Sedimentary context and palaeoecology of *Gigantoproductus* shell beds in the Mississippian Eyam Limestone Formation, Derbyshire carbonate platform, central England

L. S. P. Nolan1*, L. Angiolini2, F. Jadoul2, S. J. Davies1, V. J. Banks3, M. H. Stephenson3 & M. J. Leng4,5

1 Department of Geology, University of Leicester, University Road, Leicester, LE1 7RH, UK
2 Università degli Studi di Milano, Dipartimento di Scienze della Terra ‘A. Desio’, via Mangiagalli 34, Milano, 20133, Italy
3 British Geological Survey, Keyworth, Nottingham, NG12 5GG, UK
4 NERC Isotope Geosciences Facilities, British Geological Survey, Keyworth, Nottingham NG12 5GG, UK
5 Centre for Environmental Geochemistry, School of Geography, University of Nottingham, Nottingham NG7 2RD, UK

*Correspondence: ln82@le.ac.uk

Abstract: A sedimentological study was conducted at two localities exposing the Mississippian Eyam Limestone Formation of the Derbyshire carbonate platform, UK. Ricklow Quarry comprises seven facies with diverse skeletal assemblages, representing deposition on the inner to middle ramp within open marine waters. Once-a-Week Quarry comprises four facies, dominated by crinoidal debris representing deposition on the inner ramp. Both localities expose *Gigantoproductus* shell beds. Palaeoecological analysis of a single shell bed from each locality enabled investigation of the rapid colonization and success of this taxon on the platform. At Ricklow Quarry, on the eastern side of a localized mud mound, both life (>72% of thin and thick-shelled brachiopods in life position) and neighbourhood assemblages are present. A low-moderate diversity community (<1.37 and <0.8 Shannon diversity index) rapidly established over relict Brigantian mud mounds. Shell beds are preluded by intervals of decreased energy that allowed larvae to settle. Once established, the dominance of thick-shelled individuals enabled baffling, potentially providing localized shelter for larvae and nearby individuals. At Once-a-Week Quarry, where no mud mound is present, only thick-shelled *Gigantoproductus* species and a low diversity community (<1.07 Shannon diversity index) exclusively comprising neighbouring assemblages (37% in life position) is present. The presence of inactive mud mounds at Ricklow Quarry appears to have been the key to the success of *Gigantoproductus* species enabling the onset of stable communities in the shelter provided by the relict mound. Once the first palaeocommunities were established, larvae dispersed and colonized higher energy settings, such as at Once-a-Week Quarry.

Received 10 February 2017; revised 12 April 2017; accepted 28 April 2017

During the Mississippian, gigantoproductid brachiopods appeared within the geological record, diversified and subsequently declined (Qiao & Shen 2015). Evaluating their palaeoenvironmental setting and palaeoecology assists in elucidating the success of the genus and the relationship of these brachiopods with local environments. The Mississippian Eyam Limestone Formation of the Derbyshire carbonate platform, central England, UK (Fig. 1), has been described by Aitkenhead & Chisholm (1982); Aitkenhead et al. (1985), and Gutteridge (1983, 1987, 1991, 1995, 2003). These authors commented on the association of *Gigantoproductus* species with mud mound deposits. Brachiopods are found in high abundance at specific intervals within the Asbian-Brigantian Monsal Dale and Eyam Limestone formations (Aitkenhead et al. 1985). Nevertheless, little detailed work has been published on the palaeoecological significance of the gigantoproductid shell beds of the Derbyshire carbonate platform, and the link between their abundance and depositional environment.

The genus *Gigantoproductus* contains the largest brachiopod specimens ever recorded (Muir-Wood & Cooper 1960) and these most commonly occur in shell beds or lenses (Ferguson 1978; Angiolini et al. 2012; Yao et al. 2016). *Gigantoproductus* is distinguished by its large size, shallow corpus cavity, irregular ribbing and fluting, and the occurrence of dorsal brachial cones (Pattison 1981; Brunton et al. 2000). The morphology of the genus is seen to vary with population density and substrate (Ferguson 1978). Four morphological sub-groups were identified by Pattison (1981), primarily based on shell curvature, ribbing and fluting, and ventral valve shell substance thickness, which, alongside other characteristics, are used as distinguishing features. Because *Gigantoproductus* were large, they presumably required a constant supply of oxygen and food, suggesting they would have thrived in shallow and agitated waters of normal salinity marine environments (Ferguson 1978). Graham et al. (1995) suggested that the large size of *Gigantoproductus* may be attributed to higher levels of atmospheric oxygen during the Carboniferous and their diversification has been linked to a warming climate in the late Visean (Brezinski & Kollar 2012).

The Derbyshire carbonate platform formed on the eastern margin of the Laurasian landmass, 4° south of the equator (Scottese & McKerrow 1990). *Gigantoproductus* species first appeared in the middle Visean, and reached their peak diversity and abundance in the late Visean (Fig. 2) when they were distributed along shallow shelf environments around the Palaeotethys Ocean by the warm circum-Palaeotethys
currents (Qiao & Shen 2015). These brachiopods are also preserved in rocks from Eurasia and Nova Scotia (Qiao & Shen 2015), as well as in Serbia and Kazakhstan, that would have been located to the north of Palaeotethys (Ruban 2015). Changes in the abundance of Gigantoproductus appear to have coincided with the palaeoclimatic shift from greenhouse to icehouse conditions in the Late Mississippian (Qiao & Shen 2015). The extinction of the genus Gigantoproductus in the late Serpukhovian (Fig. 2) may be linked to the cooling of tropical oceans and expansion of the Gondwana glaciation.

Whilst Gigantoproductus species in the Eyam Limestone Formation are noted as commonly associated with localized mud mounds (Aitkenhead & Chisholm 1982; Gutteridge 1983), the significance of this association and exact location of Gigantoproductus relative to the mounds is not clear. We explored the relationship between the inactive mud mounds, which effectively generated a relict topography and influenced deposition, and the nearby, overlying shell beds and lenses at two key localities on the Derbyshire carbonate platform which are comparable in age, but have different geological settings relative to the mounds. Using field observations and thin section analysis, the sedimentary evolution of the Eyam Limestone Formation was investigated. This sedimentological analysis is combined with a palaeoecological study of the beds dominated by species of the genus Gigantoproductus that enables a better understanding of their strategy of rapid colonization and the success of this genus on the Derbyshire carbonate platform.

Stratigraphy and lithofacies

Sedimentation across the Derbyshire carbonate platform began in the late Tournaisian as sea level rose and a marine transgression flooded the Lower Palaeozoic basement (Aitkenhead & Chisholm 1982). The platform formed around a basement high that comprised three half-grabens (Smith et al. 1985). It is divided into two provinces (Fig. 1D): (1) the on-shelf province was characterized by shallow water deposition; and (2) the off-shelf province represented a deeper water setting (Aitkenhead et al. 1985). The Peak Limestone Group of the Derbyshire carbonate platform (on-shelf province) consists mainly of marine carbonate facies interbedded with marine shales and minor volcanic deposits (Aitkenhead et al. 1985). The oldest formation in the Peak Limestone Group, the Woo Dale Limestone Formation, was deposited during the Chadian to Holkerian (Schofield & Adams 1985). Dolostones and limestones at the base of the formation pass upward into coarse-grained limestone with planar cross-bedding and lenticular-irregular bedforms (Aitkenhead et al. 1985; Schofield & Adams 1985, 1986). These on-shelf limestones are overlain by
Gigantoproductus shell beds, Mississippian Eyam Limestone Formation, Derbyshire carbonate platform

The Eyam Limestone Formation comprises thinly bedded, cherty, bioclastic limestone with fossiliferous beds of brachiopods, corals and crinoids, a few dark mudstone intercalations and localized mud mounds along with their associated facies. In the centre of the platform (around Monyash; Fig. 1B) the formation was deposited on an easterly dipping intraplatform carbonate ramp that passed laterally into the Stanton intraplatform basin (Fig. 1B) and which probably formed due to the localized subsidence of the basement (Gutteridge 1987). To the south of the carbonate platform massive carbonate mud mounds (described below) overlay these beds, whereas in the central and northern parts they occur at the base of the formation (Aitkenhead & Chisholm 1982). Mud mounds with evidence of a significant period of subaerial exposure prior to deposition of the overlying beds (Aitkenhead et al. 1985; Gutteridge 1991) led Gutteridge (1995) to propose a revision of the boundary between the Monsal Dale Limestone and the Eyam Limestone formations. This revised boundary has not been formally adopted; however, evidence indicating subaerial exposure of mound facies was observed at one of the study sites in this current study and was used as the formation boundary herein. The fossiliferous beds, rich in gigantoproductid brachiopods, were identified by Gutteridge (1983) as the fossil packstone sub-facies of an irregularly bedded bioclastic facies.

The mounds present within both the Monsal Dale and Eyam Limestone formations are the Type 3 build-ups (crinoid-brachiopod-fenestrate bryozoan) described by Bridges et al. (1995). They are, therefore, not Waulsortian type mounds which were described in Dove Dale at the platform edge by Bridges & Chapman (1988). The mud mound facies occur in the on-shelf settings of the Derbyshire carbonate platform within the shelf interior, at the platform margins and in the shallow to middle section of the intraplatform ramp (Gutteridge 1995). Three facies related to the mud mounds were recognized by Gutteridge (1995): bryozoan wackestone/mudstone (mound core facies); bioclast intraclast wackestone/packstone (mound-flank facies); and crinoidal grainstone (intermound facies). The mound cores are crossed by fractures that show evidence of formation at different stages of lithification and indicate that surface microbial binding probably stabilized the mud mound. The mounds pass laterally and vertically into inter-mound facies dominated by crinoid fragments derived from crinoid ‘thickets’ around the mounds. The mud mounds in the study area developed on the shallow part of the intraplatform ramp (Gutteridge 1995) and their geometry was controlled by water depth. Towards the east, and into deeper water, the mud mounds increase in thickness but become more laterally restricted. The present-day dip of exposed bedding reflects that of the original flank slopes of the mud mound at progressive growth stages. Concentrations of brachiopods hosted in scour features occur on the sides of the mud mounds (Gutteridge 1990), but these are distinct from the brachiopod shell beds discussed within this paper, which are observed onlapping or overlying the mounds. It is most likely that the relationship of the whole-fossil packstone beds with the mud mounds resulted from the local palaeogeography with the mound topography enabling shallow lagoons to form around distances and are interpreted as the transition from shallow to deeper water deposition (Aitkenhead et al. 1985).

Shelf limestones of the Asbian and Brigantian sub-stages are characterized as regressive cyclic sequences (Bridges 1982; Walkden 1987). Characteristically, the Bee Low Limestone Formation comprises thickly-bedded, fine- to medium-grained calcarenites. Scattered crinoid debris are common, with other biota, including corals, brachiopods, foraminifers and ostracods, also present (Aitkenhead et al. 1985). The overlying Monsal Dale Limestone Formation comprises two main facies: (1) upper, heavily bioturbated, thickly-bedded packstone to wackestone; and (2) skeletal grainstone (Cox et al. 1977). Fossiliferous beds are common (Aitkenhead et al. 1985), as are localized carbonate mud mounds (Gutteridge 1995). The formation is laterally variable, with common surfaces preserving features that indicate subaerial exposure, which pass laterally into thinly bedded, finer grained limestones without subaerially exposed surfaces. These lateral changes occur over short distances and are interpreted as the transition from shallow to deeper water deposition (Aitkenhead et al. 1985).

The Eyam Limestone Formation comprises thinly bedded, cherty, bioclastic limestone with fossiliferous beds of brachiopods, corals and crinoids, a few dark mudstone intercalations and localized mud mounds along with their associated facies. In the centre of the platform (around Monyash; Fig. 1B) the formation was deposited on an easterly dipping intraplatform carbonate ramp that passed laterally into the Stanton intraplatform basin (Fig. 1B) and which probably formed due to the localized subsidence of the basement (Gutteridge 1987). To the south of the carbonate platform massive carbonate mud mounds (described below) overlay these beds, whereas in the central and northern parts they occur at the base of the formation (Aitkenhead & Chisholm 1982). Mud mounds with evidence of a significant period of subaerial exposure prior to deposition of the overlying beds (Aitkenhead et al. 1985; Gutteridge 1991) led Gutteridge (1995) to propose a revision of the boundary between the Monsal Dale Limestone and the Eyam Limestone formations. This revised boundary has not been formally adopted; however, evidence indicating subaerial exposure of mound facies was observed at one of the study sites in this current study and was used as the formation boundary herein. The fossiliferous beds, rich in gigantoproductid brachiopods, were identified by Gutteridge (1983) as the fossil packstone sub-facies of an irregularly bedded bioclastic facies.

The mounds present within both the Monsal Dale and Eyam Limestone formations are the Type 3 build-ups (crinoid-brachiopod-fenestrate bryozoan) described by Bridges et al. (1995). They are, therefore, not Waulsortian type mounds which were described in Dove Dale at the platform edge by Bridges & Chapman (1988). The mud mound facies occur in the on-shelf settings of the Derbyshire carbonate platform within the shelf interior, at the platform margins and in the shallow to middle section of the intraplatform ramp (Gutteridge 1995). Three facies related to the mud mounds were recognized by Gutteridge (1995): bryozoan wackestone/mudstone (mound core facies); bioclast intraclast wackestone/packstone (mound-flank facies); and crinoidal grainstone (intermound facies). The mound cores are crossed by fractures that show evidence of formation at different stages of lithification and indicate that surface microbial binding probably stabilized the mud mound. The mounds pass laterally and vertically into inter-mound facies dominated by crinoid fragments derived from crinoid ‘thickets’ around the mounds. The mud mounds in the study area developed on the shallow part of the intraplatform ramp (Gutteridge 1995) and their geometry was controlled by water depth. Towards the east, and into deeper water, the mud mounds increase in thickness but become more laterally restricted. The present-day dip of exposed bedding reflects that of the original flank slopes of the mud mound at progressive growth stages. Concentrations of brachiopods hosted in scour features occur on the sides of the mud mounds (Gutteridge 1990), but these are distinct from the brachiopod shell beds discussed within this paper, which are observed onlapping or overlying the mounds. It is most likely that the relationship of the whole-fossil packstone beds with the mud mounds resulted from the local palaeogeography with the mound topography enabling shallow lagoons to form around distances and are interpreted as the transition from shallow to deeper water deposition (Aitkenhead et al. 1985).

The Eyam Limestone Formation comprises thinly bedded, cherty, bioclastic limestone with fossiliferous beds of brachiopods, corals and crinoids, a few dark mudstone intercalations and localized mud mounds along with their associated facies. In the centre of the platform (around Monyash; Fig. 1B) the formation was deposited on an easterly dipping intraplatform carbonate ramp that passed laterally into the Stanton intraplatform basin (Fig. 1B) and which probably formed due to the localized subsidence of the basement (Gutteridge 1987). To the south of the carbonate platform massive carbonate mud mounds (described below) overlay these beds, whereas in the central and northern parts they occur at the base of the formation (Aitkenhead & Chisholm 1982). Mud mounds with evidence of a significant period of subaerial exposure prior to deposition of the overlying beds (Aitkenhead et al. 1985; Gutteridge 1991) led Gutteridge (1995) to propose a revision of the boundary between the Monsal Dale Limestone and the Eyam Limestone formations. This revised boundary has not been formally adopted; however, evidence indicating subaerial exposure of mound facies was observed at one of the study sites in this current study and was used as the formation boundary herein. The fossiliferous beds, rich in gigantoproductid brachiopods, were identified by Gutteridge (1983) as the fossil packstone sub-facies of an irregularly bedded bioclastic facies.

The mounds present within both the Monsal Dale and Eyam Limestone formations are the Type 3 build-ups (crinoid-brachiopod-fenestrate bryozoan) described by Bridges et al. (1995). They are, therefore, not Waulsortian type mounds which were described in Dove Dale at the platform edge by Bridges & Chapman (1988). The mud mound facies occur in the on-shelf settings of the Derbyshire carbonate platform within the shelf interior, at the platform margins and in the shallow to middle section of the intraplatform ramp (Gutteridge 1995). Three facies related to the mud mounds were recognized by Gutteridge (1995): bryozoan wackestone/mudstone (mound core facies); bioclast intraclast wackestone/packstone (mound-flank facies); and crinoidal grainstone (intermound facies). The mound cores are crossed by fractures that show evidence of formation at different stages of lithification and indicate that surface microbial binding probably stabilized the mud mound. The mounds pass laterally and vertically into inter-mound facies dominated by crinoid fragments derived from crinoid ‘thickets’ around the mounds. The mud mounds in the study area developed on the shallow part of the intraplatform ramp (Gutteridge 1995) and their geometry was controlled by water depth. Towards the east, and into deeper water, the mud mounds increase in thickness but become more laterally restricted. The present-day dip of exposed bedding reflects that of the original flank slopes of the mud mound at progressive growth stages. Concentrations of brachiopods hosted in scour features occur on the sides of the mud mounds (Gutteridge 1990), but these are distinct from the brachiopod shell beds discussed within this paper, which are observed onlapping or overlying the mounds. It is most likely that the relationship of the whole-fossil packstone beds with the mud mounds resulted from the local palaeogeography with the mound topography enabling shallow lagoons to form around
the mound as sea level continued to rise after the period of subaerial exposure (Gutteridge 1983). The Eyam Limestone Formation is the uppermost carbonate formation of the Peak Limestone Group and is overlain by the Longstone Mudstone Formation indicating a switch to deeper water deposition (Aitkenhead et al. 1985). The platform was eventually buried by southerly prograding fluvi-deltaic systems that were deposited as water depths subsequently shallowed during the Serpukhovian and Bashkirian (Guion & Fielding 1988).

Study sites

Two sites, Ricklow Quarry and Once-a-Week Quarry, were selected for detailed study (Fig. 1). Ricklow Quarry (Fig. 3) (53.192210N, 1.754669W) is approximately 1.5 km ESE from the village of Monyash, on the northern side of Lathkill Dale. Once-a-Week Quarry (Fig. 4) (53.209364N, 1.765823W) is 1.75 km NNE of Monyash. Ricklow Quarry is disused, but was quarried for building and decorative stone used in the local area. Limestone from Once-a-Week Quarry is used for the same purposes and the site is currently undergoing a new phase of excavation.

Both localities expose sections of the Eyam Limestone Formation. Ricklow Quarry exposes the base of the formation and its contact with the underlying Monsal Dale Limestone Formation (Fig. 5). At Ricklow Quarry two shell beds are exposed. The first bed is located at the top of a large exposed section, has a minimum thickness of 2.2 m and is the subject of this study. A second bed, 1.3 m thick and containing common Gigantoproductus, lies stratigraphically c. 8 m higher and on the opposite side (SW) of Lathkill Dale, c. 80 m to the west. This bed, however, is poorly exposed and, because a detailed study was not possible, it is not discussed within this paper. At Once-a-Week Quarry, a 1 m-thick shell bed is exposed at the top of the section and a second, less prominent, 20 cm-thick shell bed also occurs c. 6.4 m from the base of the quarry (Fig. 6). A third bed is visible on the quarry floor, but as only a bedding plane view; there is a small exposure in the centre of the quarry.

Methodology

Facies

Sedimentary logs were used as a sampling framework at both study sites. Macroscale field observations made at outcrop were supplemented by petrographic analysis and facies descriptions of thin sections from these samples. The Ricklow Quarry logged section was measured from the base of the exposure on the far west side of the northern wall of the quarry and progressed laterally 18 m east, with a total thickness of 9.5 m measured. Forty-three samples were taken through the logged section and thirty-nine thin sections were made. At Once-a-Week Quarry, a 10 m-thick section was measured from a small cave in the centre of the quarry floor.
Fig. 4. Once-a-Week Quarry. (A) The extent of the logged quarry face (Fig. 6) is represented by the white line. The base of the section was exposed and logged in a small cave as shown. To access the full section, the log was measured moving systematically to the NW across the quarry face. To the SE, beyond the white marker pole, renewed quarrying has exposed more of the section. (B) A detail of a vertical section through the *Gigantoproductus* shell bed. (C) A three-dimensional view of crinoid stems predominantly aligned NW–SE.
Fig. 5. Stratigraphic section at Ricklow Quarry with skeletal abundance and facies interpretations. Relative abundances of skeletal components within thin sections of samples are represented. Section (Figs 9 and 10) One and Section Two (upper right) refer to the locations of the palaeoecological studies (Figs 5, 9 and 10). Figure numbers relating to the stratigraphic position of thin section micrographs in Figure 7 are labelled.
Fig. 6. Stratigraphic section at Once-a-Week Quarry with skeletal abundance, and facies interpretations. Relative abundances of skeletal components within thin sections of samples are represented. ‘Palaeoecological analysis’ (upper right) refers to the location of the palaeoecological studies (Fig. 11). Beds are normally graded where crinoids are abundant or very abundant. Figure numbers relating to the stratigraphic position of thin section micrographs in Figure 8 are labelled. Beds (GB) with whole (not fragmented) *Gigantoproductus* that are visible in the exposure are located on the section. Undulating bedding represents areas where localized reworking has also occurred and commonly is eroded along these planes.
Fig. 7. Thin section micrographs from the Ricklow Quarry section. All scale bars are 0.5 mm. (A) Skeletal packstone with preserved fenestellid bryozoan (by), _Tetrataxis_ foraminiferan (f) and crinoid ossicle (cr) (sample 1a, taken at height c. 1.25 m from the base of the section). (B) Rugose coral boundstone showing a large section of a well-preserved coral (co) (sample 2a at c. 1.55 m). (C) Skeletal wackestone facies showing brachiopod fragments (ba) and a micritic matrix (mm) (sample 2c at c. 1.75 m). (D) Molluscan wackestone facies with gastropod moulds (ga), skeletal fragments, foraminifera (f) and peloids (pl) within the matrix (sample 2d at c. 3.20 m). (E) The upper part of the crinoidal grainstone – rudstone dominated by crinoid debris, some with a micritic (m) envelope (sample 2i at c. 2.25 m). (F) Skeletal wackestone–packstone comprising highly fragmented shell debris (sd), including some foraminifera (f, paleotextularid) (sample 5d at c. 6.5 m). (G and H) _Gigantoproductus_ floatstone with well-preserved foraminiferan (f). In (G) there are paleotextularids at the top right and various endothyrid fragments; in (H) there is _Earlandia vulgaris_, and brachiopod (ba) fragments surrounded by micrite (m) and some sparry calcite (spc) (G), sample 7 h taken from c. 8.75 and H, sample 7 m taken from c. 8.1 m). Sample numbers are assigned to hand specimen samples and corresponding thin sections currently archived at the University of Leicester.
up through the SW quarry wall and ten samples were collected for thin section analysis. Carbonate texture classifications are based on the Dunham (1962) and Embry & Klovan (1971) systems. The skeletal components and relative abundances were estimated visually as percentages of thin section area in every thin section.

**Palaeoecology**

Palaeoecological assessments were conducted on the main Gigantoproductus-rich shell beds at each location. The palaeoecological analysis involved detailed observations from selected one-metre square vertical sections in the quarry.
Fig. 9. Schematic representation of Sections One and Two of the shell beds at Ricklow Quarry. The base of these sections represents the base of the *Gigantoproductus* shell bed. Each shell represents an identified individual and is drawn in the observed orientation. Crinoids are represented as abundance and whether ossicles or stems are present. Individuals are drawn to scale where measurements are known. Classification as life (L) or neighbourhood (N) assemblages is illustrated, and Shannon and Margalef diversity indices shown.
Two sections from the north quarry face at Ricklow Quarry were analysed and both were located at the same stratigraphic level within the shell bed. One section was located broadly in the centre of the exposed quarry wall and the second was located c. 5 m east of the first. Due to challenges with accessing a vertical quarry face, a single section was analysed at Once-a-Week Quarry.

At both study sites, all one-metre square vertical sections were divided into 10 cm divisions from the base of the section to its top, and the macrofossils within each interval were counted and classified. Brachiopod specimens were classified to species level where possible. For each fossil specimen the orientation (life or other position) was recorded, as well as whether oblique or transverse sections were present. For brachiopod specimens, the umbo orientation was noted. Where packing of the fauna was particularly close, and where fossils overlapped two areas, divisions were amalgamated to form one 20 cm division. Identification to species level was not always possible, especially where the specimens were surrounded by matrix. Where individuals were obscured by the matrix, gigantoproductids were classified as thin- or thick-shelled following the groups recognized by Pattison (1981).

Each division was classified as either a life assemblage or a neighbourhood assemblage based on the percentage of individuals in their original life position (Brenchley & Harper 1998). Where more than 70% of the organisms were in original life position, the division was classified as a life assemblage; where this was less than 70%, the division was classified as a neighbourhood assemblage.

Diversity indices were calculated using the Shannon-Wiener and Margalef diversity calculations using PAST software (Hammer et al. 2001). For these calculations, Gigantoproductus species were grouped as thin- or thick-shelled to allow inclusion of all individuals. The Margalef index is based on the richness (this is the total number of species in a community), whereas the Shannon-Wiener index measures diversity based on the combination of richness and evenness (i.e. how evenly individuals are distributed among the different species in a community). Qualitative comments on biovolume are provided.

**Results**

**Facies types: Ricklow Quarry**

Seven main facies are identified based on texture, and skeletal and non-skeletal carbonate components.

**Skeletal packstone**

This facies (Fig. 7A) occurs only in the basal c. 1.6 m of the section (Fig. 5), with beds with thickness between 25 and 45 cm, and containing clotted peloidal micrite wackestone intraclasts with common crinoids and bryozoans (mostly fenestrate and fistuliporids). Typically, the facies is characterized by sparse ostracods and brachiopods, and rare foraminifera, calcispheres and monoxane sponge spicules. Echinoids are very rare in the lowermost sample, but common from 1.25 m where they co-occur with ugdarellid red algae. At 1 m from the base of the section the facies is a crinoidal packstone; brachiopods...
become common and detrital structureless micrite matrix is present.

Coral boundstone

This facies (Fig. 7B) occurs locally at 1.5 and 7.75 m above the base of the section forming lens-shaped beds with a maximum thickness of c. 15 cm. At 1.5 m, sparse echinoderms, ostracods and bryozoans are present with rare brachiopods, calcispheres and sponge spicules within intraclasts. Between rugose corals, patches of clotted peloidal micrite and of skeletal wackestone occur followed by blocky sparite cement. The thin (c. 12 cm) lens of this facies at 7.75 m is surrounded by skeletal packstone with sparse brachiopods and foraminifers.

Skeletal wackestone

This facies (Fig. 7C) occurs locally, c. 1.7 m above the base of the section, and is defined by the absence of molluscs, red algae and coral, whilst all other skeletal components are sparse (brachiopods, bryozoans, foraminifers, ostracods and echinoderms) or rare (debris of green palaeoberesellid algae, sponge spicules, calcispheres and trilobites). Parts of the
micritic matrix has a clotted peloidal character and evidence of burrowing. Vuggy and biomoldic dissolution porosity is present, and possible rhizoliths are observed.

**Molluscan wackestone**
This facies (Fig. 7D) characterizes the interval between 2.4 and 4.1 m above the base of the succession with abundant gastropods and bivalves. Foraminifera are identified in all samples from this facies in this interval; where they are common, at 3.25 and at 4.1 m, the assemblage is dominated by *Bradyina* and endothyrids. Other biota include common to rare ostracods, rare/sparse brachiopods, sparse calcispheres with detrital micrite and sparse peloids present in all samples. Locally this facies has a floatstone texture and shows evidence of bioturbation.

**Crinoid grainstone – rudstone**
This facies (Fig. 7E) occurs 1.85 – 2.45 m above the base of the section as a lenticular unit with a sharp erosional base. This facies is underlain by the molluscan wackestone and appears to have a transitional boundary with the overlying molluscan wackestone (Fig. 5). Cross-bedding is observed where the bed reaches its maximum thickness of 55 cm. The facies is characterized by abundant crinoid ossicles with common brachiopods and bryozoans (Fig. 7E). Other biota include ostracods and very rare foraminifers (endothyrids, *Earlandia vulgaris*, *Pseudoendothyra*, *Tetrataxis* and *Omphalotis*). Micrite matrix includes sparse peloids and clotted peloidal micritic intraclasts. Variable cements are observed including pendant vadose, equant blocky sparite and a syndetaxial cement surrounding echinoderm. Dissolution vugs, root casts, iron oxides and micritic envelopes are also present. Some brachiopods show microborings and silification.

**Skeletal wackestone – packstone**
This facies (Fig. 7F) typically contains sparse crinoids and ostracods. Brachiopods vary in abundance. Foraminifera show an initial decrease in abundance relative to the underlying facies and are typically rare to sparse. The benthic foraminifera assemblage contains endothyrids, *Tuberitina*, *Earlandia vulgaris*, palaeotextularids, rare *Tetrataxis* and *Bradyina*.

Where this facies first occurs at 4.1 m, gastropods are common and red algae fragments, such as *Fasciella* and undedrellid debris, occur as rare to sparse components in all samples; some specimens have been silicified. Sparse echioids and rare crinoids occur at the base of this facies. Bioturbation, peloids, faecal pellets, phosphate and pyrite are present in some samples.

**Gigantoproductus floatstone facies**
This facies (Fig. 7G and H) is characterized by its localized floatstone horizons, within a bioclastic skeletal packstone to wackestone matrix that contains detrital micrite, and rare peloids and faecal pellets. At the base of this facies there are several thin muddy horizons that can be traced along the exposure. *Gigantoproductus* brachiopods are abundant. Sparse foraminifers and crinoids, and sparse to rare palaeoberesellid and undegarellid algae are present in all samples. The foraminiferan assemblage comprises several *Omphalotis* and *Endothyra*, alongside *Pseudoendothyra*, *Eostafella*, *Tuberitina*, *Tetrataxis*, *Bradyina*, palaeotextularids and *Earlandia*.

### Facies Types: Once-a-Week Quarry

Four facies are recognized through the quarry section (Fig. 6). Crinoids and bryozoans are common to abundant in every thin section collected from the Once-a-Week Quarry section. The orientations of the long axes of the crinoid stems are typically between 160° – 115° with some oriented perpendicularly to the general trend. Intraclasts are commonly observed and are predominantly millimetre-sized and composed of wackestone with clotted peloidal and leiolitic micrite associated with sponge spicules. Typically, the facies at this locality comprise undulating 10 – 30 cm thin beds with normal grading of crinoids debris where they are abundant.

**Skeletal packstone-wackestone with micritic intraclasts**
This facies (Fig. 8A and B) is characterized by dominant packstone to wackestone with locally floatstone to rudstone or grainstone texture. It contains rare phosphate grains, pyrite and millimetre-sized wackestone intraclasts in blocky sparite cement. The fossil assemblage typically comprises common crinoids and bryozoans. The foraminifera are rare to very rare, but the assemblage commonly comprises *Tetrataxis*, *Tuberitina*, *Earlandia*, endothyrids, archaeodsicids and palaeotextularids.

A calcareous muddy horizon at 5.4 m separates two variants of the facies. The lower part of the facies is characterized by brachiopods, bryozoans, rare to very rare foraminifera and gastropods, sparse red algae, rare green palaeoberesellid algae, sparse ostracods and common crinoids. The facies overlying this muddy horizon is finer grained, lacking gastropods and algae with brachiopods becoming very rare. This facies also occurs at the top of the quarry section (9.75 m) where, at the macroscale, a 7 cm-thick graded bed of crinoid ossicles is noted. Here it is locally developed as a rudstone with common brachiopods, crinoids and bryozoans, with blocky sparite cement.

**Crinoidal packstone-grainstone**
This facies (Fig. 8C and D) occurs between 1.3 to 4.75 m above the base of the section and is also recognized in a thin section of a 10 cm bed at 8.6 m. It is inferred to be present between 6.45 to 9.25 m, based on the macroscale features, including the presence of lenticular bedding from 6.45 m to the bed sampled for the thin section. The orientations of the long axes of the crinoid stems are typically between 160° – 115° with some orientated perpendicular to the general trend. Intraclasts are commonly observed and are predominantly millimetre-sized and composed of wackestone with clotted peloidal and leiolitic micrite associated with sponge spicules. Typically, the facies at this locality comprise undulating 10 – 30 cm thin beds with normal grading of crinoids debris where they are abundant.

The fossil assemblage varies, but brachiopods, bryozoans, foraminifers and ostracods are always present. The foraminiferan assemblage of this facies comprises mostly archaeodsicids, *Tetrataxis* and *Howchinia* alongside endothyrids, *Valvulinella* and *Earlandia vulgaris*. 

---

Note: The text continues with descriptions of different facies types and their characteristics, including specific fossil assemblages and sedimentary features.
Calcispheres occur within all thin sections, except one sample at 3.1 m.

**Skeletal intraclastic grainstone**

This facies (Fig. 8E) occurs only once, at 4.75 m, within the section. It is characterized by its abundance of skeletal fragments and presence of wackestone intraclasts that are typically millimetres in size, and contain skeletal grains and peloids. The fossil assemblage comprises common crinoids, bryozoans (fenestellids, fistuliporids and ramose), sparse brachiopods and rare foraminifera.

**Gigantoproductus skeletal grainstone**

This facies (Fig. 8F) is characterized by abundant brachiopods, dominated by species of *Gigantoproductus*, and common crinoids within a fine- to coarse-grained bioclastic debris matrix. The texture is variable: locally, grainstone with coarse- to fine-grained skeletal fragments is intercalated with patches of packstone – wackestone and rudstone textures. Syntaxial cement around crinoids is present, possibly with micrite between gigantoproductids. Millimetre-sized intraclasts of detrital and clotted peloidal micrite are present within all samples.

A 20 cm-thick bed of this facies occurs 6.3 m above the base of the section. It contains sparse to rare foraminifera (endothyrids, *Tetrataxis*, *Tuberitina*, palaeotextularids, *Earlandia vulgaris*, *Howchinia*), sparse ostracods, rare calcispheres and sponge spicules that are associated with clotted peloidal micrite. The horizon also contains wackestone–packstone textures. A second example of this facies occurs at 9.5 m where locally it has a rudstone texture and is rich in crinoids. Here the foraminifera are very rare (though endothyrids and *Earlandia vulgaris* are identified) and bryozoans are typically fenestellids.

**Palaeoecology**

**Ricklow Quarry**

At Ricklow Quarry, brachiopod-rich deposits are found as lenses, 1 – 3 m-thick and tens of metres wide. Four species of *Gigantoproductus* are identified in the two analysed sections of the first bed (Figs 9 and 10): *G. aff. expansus* (Sarytcheva 1928), *G. gaylensis* (Pattison 1981), *G. inflatus* (Sarytcheva 1928) and *G. okensis* (Sarytcheva 1928). In addition to gigantoproductids, other brachiopods (including species of *Latiproductus* sp., other productids, chonetids and spiriferids), solitary and colonial corals, and a single gastropod specimen are present. In both sections, three to 17 individuals are present within each 10 cm division and the gigantoproductids are predominantly orientated with their umbo pointing north. At Ricklow Quarry 72% of the identified fauna were found in their original, convex-down life position.

The diversity indices through Sections One and Two (Fig. 9) are <1.37 for Shannon and <1.86 for Margalef and both sections have similar averages, Section One has averages of 0.81 and 0.88 for Shannon and Margalef respectively, and Section Two has averages of 0.85 and 0.80. In Section One, the Shannon diversity index and the Margalef index follow the same broad trends. The highest diversity index is encountered in a life assemblage identified near the base of the section (Fig. 9) and diversity indices decrease over the next three divisions into a neighbourhood assemblage. Between 70 – 160 cm, the diversity index fluctuates between 0.5 and 1.37; six of the highest diversity indices are associated with neighbourhood assemblages and three are within life assemblages for both calculated diversity indices (Fig. 8). Several of the neighbourbhood assemblages in Section One contain other productids, chonetids, spiriferids and species of *Latiproductus* alongside species of *Gigantoproductus* (Fig. 10). The presence of these other brachiopod species increases diversity indices within these divisions. Similarly, in the life assemblages with the highest diversities, combinations of other productids, *Latiproductus* sp., chonetid and spiriferids are present.

In Section Two, both methods generate similar diversity indices. There is a subtle overall decrease in diversity over the lower 1.5 m, with a higher, but variable diversity at the top despite a reduced sampling area. Two of the highest diversity indices are associated with neighbourhood assemblages and two are within life assemblages (Fig. 9). Section Two differs from Section One in that other productids represent a significant component of the individuals present in all but three divisions (Fig. 9). The lower diversity indices associated with the neighbourhood assemblages in Section Two, compared to Section One, reflect the dominance of *Gigantoproductus* and other productids (*Latiproductus* sp., chonetid and spiriferid brachiopods are absent in all but one neighbourhood assemblage). In most of Section Two, the Shannon diversity index is the same as or marginally higher than the Margalef index because the presence of productids reduces dominance of species of *Gigantoproductus* (Figs 9 and 10). At 160 cm, however, only a few individuals of thin- and thick-shelled *Gigantoproductus* spp. occur in a division and this produces a higher Margalef diversity index relative to the Shannon diversity index (Fig. 10).

Divisions are characterized by life and neighbourhood assemblages, and changes in the diversity cannot be correlated between the two sections (Fig. 9). Differences in the gigantoproductid species and other brachiopod species are also observed in both sections; for example, the productids are far more abundant in Section Two compared to Section One. Thick and thin-shelled species of *Gigantoproductus* are present within both sections at Ricklow Quarry. Thick-shelled forms dominate; thin-shelled *Gigantoproductus* species represent only 31.7% of Section One and 22% of Section Two. A small proportion (~5.5%) of shells in both sections are orientated such that a thick or thin shell cannot be determined. Bryozoans, corals and gastropods are observed, but form a minor component in both sections. Additionally, where a 100 cm width of the bed is visible (0 – 130 cm in Section One and 0 – 150 cm in Section Two), the average number of individuals present within each 10 cm interval is 10 and 12 for Section One and Two, respectively (where 100 cm width of the bed is exposed), indicating that Section Two is more densely populated.

**Once-a-Week Quarry**

At Once-a-Week Quarry three *Gigantoproductus* species are identified. *Gigantoproductus inflatus* (Sarytcheva) and *G.
okensis (Sarytcheva 1928) are present, as they were at Ricklow Quarry. Gigantoproductus elongatus (Pattison 1981) is present at Once-a-Week Quarry, but this species was not identified at Ricklow Quarry. Two species found at Ricklow Quarry, G. aff. expansus (Sarytcheva) and G. gayensis (Pattison), were not observed at Once-a-Week Quarry. Latiproductus sp., other products, spiriferids and one bryozoan colony are also found. Only thick-shelled gigantoproductids are present and dominate the biota in the section. Examining the orientation of the fauna, 37% were found in their original life position and brachiopod umbros had no preferred orientation.

The metre square section represents several neighbourhood assemblages (Fig. 11). Peak diversity (1.07 for Shannon and 1.4 Margalef) is reached at 40 – 50 cm in the section where Latiproductus sp., spiriferid brachiopods and a bryozoan colony are present. The average Shannon diversity index is 0.42 (0.5 for the Margalef diversity index) is lower than the average calculated at Ricklow Quarry, although it should be noted that this lower average is based on only six points. Diversity indices were not calculated where only thick-shelled forms (G. elongatus, G. okensis and G. inflatus) are present. On average eight individuals were identified within each 10 cm division (Fig. 11), thus demonstrating that this section is less densely populated than both Ricklow Quarry sections.

Interpretations

Facies

Depositional environment and evolution at Ricklow Quarry

The seven facies are grouped into three main facies associations that are related to their depositional environments: the mound-flank facies; the inner to middle ramp facies, and the mid ramp facies associations. The skeletal assemblage identified indicates generally subtidal open marine waters, mostly of normal salinity, but with possible variations.

The skeletal packstone facies at the base of the section represents a mound-flank facies association. The abundance of bryozoan and crinoid debris reflects their existence fringing the mud mound which lies directly adjacent to the Ricklow Quarry section (Gutteridge 1995). The clotted peloidal micrite and wackestone intraclasts that are present here may be reworked from the adjacent mounds into the flanks. However, as these types of intraclasts are also found in other horizons, they may also be in situ clotted micrite precipitation. A localized occurrence of a coral boundstone and skeletal wackestone facies is interbedded with the skeletal packstone facies. The in situ corals indicate a moderate energy, muddy depositional environment, just below the fair weather wave base (Copper 1988). The skeletal wackestone facies also forms part of the mound-flanks as its micrite content indicates deposition below the wave base. The interbedding of the skeletal packstones, wackestones and coral boundstones reflects the lateral accretion of the mud mound (Gutteridge 1995), and represents a transitional phase as the mound flank facies association transitions into the inner to middle ramp facies.

Overlying this transition zone is the inner to middle ramp facies association. This comprises three associations, the molluscan wackestone, the crinoidal grainstone–rudstone and the skeletal wackestone–packstone facies. During the deposition of these sediments, the adjacent mud mound was stable, but no longer active, partially lithified and therefore no longer contributing debris to the surrounding area (Gutteridge 1995). This is reflected in the decrease of crinoid ossicles and bryozoan debris present within the molluscan wackestone and skeletal wackestone facies. Within this facies association occurs the lenticular unit at c. 2 m, characterized by the crinoid grainstone–rudstone facies. This bed has an erosional base that suggests a channel morphology and the dimensions are within the range of tidal channels seen in Florida (Grinnell 1974); however, no other evidence of tidal influence is observed. The highly micritised grainstone facies described within the shoal facies by Gawthorpe & Gutteridge (1990) are very similar to the crinoidal grainstone–rudstone facies identified at Ricklow Quarry; however, the dimensions are different and the Ricklow Quarry unit is three orders of magnitude smaller than the shoals described by Gawthorpe & Gutteridge (1990). Furthermore, the facies described by these authors occur in the north-eastern margin of the platform with a very different structural (and therefore environmental) setting than the intraplatform ramp within which the sediments at Ricklow Quarry were deposited. This bed at Ricklow Quarry is interpreted as a depositional bar. The subtle grading towards the top of the Ricklow unit, which is then overlain by the molluscan wackestone, suggests the current velocity was decreasing as the bar was abandoned. These beds are more likely formed by current effects; their formation and size was restricted due to the lowering of sea level that occurred during their deposition prior to the Monsal Dale Limestone - Eyam Limestone formations boundary. Additionally, the effects of currents or tides may have been amplified within this region due to a potential funnelling effect caused by the geometry of the intraplatform ramp aiding the formation of such shoals in environments, which may otherwise not be suitable.

The recessive boundary observed at 2.5 m (Fig. 5) represents a subaerial exposure surface confirmed by the presence of meteoric diagenetic features, including pendant vadose cement, secondary vuggy and biomoldic dissolution porosity, and uncommon root casts and iron oxides, as observed between 1.6 and 2.35 m. This subaerial exposure, described by Adams (1980), Aitkenhead et al. (1985) and Gutteridge (1991), represents the Monsal Dale–Eyam Limestone formations boundary proposed by Gutteridge (1995).

Following subaerial exposure, the ramp was re-established and sedimentation of the molluscan wackestone facies resumed. This deposit at the start of the Eyam Limestone Formation likely represents restricted environments, including the development of 'lagoon'-like environments within the inner to middle ramp depositional environment (Gutteridge 1983), which developed due to the interaction of the low sea level (post-emergence) and the relict topography of the now inactive (though still present) mud mounds. It is noted that the sediments exposed at Ricklow Quarry lie directly to the east of a mud mound at this locality and, therefore, is on the ‘open’ side of the mound, which potentially limited the formation of 'lagoon'-like environments. However, the morphology of this mound is not fully
understood, with outcrops of mound facies to the south, west and north of the quarry itself (Fig. 1C). This suggests that the mound geometry was more complex during the time of deposition than is currently visible in outcrop. This is likely to have complicated the interplay of sea level rise with the mound geometry, therefore allowing the formation of restricted 'lagoon'-like environments.

As the ramp evolved further, the skeletal wackestone-packstone facies was deposited above the molluscan wackestone. This textural change, from wackestone to packstone, suggests a change to more open marine conditions. This switch can also be inferred by the increase in occurrence of red undgarellid algae and green paleoberesllid algae debris, and the end of the dominance of molluscs, alongside increasing energy.

The muddy carbonate horizons at the base of the Gigantoproductus floatstone facies suggest relatively low energy conditions during the initial Gigantoproductus colonization. The transition into deposition of the middle ramp facies association also includes a localized horizon of the coral boundstone facies. Deposition occurred below the active wave base with some mud present within the water column; this is indicated by the presence of the micrite rich floatstone lithofacies and the interbedding of a second occurrence of the coral boundstone facies. A continuation of open (less restricted) conditions is indicated by the presence of both green and red algal debris within several horizons, which are likely to have undergone some transportation. Brachiopods and echinoderms present within this facies indicate that normal salinity marine conditions were present throughout (Fürsich 1993; Kammer & Ausich 2006).

Depositional environment and evolution at Once-a-Week Quarry

The skeletal packstone with intraclasts, the crinoidal packstone–grainstone and skeletal packstone wackestone, present from the base of the section to 6.25 m, are collectively interpreted as an inner ramp facies association. The presence of semi-articulated crinoid stems suggests that either energy levels were sufficiently low to avoid disarticulation or that sedimentation rates were high (Cam 1968; Ausich et al. 1979; Baumiller & Ausich 1992). A high sedimentation rate would also explain the absence of corals and their scarcity at the locality in general (only one example of a coral is seen in the quarry face).

Alternations between the skeletal packstone–wackestone with intraclasts and the crinoidal packstone–grainstone, associated with an increase in size of the crinoid ossicles, suggest changes from lower to higher energy conditions, respectively. The quantity of micrite, and the abundance and size of skeletal fragments, is also used to infer changes in energy and the amount of reworking.

The sparse to rare brachiopods noted in the facies and at outcrop are not in their life position, and the fragmentation suggests some reworking. However, the macrofossil assemblage identified is assumed to be representative of the in situ community because significant transport distances between habitats are unlikely (Lane 1973; Macdonald 1976). The very rare to sparse red and green algae suggests that water depth may have varied (Madi et al. 1996), but all algae present are debris and are likely to have undergone some transportation. Therefore they cannot be used as direct or reliable indicators of water depth.

The Gigantoproductus skeletal grainstone appears at 6.25 m, where the coarse-grained, sand-sized skeletal fragments indicate high levels of reworking and increased energy levels relative to the underlying facies. The Gigantoproductus skeletal grainstone also occurs at 9.25 – 9.75 m, separated from the lower bed by the crinoidal packstone and wackestone. At the top of the section, size grading of crinoid ossicles indicates turbulent current allowed significant sorting during deposition of the skeletal packstone–wackestone with intraclasts. The presence of coarse-grained, sand-sized skeletal fragments and the relative absence of mud in the Once-a-Week Quarry section suggest a higher energy, inner ramp setting in comparison to the conditions for the Gigantoproductus shell bed at Ricklow Quarry. The orientation of crinoid stems indicates a roughly south-easterly palaeoflow as elongate stems preferentially align perpendicular and occasionally roll parallel with the direction of flow (Gutteridge 1983). The consistent orientation of crinoids through the section indicates that flow patterns were steady through the deposition of these strata.

Palaeoecological interpretation of the Gigantoproductus Floatstone Facies

Gigantoprotodids were suited for living in high-energy environments (Ferguson 1978; Harper & Jeffrey 1996) where currents ensured a constant supply of sufficient oxygen and food passing over them. The consistent brachiopod orientation in the Gigantoproductus shell bed analysed at Ricklow Quarry, with umbos oriented pointing north, suggests currents were constant. As species of Gigantoproductus tend to align with the umbo facing the current (Ferguson 1978; Shino & Suzuki 2011), it is inferred that the currents were flowing in a southerly direction.

This palaeoflow direction appears to be different to that inferred by Gutteridge (1983), who suggested there were east to west palaeocurrents on the platform during the deposition of the Eyam Limestone Formation. The mud mounds at the top of Monsal Dale Limestone Formation, one of which is exposed at Ricklow Quarry, were partially eroded during subaerial exposure (Aitkenhead & Chisholm 1982; Gutteridge 1991) and produced a relict topography on the sea floor during the subsequent transgression that re-established the inner to middle ramp facies of the Eyam Limestone Formation. Renewed deposition of inner to middle ramp facies began around the inactive mud mounds (Gutteridge 1991). Continued sedimentation partially buried and smoothed the topography, providing a suitable habitat for the gigantoproductids, which sheltered at the side of the mound (in this case the eastern side).

It is likely, therefore, that the relict topography of the mud mound influenced local current flow. It generated localized flows that were diverted around the mounds leading to north–south-oriented brachiopods at the Ricklow location. The currents produced by the presence of a relict topography around the mud mounds would have also transported the larvae that colonized the sheltered margins of the pre-existing mud mound.
Although *Gigantoproductus* species thrived in high-energy environments, quieter conditions were required to enable brachiopod larvae to settle and establish a *Gigantoproductus* community. The mud-rich horizons present at the base of the *Gigantoproductus* shell bed at Ricklow Quarry suggest low energy conditions preceded the major phase of *Gigantoproductus* colonization. The brachiopods at Ricklow Quarry occur within a micrite matrix because the large shell size allowed them to baffle mud and fine bioclasts. Their size may have provided localized areas of shelter from currents for other nearby individuals and larvae once the community is established.

The diversity indices, and their averages, throughout the three sampled sections at Ricklow (2) and Once-a-Week (1) quarries are comparable to those recorded and interpreted by Angiolini (2007) as representing low diversity palaeocommunities. The indices at Ricklow and Once-a-Week quarries would be even lower if a qualitative estimation of the biovolume, rather than only the number of individuals was considered, because the large size of species of *Gigantoproductus* meant that this genus dominated the communities. The Margalef index value underestimates the true diversity due to reduced sample size (Gamito 2010), whereas the Shannon-Wiener index reflects more clearly the dominance of the *Gigantoproductus*. Low diversities may reflect an absence of heterogeneities in the environment, particularly in the substrate and/or a high level of environmental disturbance and/or resources availability.

At Ricklow Quarry, the variation between low (<1) to moderate (considered as values >1) richness of the macrofauna, rather than a systemic change from basal low diversities to high diversities upwards, suggests the early stages of ecosystem development are not recorded. There is no evidence for an ecological transition into a climax community. In the topmost 1 m of Section One at Ricklow Quarry, Shannon-Wiener diversity values of 0.45 – 0.65 over four consecutive divisions may reflect an intermediate point in the ecological succession between the early and mature stages, as already observed in other Palaeozoic brachiopod-bearing successions (e.g. Angiolini et al. 2003; Angiolini 2007). Therefore, the palaeocommunity dominated by *Gigantoproductus* species was rapidly established, but did not evolve towards a climax. The absence of a climax phase may be due to a combination of environmental disturbance and high resources. At Ricklow Quarry rapid colonization probably lead to a taphonomic feedback where the large brachiopods species changed the environment and the nature of the substrate itself, thereby sustaining further rapid colonization by conspecific individuals, and the rich and diverse microbiota seen within the *Gigantoproductus* shell bed (e.g. Ferguson 1978).

The generally low diversity indices calculated from the Once-a-Week Quarry section through the *Gigantoproductus* shell bed, compared to values at Ricklow Quarry, may reflect transport and winnowing of the biota at the former location. The general absence of thin-shelled varieties at Once-a-Week Quarry may also reflect that the environment was suited to specifically adapted organisms, including thick-shelled species of *Gigantoproductus*, bryozoans and crinoids.

The presence of *G. elongatus* at Once-a-Week Quarry infers that these assemblages are slightly younger than the first *Gigantoproductus* bed at Ricklow Quarry. This is because *G. elongatus* appears slightly later than *G. inflatus*, *G. okensis* and *G. gaylensis* (Pattison 1981). The second *Gigantoproductus* bed at Ricklow Quarry, although poorly exposed, also contains *G. elongatus*, confirming these stratigraphic relationships. No mud mound is observed at Once-a-Week Quarry; however, geological maps indicate one large and several smaller mud mounds within its vicinity. Original field slips indicate that geologists who mapped the region observed crinoid-rich facies that they interpreted to be derived from mound flanks (Chisholm 1971–1972). The interpretation of the depositional environment places Once-a-Week Quarry in shallower water than that at Ricklow Quarry. This is consistent with the geographical location of Once-a-Week Quarry relative to the geometry of the carbonate ramp, despite the two localities not being time equivalent.

The facies observed beneath the first *Gigantoproductus* shell bed at Once-a-Week Quarry suggests lower energy conditions prior to its development. However, the absence of thin shelled gigantoproductids, such as *G. gaylensis*, the random shell and umbo orientations, a much lower percentage of brachiopods in their original life position and presence only of neighbourhood assemblages all indicate higher energy conditions, and a shallower setting on the ramp, at Once-a-Week Quarry compared to Ricklow Quarry. This is consistent with the observation that there are reduced numbers of individuals at Once-a-Week Quarry suggesting larvae had more difficulty settling here. The decline in diversity near the top of Once-a-Week Quarry, where only gigantoproductids are present, and the association with a 7 cm-thick, normally-graded, coarse-grained crinoidal bed, with no gigantoproductids, indicates that currents may have exceeded the threshold (30 – 38 cm/s) for moving/tiling of adult specimens of species of *Gigantoproductus*, experimentally obtained by Ferguson (1978).

**Conclusions**

Both of the studied localities – Ricklow and Once-a-Week quarries within the Eyam Limestone Formation – represent inner to middle ramp settings characterized by diverse facies with varied skeletal assemblages. Detailed analyses of the *Gigantoproductus* shell beds present at both quarries show that there are differences that relate to their local setting and environment. Despite these differences, shell bed occurrence is preluded by a period of decreased energy. At Ricklow Quarry, several mudstone layers occur directly at the base of the *Gigantoproductus* shell bed. In contrast, at Once-a-Week Quarry, skeletal packstone-wackestone with intraclasts facies underlie the first occurrence of the *Gigantoproductus* floatstone and the *Gigantoproductus* skeletal grainstone. These intervals of low energy allowed the deposition of fine-grained sediment and, potentially, time for the brachiopod larval stages to settle.

At Ricklow Quarry, the palaeoecological study of two sections within the 2.2 m-thick *Gigantoproductus* floatstone facies revealed life and neighbourhood assemblages, with 72% of brachiopods in life position. These assemblages, and the observed variations in diversity indices, could not be correlated between two sections analysed at the same
stratigraphic height, indicating highly localized variations across the original community. A low–moderate diversity in both of the Ricklow Quarry sections indicates a rapidly established palaeocommunity that did not reach a stable climax. Once the community was established, the large shell size of *Gigantoproductus* and the dominance of these thick-shelled forms enabled baffleing of mud and fine bioclasts, and may also have provided localized shelter for other nearby individuals and larvae. This provided a positive feedback, encouraging further colonisation. In contrast, although similarly low diversity indices are seen at Once-a-Week Quarry, a palaeoecological study shows the *Gigantoproductus* skeletal grainstone was exclusively composed of neighbourhood assemblages, with only 37% of brachiopods in life position and having no preferred orientation. Although they do not represent life assemblages, the brachiopods are not thought to have been transported far from where they were living and the absence of thin-shelled products suggested that higher energy conditions on the inner ramp were likely.

At Ricklow Quarry, the relict mud mound topography is interpreted to have provided shelter on its lee (east) side that enabled *Gigantoproductus* species, including those with thin shells, to rapidly and successfully colonise these areas. Where orientations of brachiopods could be measured, a south-directed palaeoflow is indicated at this locality, which contrasts to the easterly palaeoflow inferred by Gutteridge (1983). This suggests that the relict topography of the mud mounds (of the Monsal Dale Limestone Formation) locally influenced currents and provided a potential mechanism for the transportation of larvae during deposition of the Eyam Limestone Formation. No mud mound is present in the exposed at Once-a-Week Quarry. This, coupled with the low percentage of brachiopods in life position in the assemblages, may explain the contrast in character and palaeoecology between the *Gigantoproductus* shell beds here when compared to Ricklow Quarry.

The success of this genus on this part of the Derbyshire carbonate platform appears to be related to the location of inactive mud mounds. At Ricklow Quarry, species of *Gigantoproductus* were able to rapidly establish a significant and stable community in the shelter of the relict mud mound. In contrast, at Once-a-Week Quarry, such shelter is absent, resulting in smaller communities of lower diversity, with evidence of some reworking and the establishment of only thick-shelled brachiopods. Overall, the evidence suggests that on the intrashelf part of the Derbyshire carbonate platform, *Gigantoproductus* species were commonly associated with mud mounds in inner to middle ramp settings. However, they did not actively contribute to mound development and colonized the substrate following mud mound demise.

Acknowledgements Staff from BGS publish with the permission of the Executive Director of the British Geological Survey (NERC). All authors thank the staff and owners of Natural Stone Sales Ltd, who enabled access to Once-a-Week Quarry, and to Natural England who allowed the study of Ricklow Quarry. Thank you to Dr Peter Gutteridge and Dr Ian Chisholm who kindly spent a day in the field offering their knowledge, and to Howard Daley, Jo Miles and Michael Nolan for assistance with fieldwork. Additional thanks are given to Professor Sarah Gabbott who provided discussion and guidance, and the two reviewers of the manuscript, Professor David Harper (Durham University) and Professor Stephen Donovan (Naturalis Biodiversity Centre, Leiden) for their helpful comments.

**Funding** This work was supported by the Natural Environment Research Council (NERC) (NE/L051839/1) and the British Geological Survey.

**Scientific editing by Stephen K. Donovan**

**References**

Adams, A.E. 1980. Calcrite profiles in the Eyam Limestones (Carboniferous) of the Derbyshire Dome: petrology and regional significance. *Sedimentology*, 27, 651–660.

Aitkenhead, N. & Chisholm, J.H. 1982. A standard nomenclature for the Dinantian formations of the Peak District of Derbyshire and Staffordshire. *Institute of Geological Sciences, London*.

Aitkenhead, N., Chisholm, J.H. & Stevenson, I.P. 1985. Geology of the country around Buxton, Leek and Bakewell. *Memor for 1:50 000 geological sheet 111 (England and Wales)*. HMSO Publications, London.

Angiolini, L. 2007. Quantitative palaeoecology in the Pachycyrtella Bed. *Early Permian of Interior Oman*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 196, 99–123.

Angiolini, L., Stephenson, M., Leng, M. I., Jadoul, F., Millward, D., Aldridge, A., Andrews, J., Chenery, S. & Williams, G. 2012. Heterogeneity, cyclicity and diagenesis in a Mississippian brachiopod shell of palaeoequatorial Britain. *Terra Nova*, 24, 16–26.

Aussch. W.L., Kammer, T.W. & Lane, N.G. 1979. Fossile communities of the Borden (Mississippian) Delta in Indiana and northern Kentucky. *Journal of Paleontology*, 33, 1182–1196.

Baumiller, T. K. & Ausich, W. I. 1992. The broken-stick model as a null hypothesis for crinoid stalk taphonomy and as a guide to the distribution of connective tissue on fossils. *Paleobiology*, 18, 288–298.

Brenchley, P.J. & Harper, D.A.T. 1998. Palaeoecology: Ecosystems, environments and evolution. *Chapman & Hall*, London.

Breznik, D.K. & Kollar, A.D. 2012. Palaeoecologically induced size increase in the early Carboniferous brachiopod clade *Gigantoproductus*. *Geological Society of America Abstracts with Programs*, 44, 83.

Bridges, P.H. 1982. The origin of cyclothems in the late Dinantian platform carbonates at Crich, Derbyshire. *Proceedings of the Yorkshire Geological Society*, 44, 159–180, https://doi.org/10.1144/pygs.44.2.159

Bridges, P.H. & Chapman, A.J. 1988. The anatomy of a deep water mud-mound complex to the southwest of the Dinantian platform in Derbyshire, UK. *Sedimentology*, 35, 139–162.

Bridges, P.H., Gutteridge, P. & Pickard, N.A.H. 1995. The environmental setting of the Early Carboniferous mud-mounds. *In: Monty, C.L.V., Bosence, D.W.J., Bridges, P.H. & Pratt, B.R. (eds) Carbonate mud-mounds: their origin and evolution*. International Association of Sedimentologists Special Publications, 23, 171–190.

Brunton, C.H.C., Lazarre, S.S. & Grinnell, R.E. 2000. Productida. *In: Kaesler, R.L. (ed.) Treatise on Invertebrate Paleontology. Part H. Brachiopoda, Revised Geological Society of America and The University of Kansas, Boulder and Lawrence, USA*.

Cain, J.D.B. 1968. Aspects of the depositional environment and palaeoecology of mudlimestone. *Scottish Journal of Geology*, 4, 191–210, https://doi.org/10.1144/sjg04030191

Chisholm, J.I. 1971–1972. 1:10,000 Geological Map of SK 16 NE [ ] (Composite). Ordinance Survey, Southampton, Provisional edition.

Cohen, K.M., Finney, S.C. & Husband, P.L. & J.-X. 2013. The ICS International Chronostratigraphic Chart. * Episodes*, 36, 199–204.

Copper, P. 1988. Ecological succession in Phanerozoic reef ecosystems: is it real? *Palaeo*, 3, 136–151.

Cox, F.C., Bridge, D. McC., Chisholm, J.I. & Aitkenhead, N. 1977. The limestone and dolomite resources of the country around Monyash, Derbyshire. *Description of 1:25 000 resource sheet SK 16*. Institute of Geological Sciences, London.

Dunham, R.J. 1962. Classification of carbonate rocks according to depositional texture. *American Association of Petroleum Geologists Memoir, 1*, 108–121.

Emby, A.F. & Klovain, E.J. 1971. A Late Devonian reef tract on northeastern Banks Island, N.W.T. *Bulletin of Canadian Petroleum Geology*, 19, 730–781.

Ferguson, J. 1978. Some aspects of the ecology and growth of the Carboniferous gigantoproductids. *Proceedings of the Yorkshire Geological Society*, 42, 41–54, https://doi.org/10.1144/pygs.42.1.41

Fürsich, F.T. 1993. Palaeoecology and evolution of Mesozoic salinity-controlled benthic macroinvertebrate associations. *In: C.H.C., Lazarev, S.S. & Grant, R.E. (eds) Treatise on Invertebrate Paleontology. Part H. Brachiopoda, Revised Geological Society of America and The University of Kansas, Boulder and Lawrence, USA*.

Garmony, S. 2010. Caution is needed when applying Margalef diversity index. *Ecological Indicators*, 10, 550–551.

Gawthorpe, R.L. & Gutteridge, P. 1990. Geometry and evolution of platform-margin bioclastic shoals. *Derbyshire, UK. Special Publications of the International Association of Sedimentologists*, 9, 39–54.

Grisham, J.B., Aguilar, N.M., Dudley, R. & Gans, C. 1995. Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature*, 375, 117–120.

Grinell, J.R.S. 1974. Vertical orientation of shells on some Florida oyster reefs. *Journal of Sedimentary Petrology*, 44, 116–122.
