

Macrofossils and their palaeoecology in deltaic sequences of the Lower Carboniferous Yoredale Series, Yorkshire, England

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Abstract

Deltaic sequences of the 5-Yard Limestone cyclothem forming part of the Yoredale Series, have been studied at different localities in Wensleydale and Bishopdale, N. Yorkshire. The northernmost, Wensleydale sections contain upward coarsening clastic sequences that are characterized by gradational passages from one lithology into another, suggesting slow deltaic progradation. Highly fossiliferous, calcareous shales, deposited in a shallow, open sea, pass up into less fossiliferous, sometimes evaporitic shales indicating a restricted connection with the sea. The latter show an increase of silt content, ultimately merging into fine-grained sandstones of the delta plain facies. A different general picture is found in the Bishopdale sections located in the south. These locations apparently were frequently subject to fluctuations in sediment input and water turbulence, which resulted in periods of abundant algal growth, explosive colonization by the probably opportunistic brachiopod *Gigantoproductus* and minor transgressions of the sea. It is suggested that current patterns and sediment influx from the north initiated growth of a coastal barrier, causing development of different environmental conditions in the northern and southern part of the area. Due to partial separation from the sea, the northern part changed into a lagoon with variable salinity conditions, while progradation of the delta was slow enough to permit small-scale transgressions over the southern part of the area, eventually followed by deposition of fine-grained, evenly laminated sandstones and medium-grained, cross-bedded sandstones characteristic of a seaward prograding barrier beach.

Introduction

Palaeogeographical and sedimentary setting

In the Devonian Great Britain was on an area of high relief with uplands and intermontane basins in England and Wales, and strongly uplifted mountain chains adjacent to major interior basins in Scotland dating back to the Caledonian Orogeny (Ziegler, 1981). A slow pelagic marine sedimentation started in the Middle Devonian and persisted to the Carboniferous, known as the 'bathyal lull'

(Goldring, 1967). This bathyal interval was diachronous and spread across the British continental shelf shorewards from south to north (Johnson, 1982). Maximum development of this bathyal interval took place at approximately the same time as the initiation of block and basement extensional tectonics in northern Great Britain, caused by tensional stress in the upper crust (Leeder, 1976). Under this tensional stress the structurally positive Caledonian granite intrusions tended to be uplifted forming horst blocks while the intervening regions not underlain by buoyant granite intrusions formed

graben-like basins. Initially, during the Dinantian, basins subsided while the bounding blocks remained emergent, forming islands. Later as the basins filled with sediment, the difference in structural behaviour between blocks and basins decreased.

The type area of the Yoredale succession is in Wensleydale, situated on the Askrigg Block. The Yoredale beds were first described by Sedgwick (1835) and in more detail by Phillips (1836). The cyclothems are named after the basal limestones which are largely bioclastic and represent a continuation of the shallow Dinantian seas not far south of the Carboniferous equator (McElhinny, 1973). Those seas were periodically invaded by muds, then silts and sands and finally the sediment surface emerged above water level when rootlet beds and coals were established. Then the supply of detritus ceased and with subsidence, clear limestone forming seas were re-established. The source of clastic sediments is deduced to be somewhere to the north or north-east (the range of the Caledonian chain from Ireland to Scotland and Norway).

Several different hypotheses have been proposed to account for the cyclic sedimentation that characterizes the Yoredale Series. According to Bott & Johnson (1967) cyclothems are formed in a subsiding region by repeated subsidence of the crust along fault lines. The mantle flow theory would provide a mechanism for tectonic control of cyclic sedimentation. Ramsbottom (1973) on the other hand, who traced and correlated six 'major cycles' of sedimentation in the British Dinantian succession, concluded that the major influence on Dinantian sedimentation was repeated eustatic change in sea level. Ramsbottom's system differs from that of six regional stages proposed by George et al. (1976). The latter is founded not only on a single principle of eustasy, but on a pragmatic appeal to any convenient source of evidence that may be available, mainly biostratigraphical but also tectonic. Johnson (1982) argued that a eustatic origin for deepening of the sea is ruled out. In his view the bathyal transgression which started in the Middle Devonian must have had a tectonic origin, because it produced progressive northward epeirogenic sinking of the seafloor. He suggested the Gulf

Coast region of U.S.A. as a modern analogue of the Carboniferous shelf across Great Britain, being an 'Atlantic type' continental margin developing stability in maturity.

Methods of study

The purpose of this study was to make a reconstruction of the continuously changing environment of the Yoredale delta complex, based on macrofaunal and lithological data. In contrast with the basal limestones and massive sandstones of the Yoredale cyclothems, the shale sequences in between are often badly exposed. Only a few of the sections described by Moore (1958) contain reasonably continuous shale exposures with distinct changes in macrofauna. Five of these sections, situated at different localities in Wensleydale and Bishopdale and all belonging to the same, 5-Yard Limestone cyclothem, have been selected in order to make a three-dimensional palaeo-environmental study (Fig. 1). Samples have been taken from different stratigraphical units above the 5-Yard Limestone and studied in thin-section. The lowest fossiliferous shale successions have been divided into 'topozones' for descriptive and reference purposes. This zonation is based on differences in macrofauna and lithology and should not be confused with zonation based on faunal succession (e.g. Ferguson, 1962). These topozones have subsequently been divided into several subzones which do not have any necessary relation with macrofauna or lithology. The density of several taxa occurring in these subzones is converted to the number of specimens per 2 or per 5 kg sample, shown in Figs 3, 4, 6, 7 and 8. The density and size-frequency distribution of the brachiopod *Gigantoproductus* in section 5 have been examined by bulk-sampling a vertical series of subzones in topozone 5. In order to find a possible relation between the orientation of *Gigantoproductus* and dominant palaeo-currents, the direction of shell apertures in different subzones of the same series was measured with a compass and rose-diagrams were produced (Fig. 9).

The material described herein is housed in the

collections of the Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands, under reference numbers RGM 350.000-350.232.

Studied sections

Section 1 (locality 27 of Moore, 1958)

This is the northernmost section situated in Wensleydale (Fig. 1). A coarsening-upward sequence is easily recognized here. The lithology shows a gradual change from calcareous mudshales through silty shales in to massive sandstones (Fig. 2). The occurrence of macrofossils is limited to the lower part of the section, which is divided into five topozones (Fig. 3).

Topozone 1 is characterized by a highly dense and diverse macrofauna in a calcareous mud matrix (Table 1A). Articulated bivalves and brachiopods, including many productaceans with their spines intact, as well as solitary rugose corals with the calyx pointing upwards are common, suggesting burial in life position. The brachiopod *Schizophoria resupinata* (Martin) is the most abundant macrofossil in topozone 1. Its indigenous nature is indicated by the fact that both valves are normally present and that different growth stages are abundant. Some appear to have been attached to flat-lying shells of the same species, a phenomenon already described by Ferguson (1962). Complete bryozoan fronds and large crinoid stem fragments are common and probably formed part of autochthonous populations. The calcareous mud substrate furthermore seems to have been suitable for colonization by vagile benthic organisms such as holothurians, trilobites and echinoids, fragments of which are abundant. All these lines of evidence suggest that mud sedimentation took place at a slow rate in fairly turbulent, well aerated water with a normal marine salinity.

Changes in facies conditions must have caused a considerable decrease of faunal density and diversity in topozone 2. Several elements of the former fauna, including trilobites crinoids, rugose corals and many brachiopod genera, show a distinct decline in number of individuals, or even complete extinction (Fig. 3).

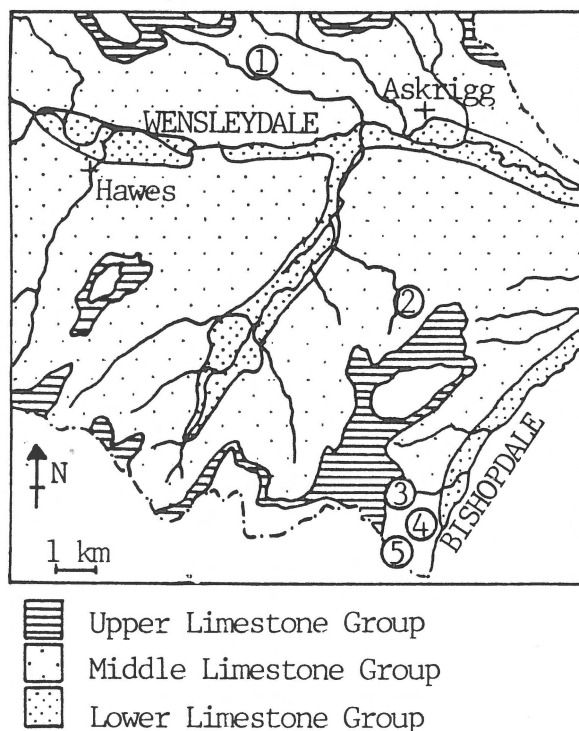


Fig. 1. Geological sketch-map of Upper Wensleydale with outcrops of the Lower, Middle and Upper Limestone Groups (after Moore, 1958). The positions of the five studied sections are marked with circles.

Increase in water turbulence and salinity is indicated by a higher content of shell fragments and by the appearance of evaporitic dolomite crystals in the mud matrix of topozone 3. Gastropods, non-fenestrate bryozoa and the small-sized brachiopods *Crurithyrus urei* (Fleming) and *Plicochonetes buchianus* (de Koninck) have a common occurrence in this topozone, and thus seem to have tolerated slightly increased salinity conditions and current actions. Spirorbid worms are fairly common too, indicating early lithification of the sediment. This process probably rendered the substrate unsuitable for vagile benthic organisms such as holothurians, which are usually found on soft, fine-grained substrates. Current actions have caused selective transport and deposition of fossil material including fragments of shells, crinoids and echinoids, fish plates and ostracods.

Topozone 4 has a more terrestrial character,

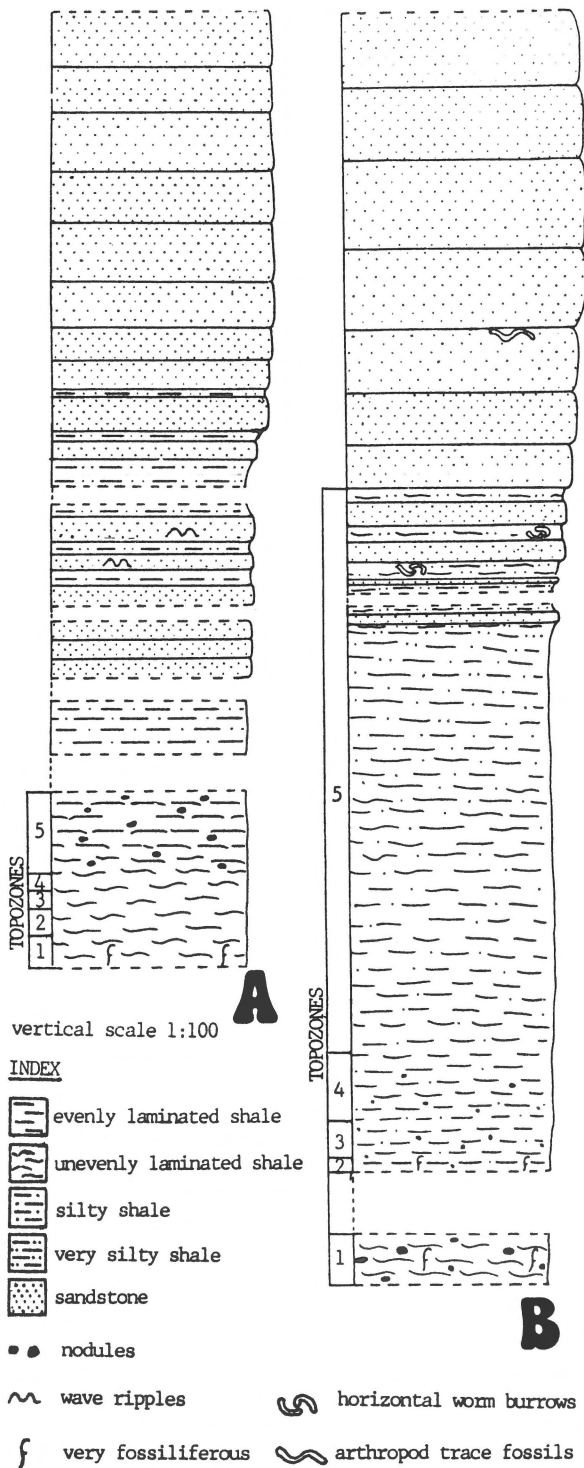


Fig. 2. Columns of sections 1(A) and 2 (B). The positions of the topozones in the shale sequences are given.

with plant impressions indicating vegetation here or nearby. The shales are fissile along domical structures, which may originate from encrusting blue-green algae which formed part of a tidal flat community (Ramsbottom, 1978). The impoverished fauna is confined to spirorbid worms, orthocones, and only few brachiopods, bivalves and gastropods which may not be indigenous.

Topozone 5 is distinguished by a considerably higher percentage of evaporitic dolomite reflecting hypersaline lagoon conditions. Microscopic intraclasts are detectable in a matrix of dolomite rhombs. These clasts contain sponge spicules, gastropod nuclei and few other bioclasts embedded in a non-dolomitic mud matrix, and presumably originate from older, less evaporitic sediments. Nodules varying in diameter up to ca. 25 cm are randomly distributed in this topozone, and show a great similarity in shape with algal spheres of the Southernness Algal Beds of the Kirkbean outlier on the NW-shore of the Solway Firth, Southern Scotland (Frölicher, 1977). Sponges on the other hand would have also been abundant in quiet Carboniferous lagoonal environments (Hudson, 1929). Since the occurrence of sponge spicules is confined to intraclasts that probably originate from older sediments, and no internal growth structures are found, it is assumed that the nodules represent the nodular growth habit of encrusting algae.

Bellerophontacean gastropods including *Euphemites urei* (Fleming) and *Knightites exilis* (de Koninck) are common at one particular horizon, associated with small, rounded inclusions (diameter ca. 5 mm) which presumably are plant seeds belonging to the order Pteridospermophyta. The gastropods may have been able to resist fairly strong salinity fluctuations which may be related with an infaunal mode of life. Although bellerophontacean gastropods have long been categorized as herbivorous hardground dwellers and are typically illustrated as grazing along seaweed fronds (e.g. Bretsky, 1969), other authors considered them to be infaunal deposit feeders (Rollins et al., 1971), strong evidence of which was later found in a morphological analysis of their internal shells (Harper & Rollins, 1983).

The unfossiliferous, micaceous shales somewhat higher in the column reflect an evident increase in

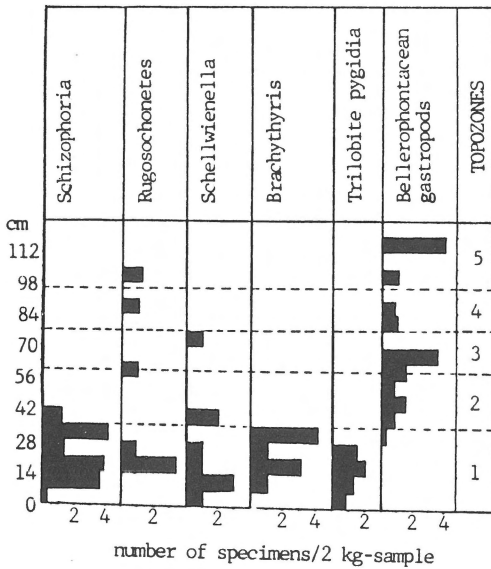


Fig. 3. The density of some fossil groups in the lower part of section 1. The number of specimens was counted in 2 kg-samples from a continuous series of subzones (7 cm).

detrital influx and rate of deposition, which would have made the environment unsuitable for living organisms. Even so, traces of horizontally moving organisms have been preserved on the surface of thin sandstone bands alternating with these shales. These organisms were probably able to survive during periods of relatively low sediment input. Locally preserved wave ripples within the shale-sandstone alternations indicate deposition in shallow water. The minor cyclicity that is recognizable in this part of the column ultimately passes up into massive, fine-grained sandstones with a horizontal lamination.

Section 2 (locality 36 of Moore, 1958)

This section is located south of the river Ure in Wensleydale (Fig. 1), and is also characterized by a distinct coarsening-up from non-silty shales into fine-grained sandstones (Fig. 2).

Topozone 1 is formed by highly fossiliferous, calcareous shales that contain silicified nodules which, considering the total absence of silicified

sponge spicules, are assigned to nodular algae. Due to heavy weathering only a minor part of the macrofossils could be identified (Table 1B). The fossil fauna is dominated by complete fronds of fenestrate bryozoa, associated with large crinoid stem fragments and generally large, costate brachiopods, e.g. *Marginicinctus marginicinctus* (Prout). The high density of suspension feeders, most of which appear to have undergone little or no post-mortem transport, suggests that there was a low rate of mud sedimentation in fairly turbulent water carrying plenty of food particles in suspension. Accumulation of bryozoan fronds on the bottom may have provided a good substrate for attachment of epifaunal organisms, but at the same time would have rendered the substrate uninhabitable for shallow-burrowing infauna. Trilobite and holothurian fragments are very sparse. Only the trilobite genus *Namuropyge* occurs sporadically and, when present, is usually found in a reef facies. Apparently this genus has been able to find suitable niches in between the bryozoan colonies.

Study of thin sections has revealed that the calcareous sediment contains much organic matter, chert-filled bioclasts and traces of vertical rootlets. The large number of gastropods that are present in all growth stages would imply that vegetation was prolific (Black, 1954), which is confirmed by the abundance of well preserved leaflets.

Topozone 2 is characterized by a considerably less dense macrofauna, accompanied by a more even lamination and a higher silt content. Quartz grains floating in a slightly dolomitic mud matrix, thus deposited at the same time as the mud, indicate that this sediment was deposited under quiet lagonal conditions. Turbulence, rate of deposition and salinity may well have varied on a small scale, so that many different habitats were available for a diversity of faunal groups (Table 1B). Shallow-burrowing organisms, e.g. trilobites, holothurians and semi-infaunal brachiopods such as *Pugnoides* are fairly common (Fig. 4); their activities are reflected by small, circular to cylindrical concretions. The indigenous nature of most brachiopods is indicated by the fact that most shells are articulated and do not show any signs of post-mortem transport. Fenestrate bryozoa are less abundant than in the

Table 1. List of fossils found in sections 1, 2, 3 and 5, the topozones of which are defined in Figs 2 and 5. Symbols: + at least 1 specimen found, c commonly found, ? presence uncertain, - not found.

A. Section 1						
Topozone	1	2	3	4	5	
BRACHIOPODS						
<i>Actinoconchus lamellosus</i> (L'Eveillé)	+	+	+	-	-	
<i>Antiquatonia</i> sp.	+	+	-	-	-	
<i>Avonia youngiana</i> (Davidson)	-	-	+	-	-	
<i>Brachythyris pinguis</i> (Sowerby)	+	-	+	-	-	
<i>Cleiothyridina deroissyi</i> (L'Eveillé)	+	+	+	-	-	
<i>Composita</i> sp.	+	+	+	+	-	
<i>Crenispirifer angulata</i> (King)	-	-	+	-	+	
<i>Crurithyris urei</i> (Fleming)	+	+	c	-	-	
<i>Echinoconchus punctatus</i> (Sowerby)	-	+	-	-	-	
<i>Eomarginifera setosa</i> (Phillips)	+	+	+	-	+	
<i>Leptagonia analoga</i> (Phillips)	+	+	-	-	-	
<i>Marginicinctus marginicinctus</i> (Prout)	-	-	-	-	+	
<i>Martinia glabra</i> (Sowerby)	-	+	+	-	-	
<i>Megachonetes</i> sp.	+	-	-	-	+	
<i>Overtonia fimbriata</i> (Sowerby)	+	-	-	-	-	
<i>Plicochonetes buchianus</i> (de Koninck)	+	+	c	+	+	
<i>Productids</i>	c	c	+	+	+	
<i>Productina margaritacea</i> (Phillips)	+	+	-	-	-	
<i>Rhipidomella michelini</i> (L'Eveillé)	+	+	+	+	-	
<i>Rugosochonetes celticus</i> Muir Wood	-	+	-	-	-	
<i>R. hardrensis</i> (Phillips)	+	+	+	+	+	
<i>Schellwienella crenistria</i> (Phillips)	c	+	+	-	-	
<i>Schizophoria resupinata</i> (Martin)	c	+	-	-	-	
<i>Semiplanus</i> sp.	-	-	-	+	+	
<i>Shumardella missouriensis</i> (Shumard)	+	-	-	-	-	
<i>Sinuatella sinuata</i> (de Koninck)	+	+	-	-	+	
<i>Stenosisma</i> sp.	+	-	-	-	-	
<i>Tylothyris laminosa</i> (M'Coy)	+	-	+	-	-	
BIVALVES						
<i>Amusium concentricum</i> Hind	+	-	-	-	-	
<i>Aviculopecten clathratus</i> (M'Coy)	-	-	+	-	-	
<i>A. forbesii</i> (M'Coy)	+	-	-	-	-	
<i>A. gentilis</i> (Sowerby)	-	-	-	+	-	
<i>A. macrotis</i> (M'Coy)	+	-	-	-	-	
<i>A. nobilis</i> (de Koninck)	-	-	-	+	+	
<i>A. stellaria</i> (Phillips)	-	-	-	-	+	
<i>Parallellodon semicostatus</i> (M'Coy)	+	+	-	-	-	
<i>Pinna</i> sp.	-	-	-	-	+	
<i>Pseudamusium anisotum</i> (Phillips)	+	+	-	-	+	
<i>P. concentricolineatum</i> Hind	+	-	-	-	-	
<i>Sanguinolites</i> sp.	+	-	-	-	-	
GASTROPODS						
<i>Borestus</i> sp.	-	-	+	-	-	
<i>Donaldina costatula</i> (Donald)	-	+	+	-	-	
<i>D. nana</i> (Donald)	-	-	+	-	-	
OTHER FOSSIL GROUPS						
<i>Bryozoa</i> (fenestrate)	+	-	-	-	-	
<i>Bryozoa</i> (non-fenestrate)	+	c	-	-	-	
Fish plates	-	-	c	c	+	
<i>Holothurian sclerodermites</i>	c	c	-	-	+	
<i>Rugose corals</i> (solitary)	c	+	+	-	-	
<i>Trilobite fragments</i>	c	+	+	-	-	
topozone	1	2	3	4	5	
B. Section 2						
topozone	1	2	3	4	5	6
BRACHIOPODS						
<i>Actinoconchus lamellosus</i> (L'Eveillé)	-	-	-	+	-	-
<i>Antiquatonia</i> sp.	-	+	+	+	+	-
<i>Avonia youngiana</i> (Davidson)	+	-	-	-	+	-
<i>Brachythyris pinguis</i> (Sowerby)	+	-	-	-	-	-
<i>Chonetipustula carringtoniana</i> (Davidson)	-	-	-	?	-	-
<i>Cleiothyridina deroissyi</i> (L'Eveillé)	-	-	+	-	-	-
<i>Composita</i> sp.	-	+	+	-	-	-
<i>Crurithyris urei</i> (Fleming)	-	+	+	c	+	-
<i>Eomarginifera setosa</i> (Phillips)	+	+	+	c	+	-
<i>Gigantoproductus</i> sp.	-	-	-	+	+	-
<i>Lingula</i> sp.	-	+	+	+	-	-
<i>Linoproductus corus</i> (D'Orbigny)	-	-	-	-	?	-
<i>Marginicinctus marginicinctus</i> (Prout)	c	+	+	?	+	-
<i>Megachonetes</i> sp.	+	+	+	-	-	-
<i>Plicochonetes buchianus</i> (de Koninck)	+	+	-	-	-	-
<i>Productids</i>	+	+	+	+	+	-
<i>Pugnoides pleurodon</i> (Phillips)	-	+	+	+	-	-
<i>Rhipidomella michelini</i> (L'Eveillé)	-	+	-	-	-	-
<i>Rugosochonetes celticus</i> Muir Wood	+	+	+	-	-	-
<i>R. hardrensis</i> (Phillips)	-	+	-	-	+	-
<i>Schellwienella crenistria</i> (Phillips)	-	+	+	+	-	-
<i>Schizophoria resupinata</i> (Martin)	-	-	?	-	-	-
<i>Setigerites setiger</i> (Hall)	?	-	-	-	-	-
<i>Shumardella missouriensis</i> (Shumard)	-	-	-	-	+	-
<i>Sinuatella sinuata</i> (de Koninck)	-	+	+	+	-	-
<i>Stenosisma</i> sp.	-	+	+	+	-	-
<i>Tylothyris laminosa</i> (M'Coy)	-	-	+	-	-	-

Table 1. (continued)

<i>Eomarginifera setosa</i> (Phillips)	+	+	+	+	-
<i>Gigantoproductus</i> sp.	-	-	-	+	c
<i>Marginicinctus marginicinctus</i> (Prout)	+	-	+	-	-
<i>Overtonia fimbriata</i> (Sowerby)	-	-	-	-	?
<i>Plicatifera</i> sp.	-	-	-	+	+
<i>Plicochonetes buchianus</i> (de Koninck)	-	+	-	-	-
<i>Productina margaritacea</i> (Phillips)	-	-	-	+	-
<i>Pugnoides pleurodon</i> (Phillips)	+	-	-	-	-
<i>Rhipidomella michelini</i> (L'Eveillé)	-	-	-	+	+
<i>Rugosochonetes celticus</i> Muir Wood	+	+	+	+	-
<i>R. hardrensis</i> (Phillips)	+	-	+	?	-
<i>Schellwienella crenistria</i> (Phillips)	-	-	-	+	+
<i>Stenosisma</i> sp.	+	+	-	+	-
<i>Tornquistina polita</i> (M'Coy)	-	-	-	-	?
<i>Tylothyrus laminosa</i> (M'Coy)	+	+	-	+	+
BIVALVES					
<i>Aviculopecten nobilis</i> (de Koninck)	-	-	-	+	-
<i>Edmondia maccoyii</i> Hind	-	+	+	-	-
<i>Pseudamusium anisotum</i> (Phillips)	-	-	-	+	-
<i>Sanguinolites plicatus</i> (Portlock)	-	-	-	+	+
<i>Streblopteria ornata</i> (Etheridge)	+	-	-	-	-
GASTROPODS					
<i>Borestus</i> sp.	-	-	-	+	-
<i>Donaldina nana</i> (de Koninck)	-	-	-	+	-
<i>Euphemites urei</i> (Fleming)	+	-	+	+	-
<i>Ianthinopsis rectilinea</i> (Phillips)	-	-	-	+	-
<i>Knightites exilis</i> (de Koninck)	+	-	-	+	-
<i>Naticopsis planispira</i> (Phillips)	-	-	-	+	-
<i>Platyzona tornatilis</i> (Phillips)	-	-	-	+	-
<i>Straparollus</i> sp.	-	+	-	+	-
OTHER FOSSIL GROUPS					
Bryozoa (fenestrate)	+	c	-	+	-
Bryozoa (non-fenestrate)	-	-	-	-	+
Crinoids (single ossicles)	-	+	+	c	-
Crinoids (longer stem fragments)	-	-	-	-	-
Fish plates	-	-	-	c	c
Holothurian sclerodermites	+	+	+	+	-
Plant leaflets	+	+	+	+	-
Rugose corals (solitary)	-	+	-	+	+
Trilobite fragments	-	-	-	+	-
topozone	1	2	3	4	5

topozone below, but are still fairly common, suggesting good aeration in some parts of the lagoon.

Ascending the sequence, fossil diversity decreases with a gradual increase in silt and dolomite content. The mud matrix of topozone 3 contains ca. 15 vol% of quartz and ca. 5 vol% of dolomite rhombs. Included bioclasts often show complete pyritisation which, together with a scarcity of fossil

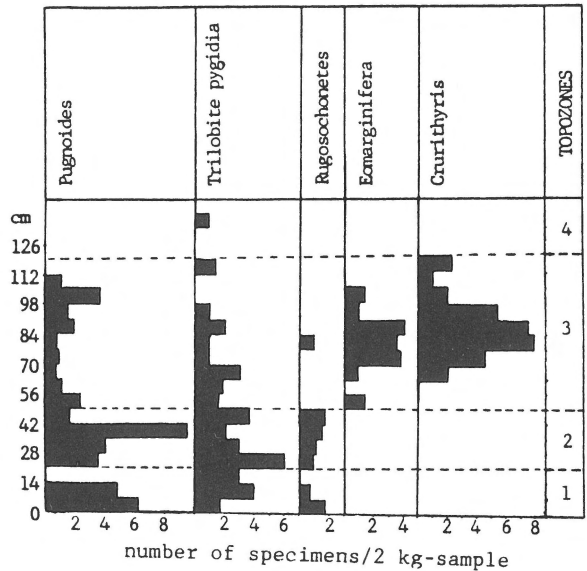
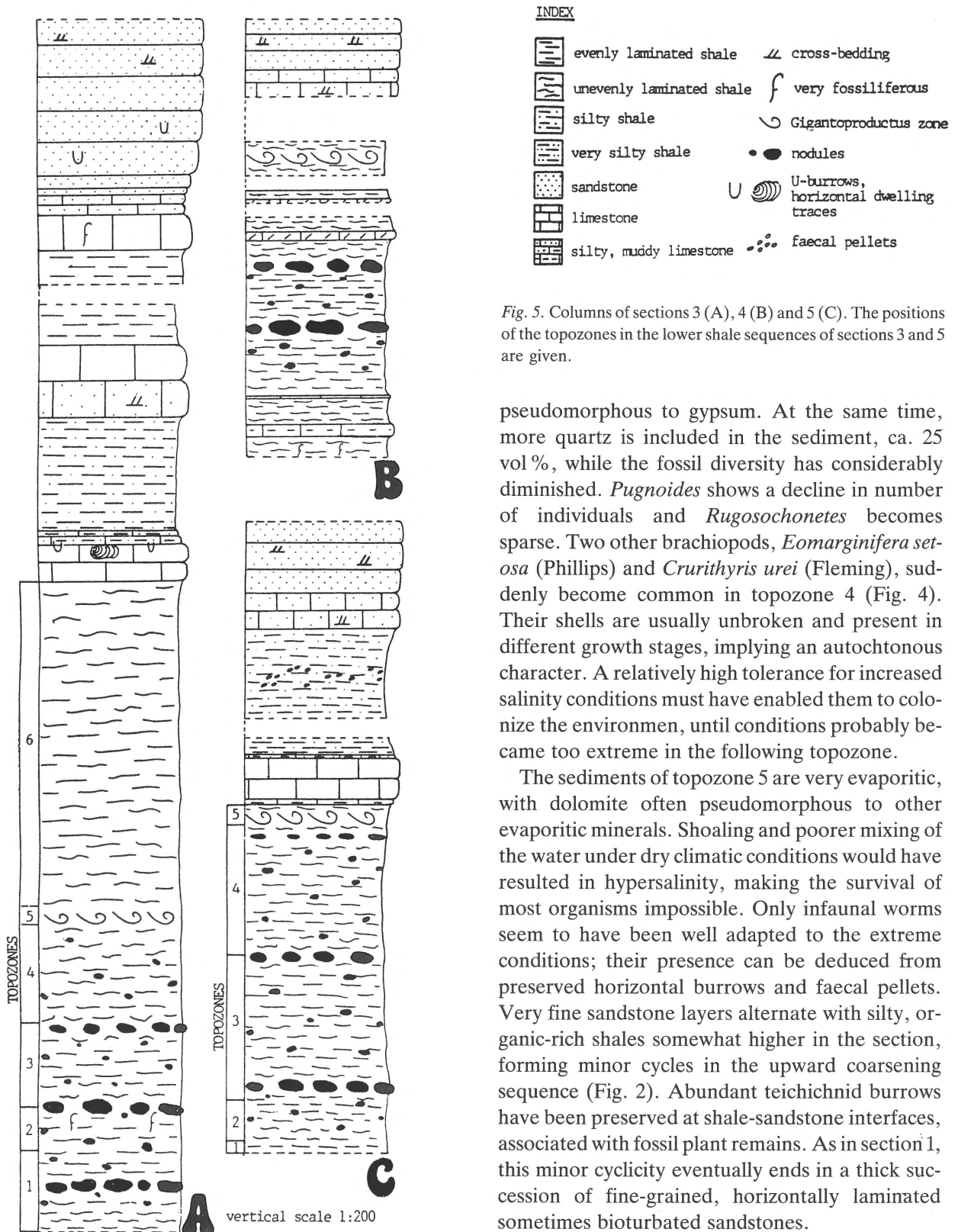


Fig. 4. The density of some fossil groups in topozones 2-5 of section 2. The number of specimens was counted in 2 kg-samples from a continuous series of subzones (7 cm).

debris, indicates sedimentation in very quiet, often poorly aerated lagoon water. The distinct decline in the number of suspension feeders, including bryozoans, crinoids, rugose corals and brachiopods, is probably coupled with less mixing of the water. *Pugnoides pleurodon* (Phillips) and *Rugosochonetes celticus* Muir Wood are the most common brachiopods (Fig. 4). Their undamaged, articulated shells appear to have been buried in life position, from which may be inferred that they found suitable habitats in some, better mixed parts of the lagoon. Herbivorous gastropods and plant remains are much rarer here than in the calcareous shales of topozone 1, suggesting that the local environmental conditions were not conducive for a rich vegetation. Besides absence of nearby land vegetation no signs of extensive algal growth have been found. Fragments of mud-feeding holothurians are largely confined to the finer grained sediment of topozone 2, while trilobites remain fairly common at places and seem not yet to have been hampered by the gradually changing conditions. Further increase of salinity is inferred from thin sections of topozone 4, where dolomite is present in the form of crystal rhombs and is sometimes



Section 3 (locality 51 of Moore, 1958)

Section 3 is located in the south-western part of Bishopdale (Fig. 1). Topozone 1 consists of dark grey, finely laminated shales that are rich in organic matter. Nodules with a diameter up to ca. 10 cm occur throughout these shales, while larger ones are mainly confined to one horizon at the top of the topozone (Fig. 5). On the basis of their growth habit and internal growth structures, that are sometimes visible, these nodules are assigned to algae. Macrofossils are sparse, mainly consisting of bivalves. The occasional presence of articulated, often pyritised ostracod shells points to quiet, badly aerated bottom conditions.

More macrofossils appear in the uppermost part of topozone 1, ranging into the calcareous and fossiliferous shales of topozone 2 (Fig. 6; Table 1C). The brachiopods *Rugosochonetes celticus* Muir Wood, *R. hardrensis* (Phillips) and *Crurithyris urei* (Fleming) are the most common early colonists, associated with trilobites, holothurians and few bellerophontacean gastropods. *Rugosochonetes* abruptly declines in numbers at the top of topozone 1, where several other genera take over.

The considerable increase in fossil density and diversity in topozone 2 may be related to a reduced sedimentation rate and increased water turbulence, which better mixed and aerated the basin water. The common occurrence of foraminiferids suggests that there was an open connection with the sea, resulting in a normal marine salinity. This would have allowed colonization by many stenohaline organisms, including solitary rugose corals. The abundance of shell debris and single crinoid ossicles gives evidence of fairly strong current action. Burrowing activities of trilobites, holothurians and other (semi-)infaunal living animals have locally disturbed the original lamination. Many of these faunal elements, although less dense, occur in topozone 3. The large brachiopod *Gigantoproductus*, which is absent in the lowermost part of the sequence, gradually becomes more common and is present in different growth stages. The fauna remains fairly diverse throughout topozone 3 and seems not to have been dominated by any one or only few elements.

The algal nodule beds that demarcate topozone 3 are characterized by relatively high abundance of fossil debris and a scarceness of intact macrofossils. It thus seems likely that these algal beds were formed during periods of highly turbulent water. A temporarily slow sedimentation rate in relatively clear water may have stimulated abundant algal growth.

Dark grey, organic-rich and generally finely laminated shales are found on top of the highest algal nodule horizon, forming topozone 4 (Fig. 5). This topozone is characterized by a scarcity of macrofossils; such as there are consist of articulated brachiopods, bivalves, bryozoa, gastropods and plant leaflets, while small, irregularly shaped algal nodules occur sporadically. The common occurrence of ostracods on the other hand, which usually show well preserved, often pyritised, articulated shells, would indicate that deposition took place under quiet, oxygen-poor conditions which were favourable for pyrite to develop.

The lighter grey, coarser laminated shales of topozone 5 are characterized by a higher lime content and an abundance of differently sized shells of *Gigantoproductus*. From the co-occurrence of different developmental stages and absence of any signs of transport it is concluded that most shells were buried in life position. It is not unlikely that *Gigantoproductus* acted as an opportunist (J. Pattison, personal communication). It may have taken advantage of a reduced sedimentation rate and increased current actions supplying sufficient food, associated with a scarcity of other benthic suspension feeders. Opportunistic species generally have little tolerance for the presence of other organisms (McCall, 1977). Only a few brachiopods and other faunal groups that generally require high energy water, e.g. bryozoa and rugose corals, are present in the same horizons.

From the base of topozone 6, there is an abrupt decline in the number of individuals of *Gigantoproductus*, presumably due to a sudden onset of unfavourable circumstances. As an opportunist, its populations would have been very unstable and thus would have become extinct very quickly (Levinton, 1970). The calcareous mud-shales of topozone 6 are characterized by a coarse, uneven lamination and a scarcity of macrofossils.

The muddy, slightly fossiliferous limestone on top of topozone 6 reflects a minor transgression. Infaunal deposit feeders have left U-burrows and horizontal dwelling traces in the uppermost part of this limestone. A successive regressive period is reflected by the silty, micaceous shale sequence on top of the limestone. The very high influx and rate of deposition of silts and clays during this period probably excluded all faunal life.

Several other transgressive and regressive periods are recognizable in the upper part of the column, represented by alternations of limestones and shales (Fig. 5). A final regression resulted in deposition of a thick succession of fine-grained, evenly laminated sandstones followed by medium-grained, well-sorted sandstones. The latter exhibit parallel, slightly inclined laminations and scour surfaces resembling those of beach barrier deposits. The common occurrence of vertical burrows point to deposition in a shallow, intertidal environment (Seilacher, 1967; Heckel, 1972).

Section 4 and 5 (localities 54 and 55 of Moore, 1958)

Both sections are only a relatively short distance from section 3 in Bishopdale (Fig. 1). They show an overall picture that is similar to that of section 3 (Fig. 5). Section 4 is very limited in outcrop, especially its calcareous shale units, which are heavily eroded and weathered. Because of the fact that sections 4 and 5 seem to have many elements in common, only section 5 will be described.

The lowest topozone of section 5 consists of dark grey, finely laminated mudshales, rich in organic matter. Macrofossils, which are sparse and sometimes pyritised, include articulated brachiopods, bivalves, bryozoan fragments and plant leaflets (Table 1D). Deposition of clay would thus have taken place under quiet, sometimes anaerobic conditions, which inhibited the decay of organic matter and allowed pyritisation of bioclasts. The abundance of entire shells of *Crurithyris* may be explained by the fact that this relatively small-sized brachiopod probably lived attached to floating seaweeds or other plant remains in the upper, better aerated parts of the water (Fig. 7).

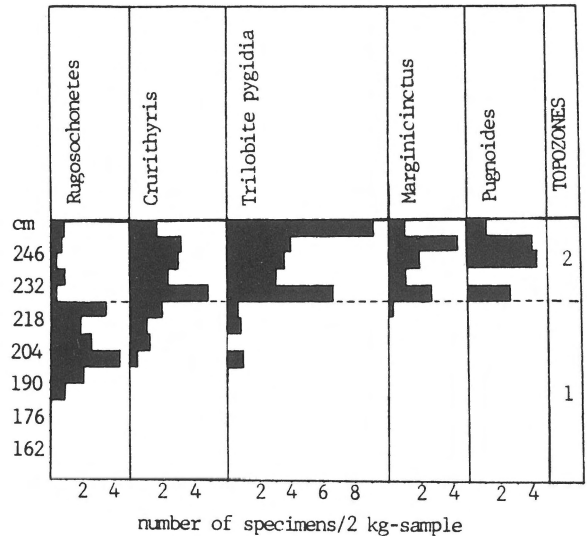


Fig. 6. The density of some fossil groups in topozones 1 and 2 of section 3. The number of specimens was counted in 2 kg-samples from a continuous series of subzones (7 cm).

Topozone 2 is characterized by a slightly higher fossil density and occurrence of algal nodules varying in diameter up to ca. 20 cm. The latter remain common in topozones 3 and 4. The fossil fauna is dominated by suspension feeders requiring a fair degree of water turbulence. Fragments of fenestrate bryozoa are common, while intact bryozoan fronds are occasionally found, almost certainly indigenous in origin. In addition to several mostly articulated brachiopods and bivalves, solitary rugose corals occur in this topozone, which seem to have been buried in life position. Ripple-marks in the unevenly laminated sediments point to a fair degree of wind-generated wave activity in the palaeo-environment.

The algal bed at the bottom of topozone 3 contains very large nodules with a maximum diameter of 45 cm. They are surrounded by very fossil-poor, finely laminated shales that were probably deposited under quiet, reducing conditions, as indicated by the presence of pyritised bioclasts. A second algal nodule bed separates topozone 3 from the fossiliferous shales of topozone 4. As argued in the earlier description of section 3, the algal nodule beds may reflect periods of temporarily increased water turbulence, although fossil debris is only abundant in the second algal horizon.

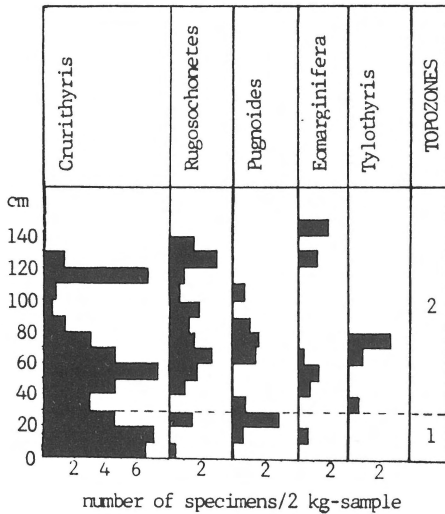


Fig. 7. The density of some fossil groups in the lowest two topozones of section 5. The number of specimens was counted in 2 kg-samples from a continuous series of subzones (10 cm).

The lower- and topmost parts of topozone 4 are characterized by a fairly dense and diverse marine fauna (Table 1D). Most brachiopods, bivalves, gastropods and rugose corals do not show any sign of post-mortem transport, and probably formed part of autochthonous populations. Their growth would have required good mixing of the basin water to supply sufficient oxygen and food in suspension. Concentrations of very fine fossil debris evidences fairly strong current action.

The middle and by far the largest part of topozone 4 consists of largely unfossiliferous mud-shales that were probably deposited under the same environmental conditions as topozone 3.

Topozone 5 is characterized by distinctive lighter grey and more coarsely laminated calcareous shales, implying significant changes in the palaeo-environment. The abundance of fossil debris including fish plates reflects a high water turbulence, while the lime content would indicate a considerably reduced sedimentation rate of mud, thus allowing precipitation of lime. These conditions apparently were suitable for rapid colonization by *Gigantoproductus*. Other brachiopods, bryozoa, rugose corals and trilobites seem to have been strongly restricted in number by the high densities of *Gigantoproductus* shells. The density of *Gigan-*

toproductus has been measured in 5-kg samples taken from a vertical series of subzones (Fig. 8A). It shows a rapid increase with a maximum of 37 shells per 5-kg sample. Clearly, some kind of adverse event must have caused an abrupt decline in its density, as in topozone 5 of section 3, quickly followed by complete elimination. Besides the density, the distribution of different growth stages in the fossil population of *Gigantoproductus* has been examined in two subzones of the same series (Fig. 8B). Two size-frequency histograms, based on the maximum width, show respectively the size distributions of a relatively immature, still growing population and a more mature population. It appears that a general shift from small to larger sized individuals took place during growth of the population. Shells with a maximum width less than 3 cm are absent. This may be explained by the fact that young, gently concavo-convex shells must have had a less stable position in the sediment than full-grown, differentially thickened, strongly concavo-convex adult shells, and would therefore have been more vulnerable to currents or possible predators. Furthermore, young shells presumably formed a minor part of the total population, as a result of rapid growth in early stages, which strategy would be characteristic of opportunists, thus enhancing their chance of survival (Levinton, 1970). At first sight *Gigantoproductus* seems to have had one or more preferential orientations, probably strongly related to the directions of dominant water flows in the palaeo-environment. To elucidate this, the orientation of a large number of specimens present in three different subzones was measured. The lowest of these subzones contain shells which are dominantly orientated with their apertures pointing in one direction, suggesting a dominant palaeo-current from the north-east (Fig. 9A). Shells in the other two subzones, where *Gigantoproductus* reaches a maximum abundance, show a tendency to turn their apertures to one of two opposite directions, the north-east and south-west, which suggests tidally influenced palaeo-currents (Fig. 9B, C). It is probable that young shells rested freely on the mud substrate and were able to choose their orientation, probably best serving their water circulatory system by facing into the dominant current

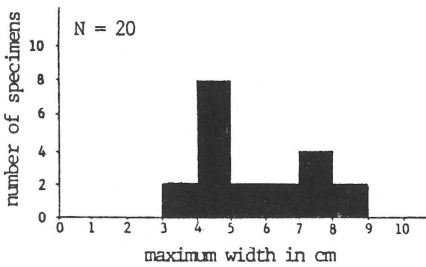
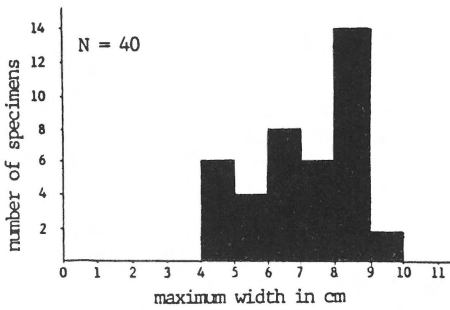
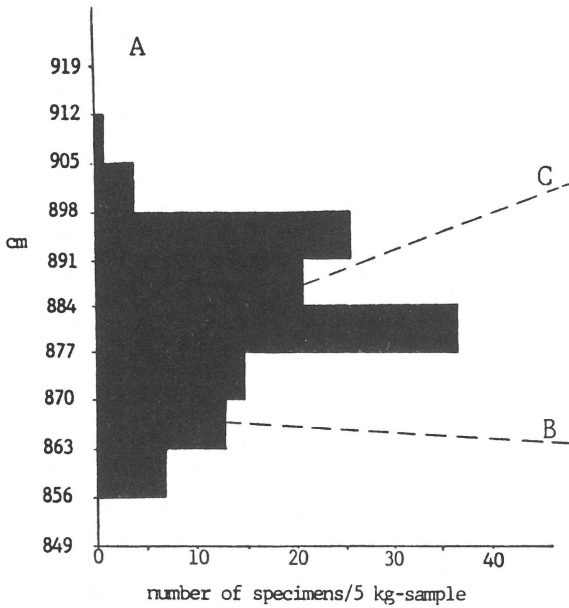


Fig. 8. Histograms showing the density and maximum width of *Gigantoproductus* in topozone 5 of section 5. A: density measured in 5 kg-samples from a continuous series of subzones (7 cm). B and C: maximum width of specimens in two subzones of the same series, indicated by dashed lines. N is the total number of measured shells.

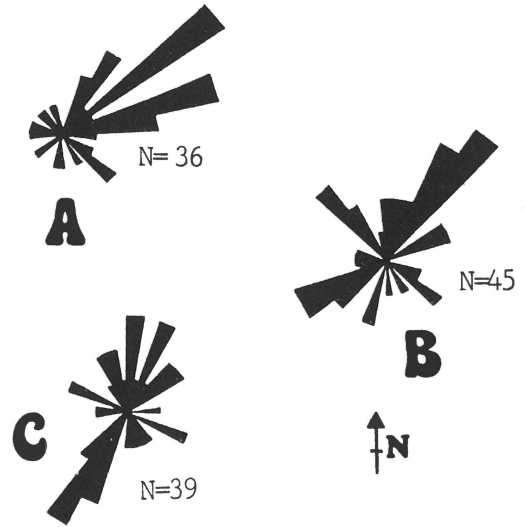


Fig. 9. The orientation of *Gigantoproductus* in subzones of topozone 5 in section 5. A: 870–877 cm, B: 877–884 cm, C: 884–891 cm. A compass was used to measure the direction to which the shell apertures were turned to. N is the total number of examined specimens.

direction(s). The development of spines, differential thickening and stronger convexity of the ventral valve during growth could be interpreted as special adaptations to a static, quasi-infaunal position, similar to the presumed life habit of many productoid brachiopods, e.g. *Waagenoconchia* (Grant, 1966). It is not likely that *Gigantoproductus*, once stabilized in the sediment, was able to adapt its orientation to changing current directions.

The thin limestone deposited on top of topozone 5 reflects a minor transgression, which may have played an important role in the elimination of *Gigantoproductus*. The limestone shows the same characteristics as that present above the *Gigantoproductus* zone in section 3 (Fig. 5), and is also overlain by an interval of silty, micaceous shale reflecting an increased terrigenous input and sedimentation rate. Small, barrel-shaped coprolites with a mean length of 1.5 mm, produced by deposit-feeding animals, were locally found in these shales. The cyclothem ends with silty, often cross-bedded limestones and fine- to medium-grained, bioturbated sandstones with parallel, slightly inclined

laminations and scour surfaces, as present in the upper half of sections 3 and 4 (Fig. 5).

Conclusions and discussion

Deltaic growth and the fossil community

The different fossil faunas that have been found in different lithological units of the 5-Yard Limestone cyclothem contain important information about the growth of the Yoredale delta and the related regression of the sea. During the initial phases of regression the sedimentation rate remained low, so that colonization by benthic suspension-feeding communities could take place. It is quite likely that the dense and highly diverse fossil faunas in the calcareous shales at the bottom of some of the sections are partly reworked and thus 'time-averaged' in the sense of Walker & Bambach (1971). Recognition of different stages of faunal succession or replacement is impossible. The low depositional rate may have caused faunal mixing and condensation, a phenomenon described by Fürsich (1978). Nevertheless it is noticeable that brachiopods with morphological adaptations to life on a soft substrate, such as development of large flat valves, are generally more common in the lowest horizons of the calcareous shale units, e.g. *Schellwienella* (Fig. 3). These may have formed part of pioneer communities that colonized the bottom shortly after deposition of terrigenous mud. Accumulation of their shells would have stabilized the substrate, successively leading to colonization by other epifaunal suspension feeders, e.g. *Schizophoria*, and more or less restricting the number of deposit feeders. Similar ecological successions controlled by autogenic effects have been described from the fossil record (e.g. Walker & Alberstadt, 1975; Johnson, 1977). This situation would be typical of a fairly turbulent, offshore-shelf area where the current pattern or a low sediment supply prevent a continuous and high sedimentation rate (Fürsich, 1978).

Later phases of regression involved shallowing of the water accompanied by an increased sedimentation rate. Degradation of the established commu-

nity would have been caused by a gradual intensification of the environmental stress gradients acting upon that community. McCall & Tevesz (1983) noted that many palaeoecological studies that have used successional concepts to explain temporal faunal change on clastic bottoms would not, in fact, truly describe palaeoecological succession, because they include an obvious and important environmental change, thus leaving little role for biotic interactions. Several problems and methods of recognition were already demonstrated by Rollins et al. (1979), using the following definition as important guideline: 'Succession is a modification of the environment by colonizers, allowing introduction of new taxa through time' (Kauffman, 1974). It thus seems plausible that the appearance of several new taxa at the top of the calcareous shale units, e.g. bellerophonacean gastropods in section 1 (Fig. 3) did not result from community succession but from community replacement initiated by the increased sedimentation rate.

As a result of repetitive and frequent episodes of increased sediment input, community control has probably been predominantly allogenic and seems to have prevented communities from becoming highly organized. Additionally, salinity fluctuations played an important role in the Wensleydale area. Some organisms, e.g. *Crurithyris* and bellerophonacean gastropods, seem to have had a relatively high tolerance for salinity fluctuations.

The shale sequences in Bishopdale do not show any sign of increased salinity conditions, but contain good evidence of open-water conditions with strong fluctuations in turbulence and sedimentation rate. Foraminiferids are common microfaunal elements in the non-silty shales of the Bishopdale sections, often associated with a diversity of ostracods. A micropalaeontological study of these fossil groups is recently undertaken by the author.

Although algal nodules occur throughout large parts of all sections, by far the largest are found in Bishopdale, being restricted to certain horizons. Dome-like stromatolites as present in topozone 4 of section 1 are commonly found in low-energy environments. Blue-green algae have produced stromatolites in a variety of environments, but are most often found in shallow marginal waters of

marine basins and saline lakes (Wray, 1978). The climatic conditions during Lower Carboniferous times would also have been very suitable for growth of calcareous algae, since maximum precipitation of calcium carbonate can be expected in the tropical, lower latitudes where relatively warm temperatures and a low carbon dioxide partial pressure are found (Fig. 1). Various other factors including light intensity and its spectral composition, substrate and water movement, may have played an important role in the occurrence, shape and size of the algal spheres. It is not unlikely that they were produced by different taxa, because there is evidence that depth limits at relatively low taxonomic levels, especially genus and species, are relatively narrow (Wray, 1972, 1978). A more profound study of the morphology and taxonomy of algal spheres occurring throughout the 5-Yard Limestone cyclothem is to appear in a future paper by the present author.

After a period of relative quiescence following several periods of abundant algal growth, the supposed opportunist *Gigantoproductus* rapidly colonized the Bishopdale area. It seems to have taken advantage of a suddenly increased water turbulence and reduced sedimentation rate, together with a lack of competition by other benthic suspension feeders.

Some twenty years ago a band of *Gigantoproductus* was found below the present base of the silty shale exposure in section 2, in between topozones 1 and 2 (Fig. 2). All the shells in this band were lying one on top of the other. It seems as though for the short period the conditions described above extended northwards into the Wensleydale area (E.N.K. Clarkson and W.B. Heptonstall, personal communication).

Measurements of the orientation of *Gigantoproductus* in section 5 has demonstrated that the shells turned their apertures in dominantly one or two opposite, tidally influenced current directions, respectively the north-east or north-east and south-west (Fig. 9). The preferential orientation of *Gigantoproductus*, linked with the direction of dominant palaeo-currents, would indirectly suggest that the main source of clastic sediments must have lain to the north-east, as already generally and independently agreed by many authors.

Depositional environments

The lithologies in the clastic sequences of the Yoredale facies can often be directly matched with those from modern river dominated deltas, e.g. the Mississippi as described by Fisk et al. (1954 and Fisk, 1961). The fossiliferous, calcareous shales which pass up into less fossiliferous, argillaceous shales in the lower part of the sections are interpreted as the prodelta facies, where the faunal content is inversely related to the silt content. Progradation of the Yoredale delta would have caused prodelta successions to become overlain by delta front and delta plain deposits, accompanied by an increase in grain size and disappearance of fauna. The delta plains of the Mississippi are open at the seaward end where they pass directly into the delta front. Interdistributary areas of fluvial-dominated delta plains are generally enclosed, shallow water environments which are quiet or even stagnant, although in the open bays of the Mississippi delta waves induce mild agitation. Flood-generated processes are the principal means of sediment supply to these areas, resulting in a wide range of facies and sequences (Elliott, 1974). The silty shales and very fine, ripple-marked sandstones in sections 1 and 2 were probably deposited in shallow water of such interdistributary bay facies, while the coarsening upwards sequence characterized by increasing thickness of the sandstone beds upwards would indicate levee progradation (Elliott, 1975, 1978).

The locations in Bishopdale have been less influenced by the prograding delta, which here is reflected in the sections by minor transgressive cycles. The unfossiliferous, silty and micaceous shales in the upper half of sections 3 and 5 (Fig. 5) may correspond to delta-front deposits. The overlying silty, sometimes cross-bedded limestones were probably deposited in a shallow marine environment situated on the seaward margin of the delta. The cross-bedded sandstones at the top of sections 3, 4 and 5 are very similar to deposits in modern nearshore, wave-dominated environments of prograding barrier beaches, e.g. the coastal barrier deposits in South- and North-Holland (Van Straaten, 1965). Elliott (1975) found similar beach cross-bedding in the uppermost sandstones of the

Great Limestone (Yoredale) cyclothem in Wear-dale, N. Pennines.

The development of different environmental conditions in the northern and southern parts of the area may be explained by growth of a coastal barrier, partially separating the northern part from the main body of the sea, thus changing it into a lagoon with variable salinity. Minor transgressions of the sea were restricted to the southern part of the area, and must be ascribed to small-scale changes in the palaeo-environment, such as variations in sediment input and subsidence of the sea floor. Moore (1958) concluded that minor rhythms often show the same characteristics as the major rhythm that includes them, except for the persistence of the limestone. Comparing the basal 5-Yard Limestone with minor limestones in the same cyclothem, however, and taking the fauna into account, this conclusion is not borne out by the new evidence. The basal limestone is characterized by a dense and diverse marine fauna, associated with an extremely low percentage of terrigenous mud. Many macrofaunal elements adapted to a slight increase of detrital input can still often be found in non-silty shales resting on the basal limestone. The minor limestones on the other hand are generally characterized by a scarcity of macrofossils and a higher content of mud and silt, while they are usually overlain by very fossil-poor, silty shales or sandstones. Major transgressions operating against delta growth would have resulted in a distinct landward shift of the coastline, while minor transgressive events interrupted the outward growth of the delta only to a small extent, and as a whole did not effect delta progradation. Finally it is concluded that progradation of the Yoredale delta remained fairly slow, allowing small-scale transgressions in the southern part and causing gradational passages from fine-grained into coarser grained sediments in the northern part of the study area.

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