seas corresponding to abiotic precipitates and trends in skeletal mineralogy (Stanley & Hardie 1998). The controls on whether calcite and/or aragonite precipitate, however, are complex and recent experimental data indicate that aragonite precipitation continues alongside calcite during 'calcite seas' in warm-water environments (Balthasar and Cusack 2015). In the TAZ the contribution from direct precipitation and from co-existing aragonitic shells would surely have been adequate to account for diagenetic early cementation (Wheeley *et al.* 2008). Mesozoic peaks of hardground occurrence (Fig.1A) may in part reflect large outcrop areas of marine sediments (Smith & McGowan 2007), but there is also a difference in the settings in which these younger examples formed. As shown by Christ *et al.* (2015), Jurassic hardgrounds are predominantly from shoal-inner platform settings or are associated with deep water Ammonitico Rosso deposits, and Cretaceous examples are predominantly from shoal-inner platform settings or the relatively deep water Chalk. In contrast the Cambrian–Ordovician examples represent a variety of deposystems but especially from deeper ramp settings (Christ *et al.* 2015). Unlike Ordovician hardgrounds he described that formed by cementation in the sub-oxic zone, Kenyon-Roberts (1995) found the Middle Jurassic hardgrounds from southern Britain were polygenetic. Some were characterized by fibrous marine cements or displayed complex zoned ferroan and non-ferroan early cements that had marine geochemical signatures. Others represented vadose subaerial cements, while yet another type was characterized by peloidal-meniscate cements, possibly microbial in origin, and resembling those described by Hillgaertner *et al.* (2001) from subtidal Lower Cretaceous and Upper Jurassic platform carbonates (Swiss and French Jura Mountains).

Although we emphasize here the critical issue of the deepening of the TAZ to explain the changes in sea floor behaviour, other changes were taking place in the carbonate system during this interval and it is important to review these as well. Early Palaeozoic metazoan evolution increased nutrient-rich organic matter and oxygen levels, and notably the increase in bioturbation changed the nature of seafloor sediments (McIlroy & Logan 1999; Bottjer *et al.* 2000; Dornbos *et al.* 2005), affecting early diagenesis. In particular, the availability of aragonite from skeletal carbonate dissolution changed during this interval. To what extent does the limited degree of cementation reflected in thin cemented layers actually relate to a limited rate of supply of calcium carbonate from skeletal dissolution, rather than to the frequency of exhumation at shallow burial depths?

Taphonomic studies have highlighted the preferential early dissolution of skeletal aragonite in sufficient quantities to skew the fossil record significantly in early Palaeozoic shallow marine settings (‘missing molluscs’, e.g. Cherns & Wright 2000, 2009). Aragonitic molluscs are diverse in the early Cambrian radiation although their fossil record is relatively sparse through the Cambrian–Early Ordovician when calcitic organisms (e.g. archaeocyathans, trilobites, brachiopods) dominate the skeletal record (Porter 2007, 2010). The skeletal contribution to carbonate deposition remained limited until the Mid-Ordovician, when limestone shell beds also increased in thickness and abundance in shallow marine successions (Kidwell & Brenchley 1994; Li & Droser 1997, 1999; Pruss *et al.* 2010). While the majority of these were brachiopod-dominated, some were mollusc-rich, mostly reperesenting locally derived storm concentrations of gastropods (Li & Droser 1999; Harper 2006, fig. 9). Even at very low rates of production relative to those of molluscs in modern marine settings, molluscan aragonite could have sourced the carbonate in diagenetic limestone–marl bedding in the Middle Ordovician of Sweden (Wheeley *et al.* 2008). Thus the question arises as to whether thicker cemented zones in mid Ordovician hardgrounds and hiatus nodules are a consequence of more skeletal aragonite becoming available for dissolution in the TAZ?

Another possibility relating to progressive increase in the thickness of the TAZ is that, if the TAZ was thin during the earliest Palaeozoic, would the residence time of aragonitic shells passing through it as sediment accumulated have been relatively short compared with intervals when the TAZ was thicker (sedimentation rate and other variables being similar), potentially allowing some aragonite to pass into the sulphate reduction zone (and become cemented into diagenetic carbonates)? We raise this because some authors have noted the presence of former aragonitic bioclasts in Ordovician hardgrounds (e.g. Palmer *et al.* 1988). Kenyon-Roberts (1995, p258) noted that some Ordovician hardgrounds commonly contained former aragonite bioclasts which had been dissolved after rare initial cementation, although not completely in the TAZ. Ordovician intraformational conglomerates from the Kanosh Formation, Utah contain abundant mollusc (bivalve, cephalopod and gastropod) bioclasts (e.g. Palmer & Wilson, 2004, figs. 9, 10). Cherns *et al.* (2008) recorded similar examples from Ordovician limestones in Sweden.

Alternatively, would a thin TAZ necessarily have favoured better preservation of shells? Wright & Cherns (2016*a*) queried whether a thin TAZ in the earliest Palaeozoic could have had a greater degree of undersaturation with respect to aragonite, compared with later thicker TAZs. Following from the Late Proterozoic when the redox boundary was close to the sediment surface (Brasier *et al*. 2011), early Cambrian biotic diversification led for the first time to an actively reworked, aerobic mixed layer, and a thin TAZ in which a lowered pH, caused by oxidation of the products of microbial degradation processes, was concentrated in a relatively narrow zone and might have led to relatively intense carbonate dissolution. This raises the possibility that even the less soluble calcitic shells could have been removed, although there are many likely variables to consider including the effect of long residence times in the TAZ in areas of low sedimentation rates. For example, could the relative paucity of skeletal grains in sediment until the Mid Ordovician, in spite of calcareous skeletons having evolved much earlier (Porter 2007; Pruss *et al.* 2010), reflect essentially a taphonomic effect? The Middle Cambrian–Lower Ordovician Alum Shale of Scandinavia is a fossiliferous, unbioturbated black shale succession, high in organic carbon and sulphur, which exhibits better preservation of the calcareous, trilobite-dominated shelly fauna in facies representing lower oxygen concentrations (Schovsbo 2001). This effect has been recorded from many shale successions whereby shells of mainly nektonic and planktonic forms settled on the dysoxic sea floor which was below the redox boundary (Cherns *et al.* 2008; Jordan *et al.* 2015). In the Alum Shale, intervals representing relatively higher oxygen concentrations have poorly preserved non-calcareous fossils such as phosphatic brachiopods, phosphatic 'ostracodes' and graptolites (Schovsbo 2001). Trilobite-rich shell concentrations within diagenetic limestone nodules in the shales ('stinkstones'; Terfelt 2003) resemble concretion-hosted shell clusters (*sensu* Tsujita 1995); they are an example of a taphonomic window where rapid burial of shell material below the TAZ led to preferential preservation (Cherns *et al.* 2008). Calcitic shell material is effectively absent outside these nodules. Schovsbo (2001) suggested that absence of shells or only patchy preservation of clusters of autochthonous phosphatic brachiopod shells in the more oxygenated shale facies could indicate general removal of calcitic fossils in the Alum Shale by sulphide oxidation. Since this effect has not been widely identified as affecting calcitic fossils elsewhere in the Palaeozoic (Cherns & Wright 2009), might it indicate a higher degree of undersaturation in the thin TAZ of the Cambrian–Early Ordovician? A further consideration here is the very low accumulation rates for the Alum Shale (< 16 mm/kyr; Thickpenny 1984, table 1), leaving shells with a likely residence time in the TAZ of up to several thousand years, even for the thin bio-irrigated layers.

CONCLUSIONS

Complex feedback relationships developed during the early Palaeozoic between evolutionary and ecological diversification, early diagenesis and niche availability. These changes also impacted considerably on skeletal abundance and carbonate deposition. Increasing biotic diversity of Cambrian– Ordovician infauna led to greater depth and intensity of bioturbation and bio-irrigation which thickened the TAZ, lowering the zone of carbonate cementation within the sediment column. Deeper and thicker, essentially nodular diagenetic limestone layers became less susceptible to frequent reworking of the cemented zone by storms and other physical processes, leading to early Ordovician decline in the FPC that had been a striking feature of offshore, subtidal facies during the earliest Palaeozoic. Further deepening of the cemented layer, and remobilization of labile skeletal carbonate, resulted in less frequent reworking, higher rates of cementation and thicker cemented layers. These, when exhumed, formed hardground substrates, increasing niche availability for sclerobiont encrusters and borers; hard substrate faunas underwent major diversification in the GOBE. Subsequent lowering of the TAZ into the later Ordovician lowered the cementation zone further such that exhumation took place far less frequently and hardgrounds declined in abundance. Widespread limestone–marl alternations represent diagenetic successions with the deeper TAZ. It is unclear whether the thin TAZ during the Cambrian–Mid Ordovician was also associated with calcite undersaturation in the sediment column.

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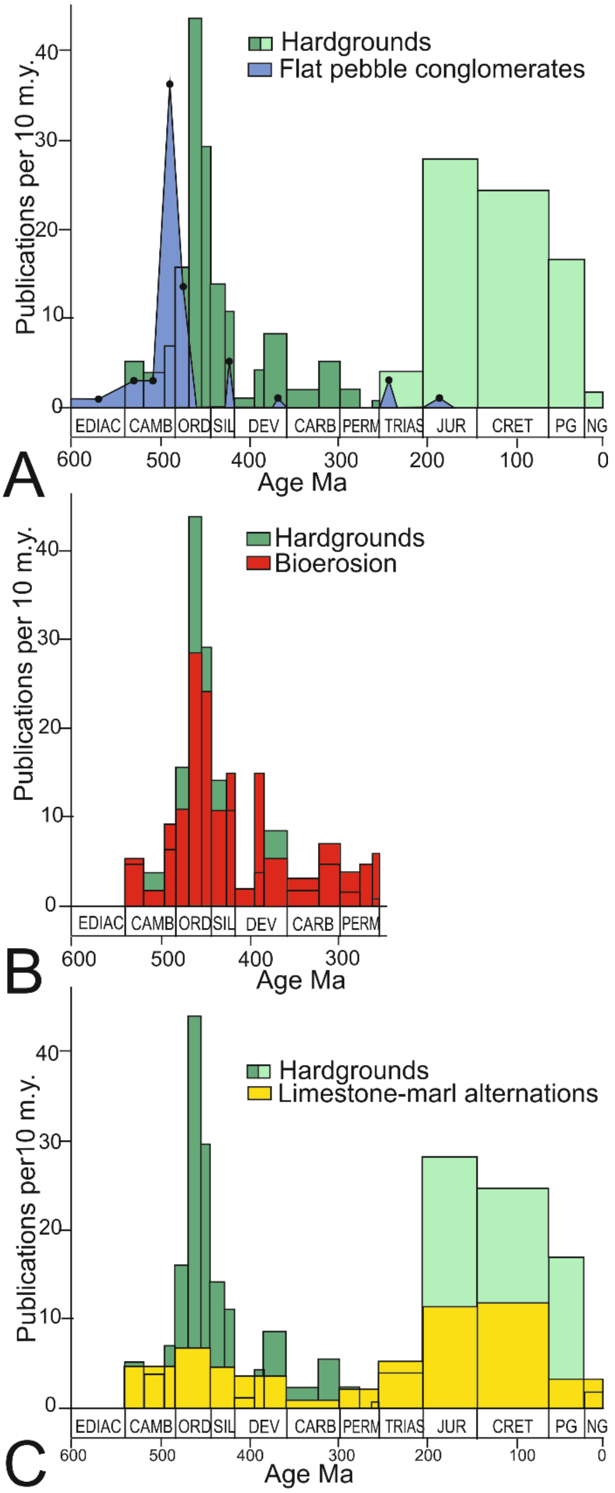

Figure 1. A, Abundance (publications as proxy by formation and normalized/10 m.y.) of subtidal flat pebble conglomerates (FPC; blue, points; data refined from Wright & Cherns (2016*b*), and submarine hardgrounds (green, histograms; based on Taylor 2008 and Wilson 2012, updated for Palaeozoic and plotted to subdivisions of periods (Lower/Middle/Upper or Lower/Upper; darker green; Cambrian data points for Lower, Middle and Upper series follow standard usage in literature, cf. ongoing stratigraphical revision into four series). Note the succession of dominance by FPC in the Late Cambrian–Early Ordovician before a steep decline, followed by hardground abundance in the Mid–Late Ordovician before a decline; hardgrounds reach their Phanerozoic peak of abundance in the Ordovician. B, The abundance (as for A) of hardgrounds and bioerosion (red) through the Palaeozoic (Wilson 2013). Note the close correlation between hardground abundance and bioerosion. C, Hardgrounds (as for A) plotted against limestone–marl alternations (LMA), data from Westphal & Munnecke (2003*b*). Note the parallel trends between these two carbonate facies, which formed in largely similar, low to temperate palaeolatitudes (Fig. 4).

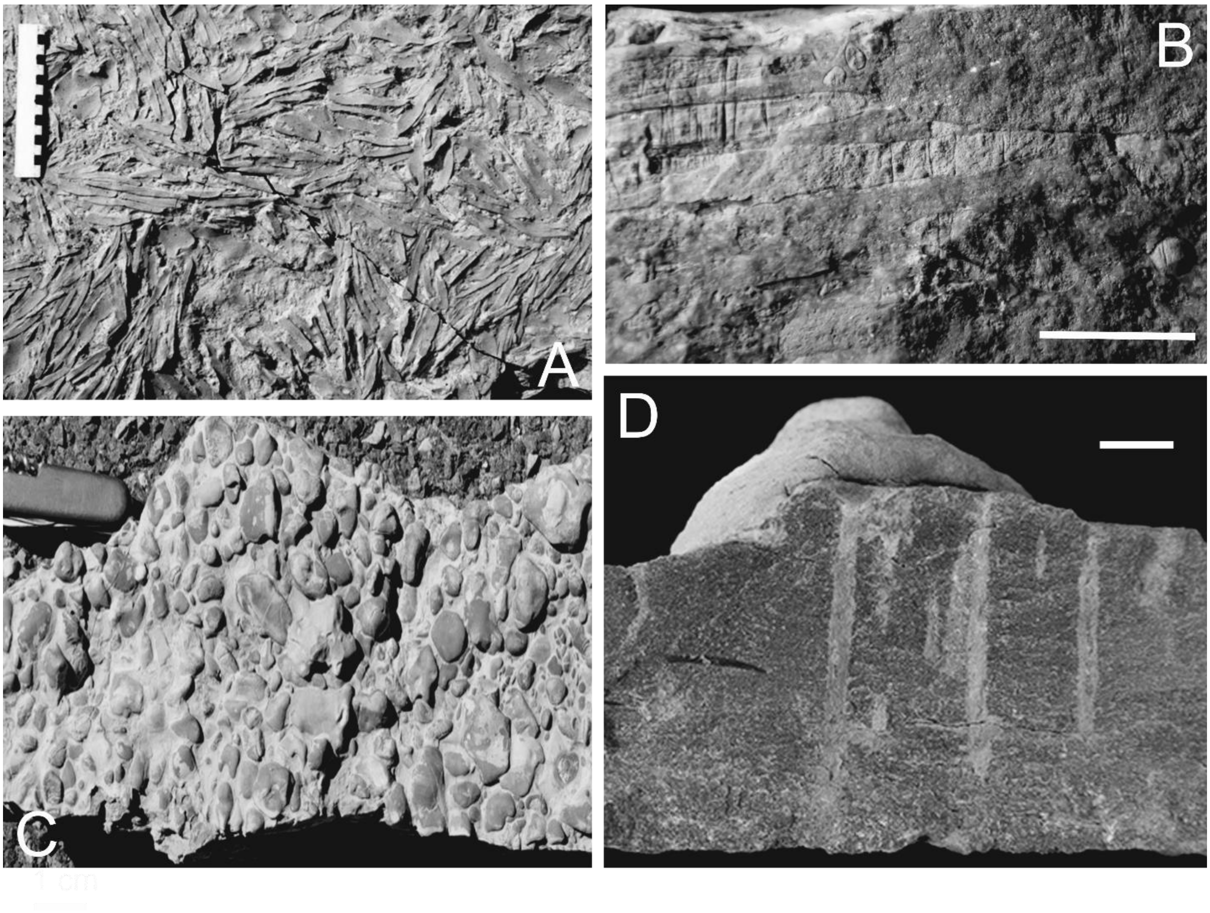

Figure 2. Field photos to illustrate Cambrian–Ordovician carbonate facies. A, Flat pebble conglomerates in plan view, Upper Cambrian, Port-au-Port Peninsula, Western Newfoundland (N..P. James);scale divisions 2cm, B, Flat pebble conglomerate in section, Upper Cambrian, Snowy Range Formation, Montana (M. A. Wilson). C, Hiatus nodules or ‘fat’ flat pebbles in plan view, Upper Cambrian, Pilgrim Formation, Wyoming (B. R. Pratt). D, Bryozoan encrusted hardground with vertical *Trypanites* borings, Upper Ordovician, Kentucky (M. A. Wilson). C and D, scale bars 1 cm.

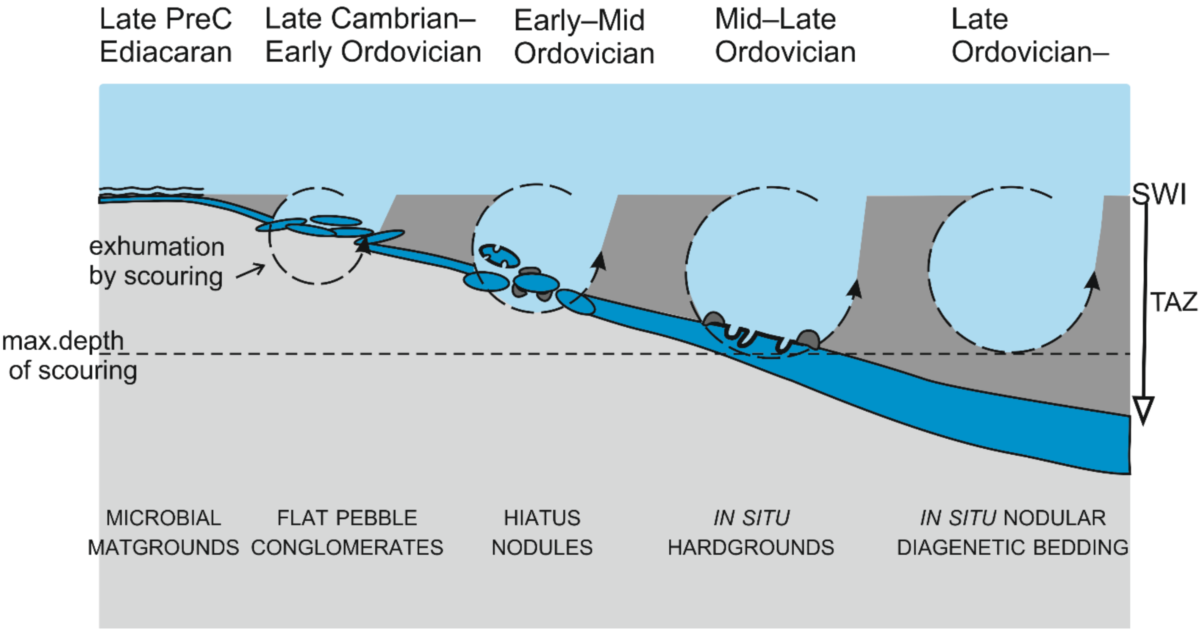

Figure 3. Diagenetic model to explain the Late Proterozoic–Late Ordovician changes in subtidal carbonate facies as a consequence of a deepening Taphonomically Active Zone (TAZ) and zone of early carbonate cementation in response to evolutionary increases in the depth and intensity of burrowing and skeletal biodiversification (model extended and amended from Wright & Cherns 2016*a*). In the Late Proterozoic (Ediacaran), widespread microbial mats and lack of bioturbation meant that the TAZ was effectively passive and the redox boundary lay close to the sea floor. Assuming the maximum depth of storm scouring remained unchanged, while the Cambrian TAZ with limited burrowing was very shallow, the thin carbonate layers were susceptible to exhumation even by minor storm disturbances, producing the flat pebble conglomerate (FPC) facies of Cambrian–Early Ordovician successions. These are replaced sequentially by the ‘fat’ thin pebbles of hiatus nodules, and then by more continuous nodular beds of submarine hardgrounds, on which hard bottom faunas of encrusting sclerobionts and macroborers diversified. Increasing skeletal carbonate input contributed to thicker carbonate layers, which were less frequently exhumed. Further deepening of the TAZ to below the depth of most storm scouring led to the decline of hardgrounds, replaced by the diagenetic successions of limestone–marl alternations (LMA) that are widespread in subtidal environments. SWI, sediment–water interface.

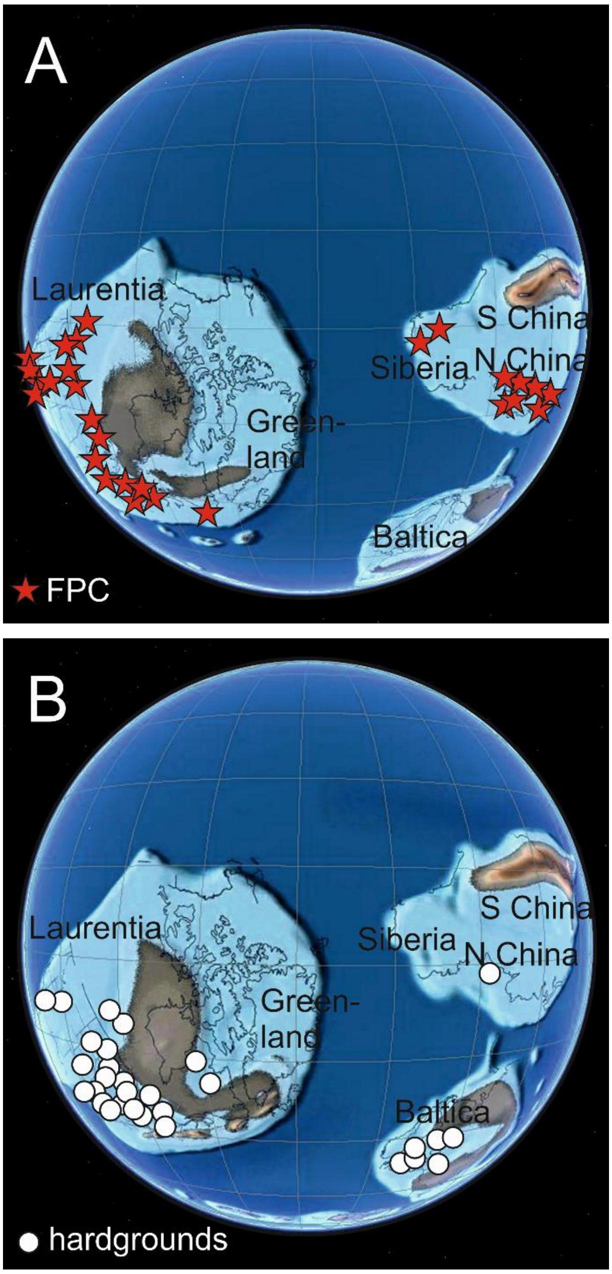

Figure 4. The palaeogeographical distribution of A, Cambrian–Ordovician flat pebble conglomerates (amended from Wright & Cherns 2016*a, b*), and B, Mid Ordovician submarine hardgrounds; data plotted onto Paleoglobe maps by C. R. Scotese, PALEOMAP Project, A, Early Ordovician and B, Mid Ordovician (Scotese & Dreher 2012).