Leaving no stone unturned: the feedback between increased biotic diversity and early
diagenesis during the Ordovician

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(Abstract)

Ordovician change in the nature of seafloor carbonates saw rapid decline of previously
widespread flat pebble conglomerates and the Palaeozoic peak abundance of hardgrounds.
The effective disappearance of flat pebble conglomerates, widely attributed to physical
disruption of substrate by bioturbation, is re-interpreted as reflecting increased depth of
carbonate precipitation below the Taphonomically Active Zone such that early lithified
carbonates were less frequently reworked by scour. With deeper, more stable zones of
cementation, exhumed limestones formed hardgrounds, whose mid Ordovician acme
supported rapid increase in epizoan diversity. Further deepening of cementation to below
normal scour accompanied post-Ordovician decline in submarine hardgrounds.

Supplementary material: database for Figure 1 is available at
http://www.geolsoc.org.uk/SUP---

The early Palaeozoic evolutionary and ecological development of benthic metazoans was
strongly affected by changes to the nature of the sea floor environment such as increased
burrowing activity (e.g. Cambrian Substrate Revolution, Bottjer et al. 2000) and widespread
development of shallow marine hard substrates (Great Ordovician Biodiversification Event
(GOBE); Harper 2006). How did those changes impact upon, and relate to, carbonate
systems and shallow sediment diagenesis? Here we consider two characteristic carbonate
facies of early Palaeozoic shelf seas: flat pebble conglomerates (FPC) and submarine
hardgrounds (carbonate cemented sea floors). Both peak in abundance before rapid decline,
the former most widespread in the late Cambrian–early Ordovician, while the latter reach
their Palaeozoic acme in the Mid-Late Ordovician (e.g. Taylor 2008, fig. 2).

Flat pebble conglomerates (locally breccias) with carbonate intraclasts (rudstones,
floatstones) are a striking feature of Late Proterozoic to early Ordovician shallow marine
carbonate successions. They were mostly deposited in subtidal, typically offshore settings
reflecting storm or tsunami reworking of shallow cemented limestone beds (Mount & Kidder
1993; Pratt 2002; Myrow et al. 2004; Pratt & Bordonaro 2007). The FPCs are variable in bed
geometry and thickness, matrix or clast supported texture, but typically have tabular, thin
(<20mm) pebble to cobble sized clasts of fine grainstone to calcimudstone (e.g. Myrow et al.
2004). This distinctive lithofacies effectively disappears from the stratigraphic record in
offshore settings after the Early Ordovician (Sepkoski 1982; Sepkoski et al. 1991; Liu &
Zhan 2009). The accepted view (e.g. Sepkoski et al. 1991) has been that with an Ordovician
increase in the extent and depth of burrowing (Droser & Bottjer 1989; Bottjer et al. 2000),
biotic mixing of the sediment would have prevented early cementation and the formation of
thin lithified zones, removing the source for FPCs after scouring by storms or tsunamis.

In the Ordovician, submarine hardgrounds become widely developed in shallow seas,
colonised by an expanding diversity of encrusting and boring epizoans (e.g. Brett &
Brookfield 1984) that form specialized new communities in the GOBE. They have been

The aim of this paper is to provide a single, geochemical explanation for both the decline of subtidal FPC lithofacies and the peak abundance of hardgrounds during the Ordovician.

**Sea floor diagenesis and changes in sea floor shallow geochemical profiles during the early Palaeozoic**

The diagenetic processes for mobilization of calcium carbonate during shallow burial have been appreciated for some time (e.g. Sanders 2003; Berkeley et al. 2008; Cherns et al. 2011). Calcium carbonate, especially the more soluble aragonite, is dissolved in the uppermost sediment layer largely as a result of acidity caused by the oxidation of H\textsubscript{2}S, and while most back-fluxes to the water column, some is re-precipitated as calcite in the sediment column in areas of increased alkalinity such as depths where sulfate reduction takes place (e.g. Sanders 2003, 2004; Fig. 1). This oxidized zone, effectively the Taphonomically Active Zone (TAZ), will be controlled by diffusion from the overlying water column, if oxygenated, and by mixing caused by bio-irrigation (mainly burrowing; e.g. Aller 1982; Aller & Aller 1998).

Organic matter accumulated more among finer grained sediment sources the microbially mediated decay processes that drive skeletal carbonate dissolution and re-precipitation (e.g. Walter & Burton 1990; Walter et al. 1993; Hendry 1993). The importance of such processes linked to the mobilization of labile carbonates in the very shallow sediment column forms 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; Munnecke & Westphal 2005).
Brasier et al. (2011) proposed that changes in the position, relative to the sea floor, of the depth of the redox boundary during the Ediacaran–early Cambrian affected the zones of early lithification in the shallow sediment column. Late Proterozoic precipitation of calcium carbonate took place at or very close (<1cm) to the sea floor (also Peters & Gaines 2012), and though the early Cambrian advent of metazoan burrowing and biomineralization depressed the zone of cementation it remained very shallow (early-mid Cambrian subtidal burrow depth <3 cm, typically mm scale: Tarhan et al. 2015; Droser & Bottjer 1988). The depth of subtidal bioturbation, and by inference the zone of cementation, remained <6 cm through to the mid Ordovician, before both bioturbation depth (<30 cm) and intensity increased significantly in the Late Ordovician (Droser & Bottjer 1989).

**Abundance of flat pebble conglomerates and hardgrounds**

Subtidal FPCs are most common in the late Cambrian–Early Ordovician, before rapid decline, and notably while the TAZ remained very shallow (Fig. 2). Their temporal record, using publications by formation as a proxy for abundance, provides a direct comparison with published data for submarine hardgrounds (Fig. 2; Taylor 2008). A peak FPC distributional map illustrates the extensive occurrence (with a latitudinal control), and suggests any bias from availability of rock formations is likely not significant (Fig. 3). In shallow carbonate epeiric seas of the North China Plate, the subsequent decline of FPCs corresponds to the decrease also in subtidal microbialites and increasing intensity of bioturbation as the shallow sea floor character changed in the late Early Ordovician (early Floian) (Liu 2009; Liu & Zhan 2009). Notably, in post-Ordovician times, minor occurrences of subtidal FPCs (Fig. 2) correspond to post-extinction events, when suppression of bioturbation would have led to shallowing of the TAZ (e.g. Wignall & Twitchett 1999; Calner 2005).
For submarine hardgrounds (carbonate cemented sea floors) the Palaeozoic peak of abundance is in the Ordovician (Taylor & Wilson 2003; Palmer & Wilson 2004; Harper 2006; Taylor 2008; Fig. 2). Early, encrusting hardground faunas are described from surfaces of cemented FPC in the late Cambrian (Brett et al. 1983). By the mid Ordovician hard substrate morphologies are variable, some largely comprising reworked, encrusted limestone nodules but others forming beds with complex hummocky and undercut surfaces; hardground biotas are notably more diverse (Brett & Liddell 1978; Brett & Brookfield 1984; Wilson et al. 1992). Taylor and Wilson (2003, p. 44) suggested that the “Ordovician was a golden age for epizoans on hard substrates” due in part to increased hard substrate availability. The appearance of encrusters makes hardgrounds more recognizable after the early Ordovician (Brett & Liddell 1978) and likely reflects the availability of more stable substrates as compared with the fragmented cemented layers characteristic earlier in the Palaeozoic.

Previously the abundance of hardgrounds had been explained by local calcite cementation sourced from carbonate released by sea-floor dissolution of aragonite in undersaturated (with respect to aragonite) Ordovician ‘calcite seas’ (Wilson et al. 1992; Taylor & Wilson 2003; Palmer & Wilson 2004; Harper 2006). Recent experimental data, however, indicate that aragonite precipitation continued alongside calcite during ‘calcite seas’ in warm water environments (Balthasar & Cusack 2015). In a study of Ordovician hardgrounds from eastern North America, Kenyon-Roberts (1995) found no direct evidence for sea floor dissolution, but did note petrographic evidence of hardground formation in shallow sub-oxic conditions below the TAZ. Cherns & Wright (2011), when comparing the taphonomy of skeletal lagerstätten between ‘aragonite’ and ‘calcite seas’, found no differences, suggesting that ‘calcite seas’ did not increase aragonitic shell dissolution.
As the depth and intensity of burrowing increased through the early Palaeozoic, the TAZ thickened and the depth at which secondary carbonate re-precipitated also deepened. This reduced the probability that lithified carbonate would be exhumed by erosional reworking caused by wave scour. The FPCs in shallow subtidal settings formed only while the TAZ was very thin, and hence the zone of cementation was close to the sediment-water interface allowing even relatively small and frequent scour events (storms or tsunamis) to exhume the cemented horizons (Late Precambrian–late Early Ordovician; Figs 2, 4). As the TAZ thickened and the depth of carbonate precipitation increased, these horizons were less likely to be reworked by scouring. The FPC facies was replaced in shallow subtidal settings by less frequently exhumed, and hence more developed and thicker, cemented horizons, which when eventually exposed by scour formed reworked concretions and hardgrounds on which hard substrate biotas expanded (Mid–Late Ordovician; Figs. 2, 4). Development of these carbonate horizons may have been facilitated by increased skeletal input through diversification and faunal expansion during this interval (Porter 2010). In more offshore settings rarely affected by wave-related erosion, the secondary carbonate could accumulate uninterrupted to produce the nodular, diagenetic bedding of limestone-marl alternations. As the TAZ deepened through the later Ordovician the cementation zone was displaced to deeper levels where reduced likelihood of exhumation led to decline in hardground abundance and more widespread development of diagenetic bedding (Late Ordovician; Fig. 3; Westphal 2006, fig. 2). An implication is that diagenetic bedding would have been preserved in shallower areas than previously, assuming that shallower sea floors were more susceptible to periodic reworking than deeper ones (Peters & Loss 2012). This hypothesis is testable if it can be demonstrated that diagenetic bedding is found in shallower settings by the Late Ordovician.
This model proposes that a single trend, namely the deepening of the zone of cementation below the TAZ, can explain the rapid decline of FPCs, and the peak abundance of hardgrounds during the Ordovician, before their subsequent decline. That progressive change was ultimately a consequence of the previously documented increased depth and intensity of bio-irrigation. Rather than destroying the potential for rapid shallow cementation (Sepkoski 1982; Sepkoski et al. 1991), lowering of the TAZ decreased the likelihood of erosional exhumation of thin cemented carbonate layers by wave scour.

Many variables affected early diagenesis during the early Palaeozoic, including increased nutrient-rich organic matter and oxygen levels in sea floor sediments as a result of metazoan evolution (McIlroy & Logan 1999; Bottjer et al. 2000, Dornbos et al. 2005). The amount of labile aragonite from skeletal carbonate dissolution also likely increased with biomineralization, although the skeletal contribution to carbonate deposition remained limited up to mid Ordovician times (e.g. Pruss et al. 2010, fig. 8). Could the thinness of limestone beds ripped up to form FPCs from latest Proterozoic to Early Ordovician be explained by lower flux of carbonate from skeletal dissolution before the GOBE rather than reflecting frequency of exhumation at shallow burial depths? Although the intensity of bio-irrigation increased markedly in the Early Cambrian, bioturbation depth (<6 cm) remained shallow through to the Late Ordovician, when both depth (<30 cm) and average ichnofabric index increased substantially (Droser & Bottjer 1989; Tarhan et al. 2015). If changes in the biogeochemical environment of the upper sediment layers were a consequence of that deeper and more intense bio-irrigation, accompanied by increased oxygenation of the seas and oversaturation (Pruss et al. 2010) that affected diagenetic carbonate precipitation, what other effects took place in terms of carbonate behaviour? The biogenically reworked mixed layer increased only slowly, from 0.2 cm in the early-mid Cambrian to 1.5 cm in the Ordovian-
Silurian (Tarhan et al. 2015). Could the presence of a thin TAZ potentially result in higher levels of acidity through sulfide oxidation and a greater degree of undersaturation with respect to aragonite, compared with today’s thicker TAZ?

Organisms with more labile, aragonitic shells (primarily molluscs) are diverse in the early Cambrian radiation although their fossils are relatively sparse in the trilobite dominated Cambrian–Lower Ordovician skeletal record (Porter 2007; Porter et al. 2010). From the mid Ordovician, skeletal material was a major contributor to carbonate sediment; limestone shell beds, most commonly brachiopod-rich, increase in proportion, thickness and abundance in shallow marine settings (Kidwell and Brenchley 1994; Li & Droser 1997, 1999; Pruss et al. 2010). Molluscs are dominant in some storm beds, most commonly representing local reworking of concentrations of dead gastropod shells accumulated in the upper sediment layers (Li & Droser 1999; Harper 2006, fig. 9). Did a thicker TAZ later in the Ordovician result in less intense sulfide oxidation, less dissolution and a longer survival time of aragonite shells in the TAZ?

The Palaeozoic decrease in abundance of hardgrounds after the Ordovician (Fig. 2) is here interpreted as reflecting the lowering of the TAZ and cementation zone to depths in the sediment column affected less frequently by wave (storm or tsunami) reworking. It might also imply that such reworking later rarely affected sediments much below the TAZ at 30cm. Mesozoic peaks of hardground occurrence (Fig. 2) may in part reflect large outcrop areas of marine sediments (Smith and McGowan 2007), such as the Cretaceous Chalk. The extensive hardgrounds of the middle Jurassic are hosted predominantly in very shallow, oolitic facies and are of much more diverse origins than those of the Ordovician (Kenyon-Roberts 1995).

Conclusions
The decline of flat pebble conglomerates and the peak abundance of submarine hardgrounds in the Ordovician are interpreted as reflecting the progressive deepening of the zone of carbonate precipitation below the TAZ, resulting in less frequent reworking of the upper part of the sediment column by scour. The deepening was a consequence of increased depth and intensity of bioturbation and bio-irrigation. This shift also created a range of more lithified substrates in subtidal settings, promoting a rapid expansion in epizoan diversity. Thus, changes in bioturbation affected carbonate diagenesis and the composition of the sea floor carbonates, and provided new niches for invertebrates.

Acknowledgments

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Figure Captions

Figure 1. Shallow burial diagenetic environment and calcium carbonate precipitation. A, labile aragonite shells (molluscs), more susceptible to early dissolution in the oxic upper sediment layers of the Taphonomically Active Zone (TAZ), release carbonate and leave moulds that are readily destroyed through bioturbation. B, calcitic shells more likely to survive early dissolution, and more rarely steinkerns of aragonitic shells; diffused carbonate precipitates in a zone of cementation in the sulfate reduction zone.

Figure 2. Abundance (using publications by formation as proxy) of subtidal flat pebble conglomerates (pale, points; supplemental information available online at www.geolsoc.org.uk/SUP0xxxx) and submarine hardgrounds (dark, histogram; based on Taylor 2008 and http://markwilson.voices.wooster.edu/bioerosion-bibliography/). Note: revision of Cambrian stratigraphy into four series is ongoing; divisions into Lower, Middle and Upper series follow standard usage in literature.

Figure 3. Palaeogeographic reconstruction for 485 Ma (Bugplates IGCP503; T.H. Torsvik 2009) showing late Cambrian–early Ordovician extent of flat pebble conglomerate facies (black stars).

Figure 4. Diagenetic model for carbonate precipitation in subtidal Palaeozoic settings, showing early Cambrian through Ordovician changes in the depth of the Taphonomically Active Zone (TAZ) and zone of cementation, susceptibility of lithified limestone layers to scouring, and distribution of flat pebble conglomerates, submarine hardgrounds and the diagenetic nodular bedding of limestone-marl alternations. SWI sediment-water interface.
Figure 1.

A

Calcitic epifauna
Aragonitic epifauna
Diffusion of carbonate
Delicate moulds destroyed by bioturbation in TAZ
(locally preserved in hardgrounds)

B

OXIC
H₂SO₄
sulfide oxidation
H₂S
sulfate reduction
ANOXIC
Calcitic shells and shell layers
Zone of cementation
Rare steinkerns of aragonitic shells

Figure 2.

![Graph showing publications over time with categories Hardgrounds and Flat pebble conglomerates.](image)

- Hardgrounds
- Flat pebble conglomerates

Age Ma

- 600
- 500
- 400
- 300
- 200
- 100
- 0

Publications

- EDIAC
- CAMB
- ORD
- SIL
- DEV
- CARB
- PERMTRIAS
- JUR
- CRET
- PG
- NG
Figure 3.

485 Ma

Laurentia

Greenland

Siberia

S China

N China

Baltica

Figure 4.

Late Precambrian–Early Ordovician | Mid–Late Ordovician | Late Ordovician...

exhumation by scouring

max. depth of scouring

SWI

FLAT PEBBLES

HIATUS CONCRETIONS

HARDGROUNDS

THICKENING AND DEEPENING OF CARBONATE LAYER
- longer residence time
- exhumation less likely

TAZ and carbonate precipitation zone

IN SITU NODULAR DIAGENETIC BEDDING
**Flat pebble conglomerates from subtidal settings (Fig. 2)**

<table>
<thead>
<tr>
<th>AGE</th>
<th>LOCATION</th>
<th>FORMATION</th>
<th>SHELF SETTING</th>
<th>PROPOSED PROCESS</th>
<th>AUTHOR(S)</th>
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<tbody>
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<td>Mesoproterozoic</td>
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<td>Subtidal within storm wave base</td>
<td>storms</td>
<td>Luo <em>et al.</em> 2014</td>
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<td>mid to outer ramp</td>
<td>storms</td>
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<td>Vendian</td>
<td>Gourma, West Africa</td>
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<td>slope</td>
<td>bottom currents'</td>
<td>Bertrand-Sarfati &amp; Moussine-Pouchkine 1983</td>
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<td>Swartpunt Fm</td>
<td>Low energy deeper ramp</td>
<td>storm</td>
<td>Narbonne <em>et al.</em> 1997</td>
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<td>ramp</td>
<td></td>
<td>Dewing &amp; Nowlan 2012</td>
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<td>Jubilee Fm</td>
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<td>subtidal shelf</td>
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