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**Trophic structure and spatial distribution of macrofaunas in the
Hurlet and Index limestones (Carboniferous: upper Viséan and
lower Serpukhovian) of Ayrshire, Scotland, UK**

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Synopsis

Explorative multivariate numerical analysis of British Geological Survey historical Biostratigraphy collections from the Carboniferous Hurlet and Index limestones, Ayrshire, yields results capable of palaeoecological interpretation. The faunas are distributed along environmental gradients within carbonate facies that systematically extended out into other sedimentary settings. Clusters of genera in higher taxa plotted on ternary diagrams of trophic structure show both units commonly include epifaunal suspension feeders, although one cluster from the Hurlet Limestone includes epifaunal detritus-suspension feeders and another from the Index Limestone includes vagrant-epifaunal detritus-suspension feeders. All the clusters include the surficial and semi-infaunal tiers, non-motile and suspension feeding categories, but they show trends of increasing ecological complexity. The geographical distribution of the clusters shows the Hurlet Limestone palaeoenvironment was most diverse around Sorn, whilst that for the Index Limestone was diverse in all three main areas of outcrop. This variation is attributed to local fluctuations in depth, sea floor conditions

and water quality. An 'embayment' in the palaeoenvironment of the Index Limestone, seen by draping the interpretations over a 3D computer model of the subsurface, was associated with the Kerse Loch Fault, where penecontemporaneous displacement and an inferred palaeotopographical fault scarp influenced marine water flow, environmental distribution and genus diversity.

Introduction

The extensive collections of the British Geological Survey (BGS) are the only remaining source of palaeontological information for many localities in the Carboniferous rocks of the Midland Valley of Scotland. They reflect the extensive exploration and exploitation of coal and other materials from the late 18th to the mid-20th century that provided a considerable amount of information on the Carboniferous geology of the region (Cameron & Stephenson 1985; Trewin & Rollin 2002; Read *et al.* 2002).

Acquired over a period of about 136 years, the specimens were identified by many palaeontologists and occur on rock samples of various dimensions from both borehole and surface exposures. They were almost exclusively collected for the purposes of biostratigraphy, which in the Scottish Carboniferous generally requires knowledge of total assemblages from beds. However, there are rare instances of collectors known to have been biased towards sampling particular fossil groups, and some taxa may also be under represented. An example of the latter is the seemingly minor occurrence of bryozoans in the materials studied compared to the significant number of genera and species known in field exposures of the mudstone and limestone facies of the Hurlet Limestone.

Although lacking the systematic sampling required for a detailed quantitative investigation, we have shown (Dean *et al.* 2010) that these historical collections are amenable to explorative multivariate numerical analysis that yields results that are capable of meaningful palaeoecological interpretation. These compare very favourably with the qualitative analyses of Wilson (1967; 1989), which arose from over forty years of experience on the Carboniferous of the Midland Valley. Moreover, they provide the platform for a deeper level of palaeoecological analysis. Here we exploit the BGS database on the macrofaunas collected from the various lithological strata comprising the Hurler and Index limestone beds (hereafter referred to as the Hurler and Index limestones) to characterise the trophic structures of associations of taxa, their links to lithofacies and their spatial distributions. The interpretation of the last of these is enhanced by draping the results over a three-dimensional computer model of part of the Ayrshire Coalfield Basin constructed as part of geological resurvey by the BGS.

Geology and lithostratigraphy

Carboniferous strata in the area of study form the southern margin of the Ayrshire Coalfield Basin (Fig. 1) and comprise the Strathclyde, Clackmannan and Coal Measures groups (Dean *et al.* 2010, fig. 2). Wilson (1989) considered that during the Tournaisian and Viséan this western part of the Midland Valley was a relatively stable, slowly subsiding area receiving little sediment in comparison with eastern areas. The base of the late Viséan Hurler Limestone marks the bounding surface between the mainly non-marine sandstones, siltstones, mudstones with volcanic rocks of the Strathclyde Group stratigraphically below it and the overlying cyclical

sequence of marine limestone-bearing strata of the Lower Limestone Formation, Clackmannan Group (Fig. 1). The Hurlet Limestone comprises the lowermost fully marine limestone unit in the Lower Carboniferous succession that can be identified and correlated across the Midland Valley (Browne *et al.* 1999). Within the area of study it is generally about 3 m thick (although it can be more than 7 m thick), light to dark grey and developed largely as compact, well-bedded limestone or calcareous mudstone with thin limestone interbeds. Mudstone and siltstone strata also occur. The Hurlet Limestone may contain very few fossils other than crinoid columnals, but in places it can be highly fossiliferous (see Simpson & MacGregor 1932; Eyles *et al.* 1949; Robertson *et al.* 1949; Dean 2002).

The Lower Limestone, Limestone Coal and Upper Limestone formations are characterised by strongly cyclical, upward-coarsening sequences of limestone, mudstone, siltstone and sandstone capped by seatearth and coal, with the proportions differing in each of the formations. The limestone units within the Lower and Upper Limestone formations represent major marine transgressions and have faunas dominated by brachiopods and molluscs, with other forms such as corals only occurring in significant numbers at a few horizons. The vertical ranges of some species have proved useful for stratigraphical correlation both locally and regionally (see Wilson 1967; 1989).

The base of the early Serpukhovian Index Limestone (Fig. 1) defines the boundary between the repeated sequences of coal-bearing strata of the Limestone Coal Formation stratigraphically below it and the overlying cycles of marine limestone-bearing strata of the Upper Limestone Formation. It served as an indicator to 19th

Century miners searching for the valuable coals and ironstones of the Limestone Coal Formation and is easily recognised over much of the Midland Valley, although calcareous strata are not well developed in eastern parts (see Wilson 1967). Up to 3 m thick in the west, the Index Limestone in the area of study is lithologically more varied than the Hurler Limestone and has a rich and diverse fauna. The unit comprises bioclastic limestone (including dolostone), argillaceous limestone, calcareous mudstone, mudstone, siltstone and minor sandstone strata (see Simpson & MacGregor 1932; Eyles *et al.* 1949; Robertson *et al.* 1949; Dean 2002). It is generally rather argillaceous at the top and bottom, and the limestone stratum is overlain by a thick marine mudstone ‘roof’ (Cameron & Stephenson 1985; Read *et al.* 2002).

Shelf palaeoenvironment and biofacies

Wilson (1967) considered the lithological differences in the marine Namurian sedimentary rocks of the Midland Valley to reflect different environmental conditions, and that these conditions were sufficiently dissimilar for local differences in the benthonic faunas to be developed. Whilst noting that many taxa occur in a wide range of rock types, he subsequently related the restricted areal distribution of certain groups of species (biofacies) in Tournaisian and Viséan strata to lateral variations in the lithologies of the individual marine cycles and he presented, in generalised diagrammatic form, the occurrence of the most commonly found marine fossils in relation to the lithology of the host rocks (Wilson 1989, fig. 9). Wilson (1989) interpreted mudstones as representing a near-shore zone, and calcareous mudstones as reflecting a zone intermediate to clearer off-shore or on-shore settings in which limestones were deposited. He argued that the mudstone provided softer substrates dominated by infaunal organisms and the limestone gave firmer substrates with

dominantly epifaunal forms.

Wilson (1989) also noted a general correspondence at some horizons (the Hurlet, Blackhall and Hosie limestones) between faunas dominated by epifaunal forms such as calcareous brachiopods, bryozoans and corals in strata of high carbonate content, and those areas with thinner successions and presumably least subsidence. This applied, in particular, to the southern and western parts of the Midland Valley, which were farthest from the inferred sources of the siliciclastic sediments believed to be transported by rivers flowing into the region from the N and NE. He did, however, recognise that the distribution of different types of benthonic faunas must have been the result of many interacting factors, and that more information and research may well lead to different interpretations.

Faunas of the Hurlet and Index limestones

In many parts of the Midland Valley, the base of the Hurlet Limestone is distinguished by a transgressive faunal sequence, the so-called Macnair Fauna (Macnair 1917; Wilson 1989, p. 104). However, in the present study area none of the elements of the Macnair Fauna have been positively identified in the mudstone strata forming the base of the Hurlet Limestone or in the limestone stratum itself, although the presence of the brachiopods *Echinoconchus* sp. and *?Pugilis* sp., and the bivalve *Sanguinolites* sp. in the said limestone may be biostratigraphically significant (see Wilson, 1989; Dean 2002).

Three biofacies were distinguished by Wilson (1989 and references therein) in the limestone and mudstone strata of the Hurlet Limestone. Biofacies 1, with dominant

Lingula, *Productus* and *Euphemites* indicated shallow, possibly locally brackish waters with a relatively high siliciclastic input. Biofacies 2, with dominant *Avonia*, *Pleuropugnoides* and *Limipecten* was regarded as indicating generally shallow shelf seas, with intermediate conditions between Biofacies 1 and 3. Biofacies 3, with dominant solitary corals (excluding zaphrentoids), *Krotovia* and *Conocardium*, indicated quiet, well-lit waters in near-shore to off-shore areas - *Conocardium* being characteristic of 'biohermal' build ups. Siliciclastic content decreases and carbonate content increases from the areas of biofacies 1 to 3 suggesting the main source of clastic inflow lay to the NW, probably from the mouth of a river system there (see Wilson 1989, fig. 8). Dean *et al.* (2010) identified three faunal groups in the Hurlet Limestone with a broad link to lithofacies that accord with the interpretations of Wilson (1989). If Biofacies 3 of Wilson (1989) equates with Group 2 of Dean *et al.* (2010) then the former may be extended (to a small degree) into an area of the Midland Valley for which no palaeoenvironmental information was previously given (see Wilson 1989, fig. 8).

The Index Limestone has a distinctive fossil content over much of the Midland Valley, with algal concretions and the brachiopod *Latiproductus latissimus* common in many places. In the mudstone immediately above and below the limestone stratum a rich and varied fauna is normally present with brachiopods and molluscs (Wilson 1967).

Whilst Wilson (1967) did not define biofacies as such in the limestone and mudstone strata of the Index Limestone, he did refer to epifaunal variation in the overlying Upper Limestone Formation as the formally named limestone beds are traced laterally

from approximately SE to NW possibly reflecting river influx into the shelf area from the north. He considered that this would, in general, reduce the salinity of the marine water and increase the siliciclastic sediment content, which in turn would influence the benthonic faunas.

Numerical analyses

The BGS macrofossil collections from the Hurlet and Index limestones

The faunas from surface exposures and boreholes in Ayrshire are mainly held in the Biostratigraphy collections in the British Geological Survey office in Edinburgh (see Dean 2002) and were collected over a period of nearly 140 years. They comprise 20 samples from 14 localities from the Hurlet Limestone and 94 samples from 53 localities from the Index Limestone (see Dean *et al.* 2010, fig. 1). The taxonomic identification of each recorded fossil is at the highest possible level of determination, which ranges from named species to phylum. The macrofaunal data from each locality can be further subdivided by sample lithology into faunas from mudstone/claystone (undifferentiated), calcareous mudstone, sandstone, siltstone, calcareous siltstone, limestone, argillaceous limestone and dolostone. As noted by Dean *et al.* (2010) the data have their limitations compared to those from a dedicated palaeoecological sampling exercise:

1. Sample sizes are highly variable and samples from the same locality are not necessarily from the same stratum, even though they may be in the same lithology. Stratal variations in species and genera are a marked feature of both limestones and are pronounced even within the same lithologies (Dr C. J. Burton, pers. comm. April 2010).

2. Taxonomic identifications in the database are made by many palaeontologists and most of the material has not formed part of a systematic taxonomic or ecophenotypic study.
3. The collections lack any taphonomic assessment.
4. Only presence/absence data are available, which severely limits the range of numerical methods that can be applied.

Numerical techniques

To try to overcome some of the problems inherent in the historical collections Dean *et al.* (2010) undertook successive analytical iterations on increasingly restricted versions of the original data sets. This restriction was done by: removing records of indeterminate taxa where named members of their larger groups were recorded from the same sample; assigning material recorded as having any level of affinity to a named species to that species if it was unequivocally identified at any locality in the species level data set; and finally, excluding any taxa that were unique to a single sample. For the lithologically fairly homogenous Hurlet Limestone, seriation, non-metric multidimensional scaling and to a more limited extent cluster analysis of the presence/absence data in samples that were not differentiated by lithology indicated three groups of faunas that corresponded well with the outcomes of the semi-quantitative analysis of Wilson (1989) noted above. This gave confidence that the data are sufficient to provide at least a broad indication of palaeoecology.

Samples from the commonly thicker, more lithologically varied Index Limestone revealed no consistent patterns of associations of taxa when different lithologies from the same locality were grouped. The inclusion of lithological data for the Index Limestone and constraining the genus level seriation by the ordering determined for the limestone samples alone resulted in the broad grouping of lithologies suggesting, as with the Hurlet Limestone, that the faunas were distributed along environmental gradients within the carbonate facies that extended into other sedimentary settings in a systematic way. Echinoids, fenestellid bryozoans, the gastropod *Naticopsis* and the brachiopods *Rhipidomella* and *?Pugnax*, were restricted to the limestone environment, whilst many of the other taxa range through increasingly coarse-grained siliciclastic settings towards the zone of river sediment influx (see Dean *et al.* 2010, figs 16–17).

In addition to the analysis of presence/absence data, a measure of diversity (i.e. genus richness) was provided by analysing the number of genera present within higher taxonomic groups in each sample. These data were amenable to analysis using cluster analysis and Principal Components Analysis (PCA), the latter providing an ordination of samples (Dean *et al.* 2010, figs 6 and 12) that broadly reflects the grouping of samples evident in the cluster analyses. These clusters from the data set in which the sample lithologies are identified provide the basis of the explicitly broad-brush analysis of faunas herein.

Patterns in the Hurlet Limestone data

Cluster analysis of the numbers of genera within higher taxa using the statistical package *PAST* (Hammer *et al.* 2001) provided three major clusters (Ht 1–Ht 3), five

sub-clusters, and five close pairings (Dean *et al.* 2010, fig. 11). The major clusters (summarised on Table 1) also define distinct fields defined by the first three principal components of a PCA (Dean *et al.* 2010, fig. 12).

Ht 1 comprises seven samples in a wide range of lithologies, all of which contain brachiopods of variable diversity. A genus of bivalve is present in all but one sample and crinoid columnals are present in five of the samples, nautiloids in two.

Ht 2 comprises seven samples in a wide range of lithologies. Six of these samples contain only brachiopod genera; the seventh also contains a gastropod genus.

Ht 3 comprises five samples, all containing crinoid columnals and all but one of which contains brachiopods with a great range of genus diversities. Two of the samples are the only ones in the Hurler Limestone to contain bryozoans. All but one sample is from limestone; the exception, an undifferentiated mudstone/claystone, is the only one in the cluster to contain just crinoid columnals.

Patterns in the Index Limestone data

For the diversity data of genera within higher taxa, cluster analysis of samples from the Index Limestone divided by lithology showed two major clusters (Ix 1–Ix 2) and eight sub-clusters (Ix 1.1–Ix 1.2 and Ix 2.1–Ix 2.6) (Dean *et al.* 2010, fig. 13; Tables 1 and 2 herein). The major clusters and, with some overlap, the sub-clusters within them are also differentiated by the first three components of the PCA plots (Dean *et al.* 2010, fig. 14).

The 38 sub-clustered samples in major cluster Ix 1 comprise a wide range of lithologies and are dominated by brachiopods, with most samples in sub-cluster Ix 1.2 being restricted to members of this phylum. The 27 sub-clustered samples in major cluster Ix 2 also comprise a wide range of lithologies and are also dominated by brachiopods, but bivalves are ubiquitous too and may be highly diverse. Gastropod genera occur in all samples in Ix 2.2–Ix 2.4. Bryozoans are restricted to Ix 2.1. Crinoid columnals occur in all the samples of Ix 2.5 and in all but one sample each of Ix 2.2 and Ix 2.4. The taxonomic compositions and lithologies represented in the sub-clusters are summarised on Table 1.

Trophic structure

The groupings of samples arising from the cluster analyses of the ‘diversity’ of genera within higher taxa provides a broad picture of the associations of taxa that avoids the ‘over-interpretation’ that might result from faunal associations identified at genus and species level. These ‘diversity’ groupings can be assessed in terms of the gross patterns of how organisms exploited their environment by looking at aspects of their trophic structure (see Scott 1978; Etter 1999 for general discussion of the principles involved). Clearly the resultant patterns are those of the preserved shelly benthos and do not take account of those groups filtered out through taphonomic processes, especially soft bodied taxa. The interpretations of feeding behaviours of the taxa present in the Hurlet and Index limestones are those of Wilson (1989).

Figure 2 summarises the distribution of the clusters of ‘diversity’ samples in the Hurlet and Index limestones, respectively, in terms of the relative proportions of suspension feeders (SUSP), detritus feeders (DET), and predators and carnivores

(PRED). In the case of the Hurllet Limestone (Fig. 2a), the relatively small number of individual samples means that these can be plotted directly on the ternary diagram, but in order to simplify the diagram for the greater number of samples in the Index Limestone data set (Fig. 2b), a 'mean value' is plotted as a generalised proxy for the sub-clusters, based on the total numbers of all genera recorded within each phylum in each sub-cluster. Figure 3 presents substrate-niche ternary diagrams for the two units illustrating the proportions of vagrant detritus feeders (VAGDET), epifaunal suspension feeders (EPSUS), and infaunal suspension feeders (INSUS). Again, the 'mean values' of the sub-clusters are plotted for the Index Limestone (Fig. 3b).

For the Hurllet Limestone, the feeding habits and substrate niche/trophic structures for the three major clusters show Ht 2 and Ht 3 dominated by epifaunal suspension feeders, but Ht 1 plots in the 'detritus-suspension' and 'epifaunal' fields of the diagrams. This cluster is the only one to contain bivalves.

For the Index Limestone, the feeding habits and substrate niche/trophic structures for the eight sub-clusters indicate that most comprise epifaunal suspension feeders.

However, Ix 2.2 plots in the 'detritus-suspension' and 'vagrant-epifaunal' fields of the diagrams. This cluster has the largest range of higher taxa, and the highest percentage of molluscan genera to all others. It is the only cluster noted as containing scaphopods and ostracods.

Bambach *et al.* (2007; see also Bush *et al.* 2007) developed a graphical means of displaying the amount of ecospace occupied by marine organisms based on their presence or absence in six categories within each of three major aspects of

autecology: tiering position in relation to the substratum/water interface; motility level; and feeding strategy. Table 2 shows the resulting patterns in each faunal cluster/sub-cluster in the Hurllet and Index limestones based on an interpretation of the autecology of the named genera in each cluster.

For the Hurllet Limestone, application of the categorisation by Bambach *et al.* (2007) strongly enhances the results shown by the ternary diagrams (Figs 2a and 3a). Whilst the diagrams indicate that all three major clusters (Ht 1–Ht 3) comprise mainly epifaunal suspension feeders, Table 2 shows that they all include marine organisms of the surficial and semi-infaunal tiers, non-motile (attached and unattached) forms, and suspension feeders. Table 2 also illustrates a trend of increasing ecological complexity from Ht 3 through Ht 2 to Ht 1, with the last mentioned including representatives from the pelagic and shallow infaunal tiers, freely fast and facultative (both attached and unattached) motile forms, and mining and predatory feeders. This is explained by bivalves and nautiloids exclusively occurring in Ht 1 (Table 1).

For the Index Limestone, application of the ecological categorisation by Bambach *et al.* (2007) again strongly enhances the results shown by the ternary diagrams (Figs 2b and 3b). Table 2 shows that sub-clusters Ix 1.1 and Ix 1.2 have in common representatives of the surficial and semi-infaunal tiers, non-motile (attached and unattached) forms, and suspension feeders. Ix 1.2, however, comprising 33 samples, is much more ecologically complex with representatives of the pelagic tier, freely fast motile forms and predators. Bivalves, nautiloids, anthozoans and trace fossils are exclusive to Ix 1.2 (Table 1) of major cluster Ix 1.

Table 2 shows sub-clusters Ix 2.1–Ix 2.6 have in common representatives of the surficial and semi-infaunal tiers, non-motile (attached and unattached) forms, and suspension feeders and miners. All but Ix 2.5 also include the shallow infaunal tier and slow, freely motile organisms. A trend in increasing ecological complexity (similar to that shown in Figs 2b and 3b) is also recognised with Ix 2.5 being faunally the most simple and Ix 2.4 and Ix 2.2 the most varied. Table 2 shows that Ix 2.4 and Ix 2.2 also include the pelagic tier, fast, freely motile forms and predators. Within major cluster Ix 2, nautiloids are exclusive to both sub-clusters, anthozoans to Ix 2.4, and scaphopods and crustaceans to Ix 2.2 (Table 1).

Wilson (1967, 1989) stated that the seas which invaded central Scotland in Viséan and Namurian times were never deep and trophic analysis shows that the fundamental biofacies of the Hurlet and Index limestones comprise mainly non-motile (attached or unattached), suspension feeding brachiopods of the surficial and semi-infaunal tiers. That the region was subject to relatively rapid fluctuations in depth, variations in sea floor conditions and water quality is shown by the variable and sporadic addition of other forms including bivalves, nautiloids, anthozoans, scaphopods, crustaceans and trace fossils that include representatives of the pelagic and shallow infaunal tiers, freely fast and facultative (both attached and unattached) motile forms and mining and predatory feeders.

The Mississippian Lower and Upper Limestone formations of central Scotland are of mixed shelf carbonate and deltaic (Yoredale-type) facies, which are common in penecontemporaneous strata in northern Britain. However, in south Cumbria, for example, the Bowland Shale Formation is of hemi-pelagic facies comprising mainly

mudstone, subordinate beds of siltstone, sandstone and limestone and ‘marine bands’ (Dean *et al.* in press). Trophic analysis by multivariate numerical methods of fossils collected systematically from these ‘marine bands’ should help to distinguish the faunal phases developed in association with the advance, acme and retreat of each marine incursion.

Two dimensional geographical distribution of the ‘diversity’ clusters

Whilst the qualitative analysis of Wilson (1989) may infer a relationship between lithofacies and the palaeoenvironment, quantitative analysis by Dean *et al.* (2010) confirms this relationship and, most encouragingly, enables subtle patterns not recognised by qualitative methods, as in the Index Limestone, to be recognised at deeper levels within it. Figures 4 and 5 respectively plot the geographical distribution of the samples within the main clusters (Ht 1–Ht 3) in the Hurlet Limestone and the sub-clusters (Ix 1.1–Ix 1.2 and Ix 2.1–Ix 2.6) in the Index Limestone identified by cluster analysis of the diversity of genera within higher taxa by Dean *et al.* (2010) and shown in Table 1. The distribution of sample localities is very largely controlled by the outcrop of the Hurlet and Index limestones in the district. These concentrate in three main areas, in the NE around Sorn, in central parts around Patna, and in the SW to the northwest of Dailly. Whilst these lithostratigraphical units may or may not subcrop at depth beneath younger rocks, the data for this study are mainly confined to the areas of outcrop, and this limits the scope for palaeoenvironmental interpretation.

The palaeoenvironment of the Hurlet Limestone shown in Figure 4 represents a combination of the faunas and lithologies in the samples comprising major clusters Ht 1–Ht 3 as discriminated by cluster analysis in Dean *et al.* (2010). Interpretation of

the relative proportion of the sample lithologies in the combined clusters at each locality suggests that the palaeoenvironment in the NE was most diverse where the range is from clearer water (with firmer substrates and dominantly epifaunal forms) through to muddy water (with softer substrates and dominantly infaunal forms) and also areas of influx of river-borne siliciclastic deposits. In the central and SW areas only the clearer water environment is inferred.

Samples from Ht 1 and Ht 2 are represented in all three main areas, but Ht 3 is restricted to the NE and SW. This cluster is the least ecologically complex in the Hurlet Limestone and includes just brachiopods, crinoids and bryozoa in mainly limestone lithologies (Table 1). Because the stratigraphical sequence of samples in the historical collection is unknown it cannot be confirmed that the trend of increasing ecological complexity from Ht 3 through Ht 2 to Ht 1 (as noted in the section on trophic analysis) represents a transgressive sequence. A more acceptable explanation of the omission of Ht 3 at Patna is Wilson's (1987) observation that the Midland Valley region was subject to relatively rapid fluctuations in depth, and variations in sea floor conditions and water quality. This may account for the local omission of this cluster in the Patna area, which where sampled did not achieve the shallowness and clarity of water attained at Dailly and Sorn.

The palaeoenvironment of the Index Limestone as shown in Figure 5 represents a combination of the faunas and lithologies in the samples comprising the sub-clusters in major clusters Ix 1 and Ix 2 discriminated by the cluster analysis of Dean *et al.* (2010). Interpretation of the relative proportion of the sample lithologies in the combined clusters suggests that the palaeoenvironment was much more varied than

that of the Hurlet Limestone. In the Patna area there is a SW to NE zonation from clear water, through the intermediate zone to muddy water. River-borne siliciclastic deposits are mapped at Sorn extending to the SE, perhaps in a channel, and flanked by gradients of increasing water clarity. Local incursions of river-borne sediment are also present along the southern margin of the study area inferred to be from the subdued relief of the Southern Uplands to the south and although the narrow basin at Dailly is dominated by the clear water environment (Ix1 cluster) there is a narrow southward gradient of slightly elevated mud content inferred to be derived from the Southern Uplands source.

Samples from sub-clusters Ix 1.2, Ix 2.4 and Ix 2.6 are represented in all three of the main areas, but Ix 1.1 is only found in the Sorn and Dailly areas, Ix 2.1 in the Patna and Sorn areas, Ix 2.2 in the Patna area, and Ix 2.3 and Ix 2.5 only in the Dailly and Patna areas. Like the Hurlet Limestone the explanation for this distribution is not considered marine transgressive, but perhaps due to rapid, possibly local, fluctuations in depth, sea floor conditions and water quality.

The distributions of environments shown in Figures 4 and 5 should not be considered static or time constrained. The depositional facies will have varied spatially and migrated temporally during the marine transgressions of the Hurlet and Index limestones.

The conditions of cyclical (Yoredale-type) sedimentation were probably similar during deposition of the Lower and the Upper Limestone formations (Wilson 1967; Read *et al.* 2002). During both intervals a major landmass occurred to the north of the

district, whilst to the south an archipelagic landmass of low relief (lying on the site of the present Southern Uplands) would probably have existed. Between these massifs was a relatively stable broad shelf area with little deposition (the Ayrshire Basin), which was separated from the rest of the Midland Valley further east by the Mississippian lava sequence of the Clyde Plateau Volcanic Formation. The latter is considered to have been a persistent topographical high (Francis 1991a; 1991b) and probably acted as a barrier to faunal migration to the Ayrshire shelf. Thus although Wilson (1989, fig. 8a; see also Wilson 1967; Read *et al.* 2002) showed an 'influx of clastics' associated with a large river system flowing off the major landmass to the north during the upward-coarsening sedimentary cycle that started with the marine transgression associated with the Hurlet Limestone, it is unlikely that the siliciclastic rocks shown in the NE area of Figure 4 are a distal representation of this river system. They probably reflect a more local source as do the siliciclastic sedimentary rocks shown in the NE area during deposition of the Index Limestone (Fig. 5).

Draping the geographical distributions on modelled three dimensional surfaces

Of particular interest in the palaeoenvironmental interpretation of the Index Limestone (Fig. 5) is the 'embayment' in the distribution of environments interpreted to the northeast of Patna in the central part of the study area. A link between the inferred depositional environments and faults with known penecontemporaneous displacement is clearly demonstrated by draping the environmental patterns summarised in Figures 4 and 5 over 3D computer models of the Hurlet and Index limestones in the subsurface, which have been developed as part of the research during current resurvey by BGS. In particular, Figure 6 shows that the palaeoenvironmental 'embayment' in the Index Limestone of the muddy water

environment that extends in a southwesterly direction into the clearer water environment, was linked to the presence of the Kerse Loch Fault. Moreover, the inset on Figure 6 (from Mykura 1967, fig. 2a) shows the coincidence of the isopach pattern in the Limestone Coal Formation and our palaeoenvironmental interpretation of the Index Limestone at the ‘embayment’. All of this suggests that movement of the Kerse Loch Fault influenced the palaeogeography, marine water flow and in turn the environments of the Index Limestone. Movement on this fault during the Carboniferous has long been known to have influenced sedimentation patterns (see Mykura 1967, pp. 27–31, fig. 2; Wilson 1989, pp. 122–123, fig. 12; Read *et al.* 2002, p. 276), and we now show that this in turn influenced the distribution of genus diversity in the benthonic faunas. Eyles *et al.* (1949) record lateral thickness variation during deposition of the Clackmannan Group across the Kerse Loch Fault and infer contemporaneous displacement. They note the thickness variation within Mississippian strata was greatest during deposition of the Upper Limestone Formation of which the Index Limestone is at the base. If fault displacement accommodated only differential basin subsidence, environmental conditions at the seabed would be unchanged and no response observed in the benthonic faunas. The ‘embayment’ of muddy conditions, defined by the subtle results of numerical analysis of faunas in the Index Limestone, demonstrate there was a ‘step-like feature in the landscape’ and more muddy conditions at the foot of a fault scarp at the Kerse Loch Fault rather than the alternative of a north-westerly shoaling sea floor (Eyles *et al.* 1949).

3D models of the subsurface in the NE (Sorn) area suggest possible coeval fault control in the NW-SE trending palaeoenvironments in both the Hurllet and Index limestones in the vicinity of the Mossbog and Auchmillan faults (see Fig. 6 for the

Index Limestone). The same also applies to the NE-SW trending palaeoenvironmental belt in the Index Limestone adjacent to the Kerse Loch Fault in the SW (Dailly) area (see also Mykura 1967, figs 2a and 13).

Conclusions

Numerical analysis of historical collections of upper Mississippian fossils from the Hurllet and Index limestones of Ayrshire provides a significantly deeper level of palaeoecological and palaeogeographical interpretation than qualitative analysis alone. Subtle patterns in the trophic structure of associated taxa based on the occurrence of genera within larger taxonomic groupings, their links to lithofacies and their spatial distributions may be characterised.

For the Hurllet Limestone, the cluster analysis of the 'diversity' of genera within higher taxa provides three major groups of samples. Two of these are dominated by epifaunal suspension feeders, whilst the third comprises epifaunal detritus-suspension feeders. All three major clusters include marine organisms of the surficial and semi-infaunal tiers, non-motile (attached and unattached) forms, and suspension feeders, but they show a trend of increasing ecological complexity ultimately to include representatives of the pelagic and shallow infaunal tiers, freely fast and facultative (both attached and unattached) motile forms, and mining and predatory feeders.

For the Index Limestone, cluster analysis provides two major groups of samples and eight sub-clusters; five of the sub-clusters comprise epifaunal suspension feeders two epifaunal detritus-suspension feeders, and one vagrant-epifaunal detritus-suspension feeders. One of the major groups includes representatives of the surficial and semi-

infaunal tiers, non-motile (attached and unattached) forms, and suspension feeders. One sub-cluster is much more ecologically complex with representatives of the pelagic tier, freely fast motile forms and predators. The second major group of samples includes six sub-clusters, which show a strong trend of increasing ecological complexity ultimately to include representatives of the pelagic tier, fast, freely motile forms and predators.

The fundamental biofacies of the Hurllet and Index limestones comprises mainly non-motile (attached or unattached), suspension feeding brachiopods of the surficial and semi-infaunal tiers. These occurred in a shallow sea over central Scotland in Viséan and Namurian times, but the sporadic inclusion of representatives of the pelagic and shallow infaunal tiers, freely fast and facultative (both attached and unattached) motile forms and mining and predatory feeders suggests relatively rapid fluctuations in depth, variations in sea floor conditions and water quality.

The palaeoenvironment of the Hurllet Limestone was most diverse in the NE of the study area where it ranged from clearer water (with firmer substrates and dominantly epifaunal forms) through to muddy water (with softer substrates and dominantly infaunal forms). Areas of river-borne siliciclastic deposits are also evident. In the central and SW areas only the clearer water environment is inferred. The least ecologically complex faunal cluster was restricted to the NE and SW. Its omission in the central area is thought due to the sea at that locality not achieving the shallowness and clarity of water attained elsewhere.

The palaeoenvironment of the Index Limestone was much more varied than that of

the Hurlet Limestone. In the central area there is a SW to NE zonation from clear water, through the intermediate zone to muddy water. River-borne siliciclastic deposits are mapped at Sorn extending to the SE, flanked by gradients of increasing water clarity. Local northward incursions of river-borne sediment from the low relief Southern Uplands that lay to the south are also present along the southern margin of the study area.

The 2D geographical distribution of the palaeoenvironments deduced from the trophic structure combined with lithological information demonstrates the influence of penecontemporaneous faulting within the Ayrshire Coalfield Basin. An ‘embayment’ in the distribution of environments in the central part of the study area links inferred depositional environments in the Index Limestone with the Kerse Loch Fault and is clearly demonstrated by draping the environmental pattern over a 3D computer model of the subsurface. In this ‘embayment’ the muddy water environment extends in a southwesterly direction into the clearer water environment linked to the fault, with known penecontemporaneous displacement, which influenced the palaeogeography, palaeotopography, marine water flow, environments and distribution of genus diversity in the benthonic faunas during deposition of the Index Limestone in the thickened sequence at the base of the south-facing fault scarp.

3D models of the subsurface also suggest possible coeval fault control of palaeoenvironments in both the Hurlet and Index limestones in the vicinity of the Mossbog and Auchmillan faults in the NE of the study area.

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Figure captions:

FIG. 1. The position of the Ayrshire Coalfield Basin (part) within central Scotland and the Carboniferous stratigraphy (including up-to-date lithostratigraphical nomenclature) relevant to the present study. See Figures 4 and 5 for the crop of the Hurlet and Index limestones.

FIG. 2. Ternary feeding habits diagrams. **(a)** Hurlet Limestone, showing the percentages of suspension feeders (SUSP), detritus feeders (DET) and predators and carnivores (PRED) in the faunas of each individual sample within each major cluster (Ht 1, Ht 2 and Ht 3). **(b)** Index Limestone, showing the percentage in each sub-cluster as a ‘mean value’ based on the total numbers of all genera recorded within each phylum in each sub-cluster. The total number of genera recorded from all the samples in each sub-cluster is : Ix 1.1 = 7; Ix 1.2 = 22; Ix 2.1 = 15; Ix 2.2 = 27; Ix 2.3 = 19; Ix 2.4 = 21; Ix 2.5 = 14; Ix 2.6 = 28. Note that the sample numbers for each

cluster in each limestone are listed in Table 1.

FIG. 3. Ternary substrate niche/trophic structure diagrams. **(a)** Hurlet Limestone, showing the percentages of epifaunal suspension feeders (EPSUS), infaunal suspension feeders (INSUS) and vagrant detrital feeders (VAGDET) in the faunas of each individual sample within each major cluster (Ht 1, Ht 2 and Ht 3). **(b)** Index Limestone, showing the percentage in each sub-cluster as a ‘mean value’ (see Fig. 2).

FIG. 4. Hurlet Limestone. The geographical distribution of the three major clusters (with sample numbers) and their palaeoenvironmental interpretation. Graticule is British National Grid. See Table 1 for sample lithologies and faunal diversity.

FIG. 5. Index Limestone. The geographical distribution of the eight sub-clusters (with sample numbers) and their palaeoenvironmental interpretation. Graticule is British National Grid. See Table 1 for sample lithologies and faunal diversity.

FIG. 6. Index Limestone. The palaeoenvironmental interpretation draped over a 3D computer model of the subsurface. Graticule is British National Grid. Note the ‘embayment’ developed in association with the Kerse Loch Fault. The inset shows isopachs in the Limestone Coal Formation in the same vicinity (from Mykura 1967, fig. 2a).

Table captions:

TABLE 1. The faunas and lithologies of samples comprising the major and sub clusters in the Hurlet (Ht) and Index (Ix) limestones identified by Dean *et al.* (2010).

Clustering achieved by using the Raup-Crick similarity index and the un-weighted pair group average algorithm. Key to lithologies: CMdst calcareous mudstone; CSst calcareous sandstone; CSlst calcareous siltstone; Dst dolostone; Lst limestone; Mdst mudstone/claystone (undifferentiated); MLst argillaceous limestone; Slst siltstone; Sst sandstone. Key to higher taxa: An Annelida; Ant Anthozoa; Bi Bivalvia; Br Brachiopoda; Bry Bryozoa; Cr Crinoidea; Cru Crustacea; Ga Gastropoda; Na Nautiloidea; Sc Scaphopoda; Tr Trace fossils.

TABLE 2. The ecological categorisation of Bambach *et al.* (2007) applied to the named genera in the major clusters of the Hurlet Limestone (Ht 1-Ht 3) and the sub-clusters of the Index Limestone (Ix 1.1-Ix 2.6). Key to ecological categories: Tiering: 1 pelagic; 2 erect; 3 surficial; 4 semi-infaunal; 5 shallow infaunal; 6 deep infaunal. Motility level: 1 freely, fast; 2 freely, slow; 3 facultative, unattached; 4 facultative, attached; 5 non-motile, unattached; 6 non-motile, attached. Feeding mechanism: 1 suspension; 2 surface deposit; 3 mining; 4 grazing; 5 predatory; 6 other.

TABLE 1

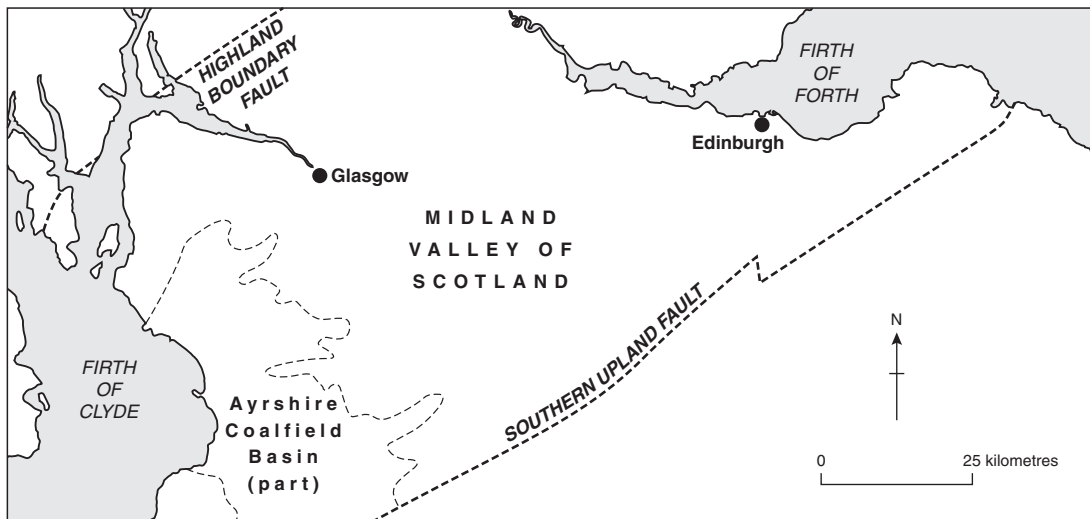
The faunas and lithologies of samples comprising the major and sub-clusters in the Hurlet (Ht) and Index (Ix) limestones identified by Dean *et al.* (2010). Clustering achieved by using the Raup-Crick similarity index and the un-weighted pair group average algorithm. Key to lithologies: CMDst calcareous mudstone; CSst calcareous sandstone; CSLst calcareous siltstone; Dst dolostone; Lst limestone; Mdst mudstone/claystone (undifferentiated); MLst argillaceous limestone; Slst siltstone; Sst sandstone. Key to higher taxa: An Annelida; Ant Anthozoa; Bi Bivalvia; Br Brachiopoda; Bry Bryozoa; Cr Crinoidea; Cru Crustacea; Ga Gastropoda; Na Nautiloidea; Sc Scaphopoda; Tr Trace fossils.

Clusters	Sample No.	Lithology	Faunal Diversity Genera per taxon	Clusters	Sample No.	Lithology	Faunal diversity Genera per taxon
Ht 1	1	Mdst/CMDst	Br 9; Bi 1; Cr 1; Na 1	Ix 1.2 (continued)	44a	Lst/MLst	Br 1
	10a	Dst	Br 1; Bi 1		45a	CMdst	Br 4
	24a	Lst	Br 2; Cr 1; Na 1		46a	Lst	Br 1
	26a	MLst	Br 3; Bi 3; Cr 1		46b	CMdst	Br 1
	52a	Lst	Br 4; Bi 1; Cr 1		47a	Mdst	Br 4
	57a	Lst	Br 3; Bi 1; Cr 1; Na 1		48b	Lst	Br 1
	64a	Slst	Br 1; Bi 1		54a	Mdst	Br 2
Ht 2	10b	MLst	Br 1	61b	CMdst	Br 1	
	12b	Lst	Br 2; Ga 1	61c	MLst	Br 2	
	55a	Lst	Br 4	61d	Slst	Br 3	
	65b	MLst	Br 2	62a	Mdst	Br 2	
	65c	CSst	Br 2	63a	Lst	Br 3	
	67a	MLst	Br 1	5d	Mdst/Slst	Br 4; Bi 6; Bry 1	
	67c	Slst	Br 1	35a	Lst	Br 3; Bi 2; Bry 1	
Ht 3	11a	Lst	Br 2; Cr 1	51c	Slst	Br 5; Bi 5; Ga 1; Bry 2	
	12a	Mdst	Cr 1	Ix 2.2	8a	Mdst	Br 5; Bi 5; Na 1; Ga 2; Sc 1; Cru 1
	36a	Lst	Br 1; Cr 1		31a	Mdst	Br 6; Bi 10; Cr 1; Na 1; Ga 3; Sc 1
	65a	Lst	Br 8; Cr 1; Bry 1	32a	Slst	Br 8; Bi 5; Cr 1; Ga 2; Sc 1	
Ix 1.1	67b	Lst	Br 3; Cr 1; Bry 2	Ix 2.3	3a	Sst	Br 3; Bi 2; Ga 1
	15a	Lst	Br 4; Cr 1		28b	CMdst	Br 3; Bi 2; Ga 2
	28c	Mdst	Br 2; Cr 1		37a	Lst	Br 6; Bi 2; Ga 1
	48a	Mdst	Br 1; Cr 1		58a	Lst	Br 5; Bi 1; Ga 2
Ix 1.2	49a	MLst	Br 4; Cr 1	Ix 2.4	16b	CMdst	Br 3; Bi 1; Cr 1; Ga 1; An 1
	54b	Lst	Br 3; Cr 1		41b	Lst	Br 3; Bi 2; Cr 1; Na 1; Ga 1; An 1
	4a	Lst	Br 3	Ix 2.5	59a	Lst	Br 3; Bi 5; Ga 2; An 1
	4c	CMdst	Br 2		27a	Mdst	Br 2; Bi 2; Cr 1
	5b	CMdst	Br 1		30b	Lst	Br 8; Bi 1; Cr 1
	5c	MLst	Br 1	Ix 2.6	38a	CMdst	Br 5; Bi 1; Cr 1
	13a	Mdst/CMDst	Br 3; Tr 1		40a	Lst	Br 5; Bi 1; Cr 1
	14a	CMdst	Br 6; Bi 1; Na 1; Ant 1		4b	Slst	Br 2; Bi 1
	17b	CMdst	Br 1	8b	Lst	Br 5; Bi 1	
	17c	Mdst	Br 3	19b	Slst	Br 3; Bi 2	
	22a	Mdst	Br 1; Ant 1	27b	MLst	Br 6; Bi 1	
	22b	CMdst	Br 1	31b	CMdst	Br 2; Bi 1	
	22c	Lst	Br 2	33b	Slst	Br 6; Bi 1	
	23b	MLst	Br 2	43b	Mdst	Br 3; Bi 8	
	23c	CMdst	Br 1	51a	Lst	Br 2; Bi 1	
	25a	Lst	Br 8	53a	MLst	Br 8; Bi 1	
	28a	Lst	Br 3	60a	Lst	Br 4; Bi 1	
30a	MLst	Br 2; Na 1					
33a	MLst	Br 3					
34a	CMdst	Br 3					
34b	Lst	Br 4					
37b	MLst	Br 1					
43a	Lst	Br 1					

TABLE 2

The ecological categorisation of Bambach *et al.* (2007) applied to the named genera in the major clusters of the Hurler Limestone (Ht 1-Ht 3) and the sub-clusters of the Index Limestone (Ix 1.1-Ix 2.6). Key to ecological categories: Tiering: 1 pelagic; 2 erect; 3 surficial; 4 semi-infaunal; 5 shallow infaunal; 6 deep infaunal. Motility level: 1 freely, fast; 2 freely, slow; 3 facultative, unattached; 4 facultative, attached; 5 non-motile, unattached; 6 non-motile, attached. Feeding mechanism: 1 suspension; 2 surface deposit; 3 mining; 4 grazing; 5 predatory; 6 other.

Cluster	Tiering						Motility level						Feeding mechanism					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Ht 1	x		x	x	x		x		x	x	x	x	x		x			x
Ht 2			x	x				x			x	x	x			x		
Ht 3			x	x							x	x	x					
Ix 1.1		x	x	x							x	x	x					
Ix 1.2	x		x	x			x				x	x	x					x
Ix 2.1			x	x	x			x		x	x	x	x	x	x	x		
Ix 2.2	x		x	x	x		x	x	x	x	x	x	x		x	x	x	
Ix 2.3			x	x	x			x	x		x	x	x	x	x	x		
Ix 2.4	x		x	x	x		x	x		x	x	x	x		x	x	x	
Ix 2.5			x	x							x	x	x	x		x		
Ix 2.6			x	x	x			x	x	x	x	x	x	x	x			



Standard Divisions			Regional Divisions		Lithostratigraphical Units	
Sub-system	Series	Stage	Series	Stage	Formations	Groups
Pennsylvanian (part)	Lower (part)	Bashkirian (part)	Westphalian (part)	Langsettian (part)	Passage Formation	Clackmannan Group
			Namurian	Chokierian-Yeadonian		
Arnsbergian	Limestone Coal Formation					
Pendleian		Lower Limestone Formation		<i>Hurlet Limestone</i>		
Mississippian	Upper	Serpukhovian	Brigantian	Lawmuir Formation	Strathclyde Group	
				Middle		Viséan
	Arundian-Holkerian	Clyde Plateau Volcanic Formation				

