Discriminating faunal assemblages and their palaeoecology based on museum collections: the Carboniferous Hurlet and Index limestones of western Scotland, UK

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Synopsis

Historic collections of Scottish Carboniferous macrofossils stored at the British Geological Survey (BGS), Edinburgh include the sole remaining sources of palaeontological data from numerous localities. Exploratory numerical analyses of such collections from the Hurlet and Index limestones of Ayrshire compare favourably with published qualitative assessments of faunal assemblages and palaeoenvironments; demonstrating that old collections can still be used in modern palaeoecological investigations. Macrofaunas from these formations comprise mainly brachiopods and molluscs and were collected from 67 localities that yielded 20 and 94 samples from the Hurlet and Index limestones respectively. Limitations of the presence/absence data were partly overcome by consolidation and restriction of aspects of the data set. Seriation indicates the lithological and environmental gradients of taxa. Cluster analysis reveals groups of samples linked to lithofacies. Principal Components Analysis (PCA) of diversity data derived from the data set in terms of

numbers of genera in higher taxa highlights differences in gross taxonomic composition in terms of trophic structure, lithology and environment.

Supplementary material: lists of localities, taxa and sample lithologies used in this study are available at http://www.geolsoc.org.uk/SUP00000.

Introduction

Carboniferous rocks at outcrop underlie much of central Scotland but are predominantly covered by Quaternary deposits, and good exposures of the sedimentary rocks are rare, especially in the economically important coal bearing Namurian and Westphalian successions. However, extensive mining, quarrying and sinking of cored boreholes associated with the exploration and exploitation of coal, ironstone and refractory materials (including limestone) from the late 18th to the mid 20th century yielded a vast amount of detailed palaeontological and stratigraphical knowledge of these rocks (Cameron & Stephenson 1985; Read *et al.* 2002; Trewin & Rollin 2002). Deep mining has ceased but the palaeontological material collected during exploration and exploitation has been retained, often as the sole remaining source of palaeontological data. This is a manifestation of a much wider phenomenon that emphasises the importance of historical palaeontological collections (e.g. see Allmon 2005). The question then arises as to whether these data from the BGS collections are sufficiently complete to render them amenable to palaeoecological analysis.

The use of numerical methods in palaeontology is well established and has been used to address a wide range of palaeontological problems (Harper 1999; Hammer &

Harper 2006). Ideally, a systematic sampling programme should be undertaken to provide data for rigorous quantitative analysis of palaeoecological data (Etter 1999). Although the BGS collections were not assembled as part of such a sampling exercise, a set of standard numerical exploratory techniques (see Hammer & Harper 2006, p. 6) was applied to the macrofaunas in these collections from the Hurlet and Index limestones in western Scotland (Figs 1, 2) to determine whether recurrent faunal assemblages could be recognised and reasonable interpretations made in terms of palaeoenvironments and lithofacies. The results of the analysis compare favourably with the published qualitative results of Wilson (1967; 1989) whose understanding was founded on a wealth of experience ‘based on innumerable observations made over forty years’ (Wilson 1989, p. 111).

The Hurlet and Index limestones: a review of the collected palaeontological materials

The Hurlet (Brigantian) and Index (Pendleian) limestones mark the bases of the Lower and Upper Limestone formations respectively (Fig. 2), and have been correlated over most of central Scotland (see Wilson 1967; 1989; Browne *et al*. 1999). Both limestones occur at the southern margin of the Ayrshire Coalfield (Fig. 1), which is a region of current geological resurvey and 3D computer modelling by the British Geological Survey. The analysis of the macrofaunal assemblages forms part of that work.

The fossils are mainly held in the Biostratigraphy collections in the British Geological Survey office in Edinburgh (see Dean 2002). They were collected from 67 localities (14 for the Hurlet Limestone and 53 for the Index Limestone) over a period of approximately 136 years. The sample localities include both borehole and surface exposures. The material from each locality was subdivided by hand specimen lithology into mudstone/claystone (undifferentiated), calcareous mudstone, sandstone, siltstone, calcareous siltstone, limestone, argillaceous limestone, and dolostone. This resulted in 20 macrofaunal samples for the Hurlet Limestone and 94 samples for the Index Limestone. Fossil content was tabulated on a spreadsheet arranged by genera and species within major groups, each determination being made to the highest level of confidence at the localities sampled. For lists of localities, taxa and sample lithologies used in this study see Supplementary material.

The data were compiled over time at the most detailed taxonomic level possible for each locality and so range from records of named species to indeterminate material ascribed only to a phylum. The limitations of the data owing to the gradual acquisition of samples to the collection rather than palaeoecologically focused bulk sampling (e.g. Etter 1999) include:

- Samples differ in dimensions from pieces of core of various diameters to hand specimens of various sizes. It cannot be discounted that at least some of the differences among samples reflect differences in sample dimension, which at present are not quantified but are very variable.
- Specimens from the same locality were not necessarily obtained from the same bed.
- Taxonomic identifications in the database were undertaken by many palaeontologists working on Carboniferous fossils since 1870. Hence they are polythetic and in most instances are not underpinned by systematic monographic studies or ecophenotypic analysis of the material. For older determinations the

taxonomy may in some cases need updating.

- The collections lack any taphonomic assessment such as the degree to which the fossils were autochthonous or allochthonous.
- Crucially, only presence/absence (binary) data are available and this provides a major limitation on the range of numerical methods that can be applied.

Consolidation and restriction of the data sets

To overcome limitations of sample size and limited taxonomic overlap between samples in the exploratory analyses, which aim to identify similarities between groups of samples, successive iterations of the analyses were undertaken on increasingly consolidated or restricted versions of the original data.

The species- and genus-level data were consolidated by removing records of indeterminate brachiopods, bivalves and gastropods where named taxa of these groups were recorded from the same sample. If a species was unequivocally identified at any locality in the species-level data set, that name was also applied to all other ‘aff.’, ‘cf.’ and ‘?’ determinations applied to that binomen. Next, all taxa restricted to a single locality were excluded so that the analyses of these ‘unique taxa excluded’ data were based solely on shared occurrences thus reducing considerably the amount of ‘noise’ in the data. In addition, the genus-level ‘consolidated’ data were further restricted to higher level taxa (essentially a mixture of phyla and classes), with the number of genera present in each group recorded rather than simple presence or absence. This provides a measure of diversity within the higher taxa and is amenable to ordination using PCA as well as cluster analysis based on quantitative data.

Numerical methodology

The consolidated data in binary (presence/absence) format was analysed using the statistical package *PAST* (*PAlaeontological STatistics*) (Hammer *et al*. 2001), which is available on the Internet as freeware, is periodically updated and refined, and is fully supported by an extensive manual.

Four data sets, comprising the Hurlet Limestone species and genera, and Index Limestone species and genera, were transferred into PAST and analysed as described below. Seriation, cluster analysis and to some extent non-metric multidimensional scaling (NMDS) proved suitable techniques for use on the binary data, whilst cluster analysis and PCA were appropriate for the diversity data within high level clades.

Seriation reorganises the original binary data matrix to group shared presences of taxa along a diagonal. Unconstrained optimization enables the ordering of both the taxa and localities to achieve a best fit and the ordering of the localities reflects their position along a palaeoecological, palaeobiogeographical and/or temporal gradient. The fewer the influencing factors (such as water depth, substrate characteristics, salinity and oxygenation), the better the clustering along the diagonal and therefore the higher the fitness criterion computed for the seriation. These fitness criteria are therefore much higher for the consolidated data than for the preliminary analyses, which included taxa unique to any one locality. For example, the species-level seriated matrices gave fitness a criterion of 0.721 for the consolidated data compared with 0.397 for the raw, unconsolidated, data for the Hurlet Limestone palaeontological data set and 0.288 cf. 0.139 for the equivalent Index limestone data set. When the samples were subdivided by lithology, consolidation generated fitness criteria on the seriations of 0.635 cf. 0.285 and 0.17 cf. 0.11 for the Hurlet and Index limestones respectively. Constraining the seriations, by fixing the ordering of samples of a particular lithology, forces the grouping of other lithologies. For example, constraining the limestone subset in the species-level seriated matrix for the Hurlet Limestone using the consolidated data set with unique taxa excluded reduced the fitness criterion from 0.635 to 0.403. However, this constrained analysis resulted in the grouping of other lithologies, suggesting ranges of lithofacies tolerance for individual species.

Q-mode analysis was used in the cluster analyses to distinguish groups of samples with similar faunas. Three similarity indices, Dice, Simpson and Raup-Crick, were employed and the clusters joined using the un-weighted pair group average (UPGMA) algorithm. The Dice coefficient was used in the NMDS where persistent patterns in the resultant two dimensional plots of ranked (rather than absolute) difference between samples were taken to reflect genuine structure within the data.

PCA is a widely used eigenvector technique, which operates on a correlation or variance-covariance matrix (Davis 1986) to identify as much of the variation in a set of data and to seek structure within the samples (see Hammer & Harper 2006). The first principal component is always orientated in the direction of maximum variation in the sample; the second and subsequent components are perpendicular to the first, explaining decreasing amounts of variation. As is common in such analyses, the first two or three eigenvectors in the present study contained most of the sample variation.

In the first instance, the ‘palaeontological’ data fields for both the Hurlet and Index limestones were analysed prior to possible links to lithology being explored. The latter involved subdividing the faunal lists from many of the localities in terms of the lithology of the rocks in which each fossil is contained. This increases the information attached to each faunal occurrence but decreases many of the sample sizes and diversities.

Results

Palaeontological data alone

Most of the Hurlet Limestone samples are lithologically homogenous and 33% of species and 36% of genera in the original palaeontological data set occur at multiple localities. By consolidating the data, the percentage of shared genera increases to 46%. Excluding taxa restricted to single localities produced minor changes in the order of the localities and higher fitness criteria in the seriated data (e.g. Fig. 3) together with more consistency of clustering among different similarity coefficients used in the cluster analyses (Fig. 4). The last of these is encouraging given the different emphases that these coefficients have in terms of co-occurrences, relative sample size or the mathematical processes involved (e.g. see Hammer & Harper 2006, pp. 212–213). Three groups of localities were consistently identified in the various seriations and are also recognised by NMDS. Group 1, which also emerges consistently in the cluster analyses (Fig. 4) comprises Carskeoch (locality 12), Daldilling (26), Nethershield (55), River Ayr (Windy Burn) (65) and Windy Burn (67); Group 2 comprises Cairnshalloch Limeworks (9), Captain’s Glen (11), Dailly Station (24), Heronspark Burn (36), Meikleholm Burn (52) and Quarrelhill Burn (57);

Group 3 comprises Auchmillanhill Bore (1), Captain’s Bridge (10) and River Ayr (Upper Heilar) (64).

These three groups of localities were discriminated purely on the basis of their faunal association but there are some broad links between these faunal associations and lithofacies:

(i) Group 1 is a fauna characteristic of clearer water conditions with a preferrence for a firm substrate. It is linked to a wide range of lithologies, particularly limestone;

(ii) Group 2 is a fauna characteristic of clear water conditions with a preferrence for a soft substrate. It is linked to an association of limestone-dominated lithofacies;

(iii) Group 3 is a low diversity fauna with a preference for muddier water conditions and a soft substrate. It is linked to a siliciclastic lithofacies.

These results closely mimic the seminal semi-quantitative analysis published by Wilson (1989), who presented, in generalised diagrammatic form (Wilson 1989, fig. 9), the occurrence of the most commonly found marine fossils of the Dinantian of central Scotland in relation to the lithology of the host rocks. He related the fossils, at group and genus-level, to the lithology they were found in (mudstones and limestones with increasing or decreasing calcareous and siliciclastic content). From this he deduced their living environments on the continental shelf, which ranged from a nearshore zone with muddy water, to offshore or nearshore zones with clearer water. The parallels between the quantitatively determined groupings of faunas recognised in the BGS collections in the present study and those recognised by

Wilson with his wealth of field experience demonstrate that geologically significant patterns can be recognised in the historical palaeontological data sets not originally collected for this purpose.

Restricting the genus-level consolidated data to higher taxonomic groups and recording the number of genera present in each group, provided a measure of diversity within the higher taxa (Fig. 5) that was amenable to cluster analysis and PCA (Fig. 6). The grouping of localities evident in the species- and genus-level analyses were not generally preserved in the cluster analyses of the quantitative data, but two large groups of localities were distinguished. These also form non-overlapping portions of the plot of the second and third components of the PCA. Some differentiation of the samples is provided by the third component. These include gastropods at localities 10, 12 and 52 with loadings around zero; anthozoans and bryozoans at localities 65 and 67 with low positive loadings; and nautiloids and others at localities 9, 24 and 57 with higher positive loadings.

In contrast, however, the picture was far from clear for the lithologically more heterogeneous Index Limestone, a thicker depositional unit with a much larger number of samples. No clear palaeoecological patterns emerged from the five associations discriminated in the solely palaeontological data by cluster analysis.

Inclusion of lithological data

Subdividing the samples on the basis of the lithology containing the fossils provides an explicit link between faunal associations and a potentially very important facet of the palaeoenvironment.

Hurlet Limestone

The unconstrained seriations of consolidated data at both species- and genus-level for all taxa from the Hurlet Limestone are very similar and have fairly low fitness criteria of 0.33 and 0.35 respectively. Excluding taxa restricted to any one locality produces a large increase in the fitness criterion to 0.635 and 0.617 respectively (Figs 7, 8). Apart from the distinction of siltstone samples in the genus-level seriation there is no grouping of samples by lithology. Constrained seriation, based on the order of the limestone samples that emerged from an unconstrained analysis of the limestone samples alone produces a grouping of the other lithologies (Figs 9, 10) albeit with lower fitness criteria than the equivalent unconstrained seriations. The seriations show that tolerance ranges of some taxa within the carbonate environments extend into other lithofacies in a systematic way across environmental gradients.

Cluster analyses of species- and genus-level data sets (all taxa and unique taxa excluded) do not reveal consistent patterns. However, recurring groupings of samples emerge from cluster analysis of the numbers of genera within higher taxa. Application of both the Dice and Raup-Crick coefficients to this 'higher taxa' data set show three major clusters (Ht 1–Ht 3), five sub-clusters (Ht 1.1–Ht 3.1), and five close pairings (Ht 1.1.1–Ht 3.1.2) (Fig. 11). The three major clusters can also be recognised on the unconstrained seriation of the whole data set and even more closely in the subset of limestone samples. Again this suggests changing co-occurrences of taxa across an environmental gradient.

The first three components of the PCA represent 93% of the variation within the ‘higher taxa’ data set from the Hurlet Limestone, with 81 % represented by Principal Component 1. The main variables along these three principal components are, in turn: (1) brachiopods; (2) bivalves; and (3) crinoids and bryozoans (with algae, foraminifera and crustaceans). The major clusters identified in the cluster analysis (Ht 1, Ht 2 and Ht 3, Fig. 13) can also be recognised on the PCA plots (Fig. 12); their distributions reflecting differences in trophic structure of the faunal associations (and therefore differences in environment). Both the cluster analysis and PCA of the diversity data reveal three major clusters that account for all but 2 of the samples. These groups cut across lithofacies but reflect differences in taxonomic composition and trophic structure.

- Ht 1 includes seven samples. The lithofacies represented are limestone (with dolostone) (57%) and argillaceous limestone, mudstone/claystone (undifferentiated)/calcareous mudstone, and siltstone (about 14% each). The fauna includes brachiopods (59% of all genera recorded within the cluster) with 1–9 genera present in each sample, bivalves (21%) with 0–3 genera, and crinoid columnals (13%) with 0–1 genera.
- Ht 2 includes seven samples. The lithofacies represented are argillaceous limestone (43%), limestone (29%) and calcareous sandstone and siltstone (14% each). The fauna includes mainly brachiopods (93%) with 1–4 genera, and gastropods (7%) with 0–1 genera.
- Ht 3 includes five samples. The lithofacies represented are limestone (80%) and mudstone/claystone (undifferentiated) (20%). The fauna includes mainly brachiopods (63%) with 1–8 genera, crinoids (19%) with one genus, and bryozoa (11%) with 0–2 genera.

Index Limestone

The fitness criteria for the unconstrained seriations of the species- (0.06) and genus- (0.11) level data sets for all taxa and even for the data with the unique taxa excluded are very low (species 0.17 and genera 0.20), and none show grouping of samples from similar lithologies. Constraining the genus-level seriation by the ordering determined for the limestone samples alone results in most of the other lithologies grouping together, but the fitness criterion is extremely low (0.10) and there is no clear relationship between lithofacies and faunas. However, the broad grouping of the lithologies suggests that some taxa were distributed along environmental gradients within the carbonate depositional setting and extended outside it into other sedimentary environments in a non-random way.

The results of cluster analyses of all the species- and genus-level data sets do not show any consistent groupings. However, cluster analysis of the higher taxa ‘diversity’ data set using both the Dice and Raup-Crick coefficients shows eight nested clusters (Ix 1.1–Ix 2.6) of three or more samples (Fig. 13) within two major clusters (Ix 1 and Ix 2), broadly reflecting differences in lithology. This suggests there is a crude link between lithology and the diversity and distribution of genera among the higher taxa.

Most of the variation in the ‘higher taxa’ data set for the Index Limestone is expressed by components 1 and 2 of the PCA which together comprise almost 89% of the variance in the data; the third component accounts for 4%. The main loadings on these components are, sequentially: (1) brachiopods and bivalves (strong positive loading); (2) brachiopods (strong negative loading); and (3) gastropods. The major and nested clusters discerned in the cluster analysis can also be distinguished to some extent on the PCA plots (Fig. 14). In general, the most calcareous mudstone faunas in the Index Limestone are mainly included in major cluster Ix 1 and are of low diversity with brachiopods the dominant or sole component and molluscs generally absent. Sandstones and especially siltstones are mainly included major cluster Ix 2 and have moderate to high diversities of brachiopods and bivalves with gastropods present in some cases.

Palaeoecological and palaeoenvironmental interpretation of the structure identified in the collections

Hurlet Limestone

The lithofacies and environmental gradients of taxa selected from the genus-level constrained seriation of the unique taxa excluded data set are shown in Figure 15. These taxa are included in the three faunal groups previously identified, and their palaeoecology accords with the interpretations of Wilson (1989).

The dominant taxa, general trophic structure and palaeoenvironment occupied by the groups of samples identified by cluster analysis of the higher taxa data set (Fig. 11) and to a large extent recognisable in the PCA plots (Fig. 12) can be summarised as follows:

- Ht 1 contains brachiopods and bivalves and, in most samples, crinoid columnals. The epifaunal brachiopods will have colonised a range of substrates depending upon whether they were pedunculate or free lying, but the bivalves are considered to represent infauna with a preference for more muddy substrates. The lithologies of the samples suggest that this major cluster represents a great range of environments, but mainly clear water in the off- or nearshore zones.

- Ht 2 is dominated by brachiopods indicating a range of substrates depending upon whether they were semi-infaunal, pedunculate or free lying. Gastropods also occur, which may have preferred to graze or plough carbonate mud.
- Ht 3 is of epifaunal forms, mainly brachiopods and crinoids most of which will have flourished on firmer substrates.

Index Limestone

Seriation of all the consolidated genus-level data with the samples constrained to the order obtained by seriating the limestone samples alone suggests that the faunal gradients within the carbonate depositional environments can be extended into increasingly coarse siliciclastic sediments. Figures 16 and 17 show this for taxa that have, respectively, an extensive and a limited range within the carbonate environment.

The major clusters and their sub-clusters identified in the cluster analysis for the higher taxa data set are at least partially recognised on the ordination of samples on the PCA and show links between faunal associations and lithologies that reflect the exploitation of subtly different environments. A detailed analysis of the composition and trophic structure of the clusters will form part of a separate study; suffice it to note here that:

Ix 1 is dominated by brachiopods and includes mainly calcareous lithofacies. The limestone lithologies indicate clearer water, the offshore or nearshore zones, firmer substrates, and dominant epifaunal forms. The slightly calcareous mudstone and mudstone/claystone (undifferentiated) lithologies provide evidence of the intermediate to muddy nearshore zones, the latter especially with less firm substrates dominated by infaunal forms. The siltstone lithology of a single sample provides almost insignificant evidence of a zone considered to represent river sediment influx.

Ix 2 is dominated by brachiopods and various molluscs. It includes mainly calcareous lithofacies, but with a significant proportion of siliciclastic sedimentary rocks. The limestone, and slightly calcareous mudstone and mudstone/claystone (undifferentiated) lithologies are indicative of the same palaeoenvironments and faunal associations as for Ix 1. The siltstone and sandstone lithologies show a siliciclastic environment in what is considered to represent a zone of river sediment influx.

Conclusions

- Exploratory numerical techniques can be successfully applied to historical palaeontological collections (not originally intended to investigate palaeoecology) to distinguish palaeoecologically meaningful faunal associations and their palaeoenvironmental setting.
- Records of sample locality and lithology (‘environmental data’) and fossil content (described by major fossil groups, genera and species) can be used; the limitations of sample size, taxonomic overlap and solely binary (presence or absence) data being minimised by excluding all ‘one off’ occurrences of fossil taxa and analysing increasingly consolidated or restricted versions of the original information.
- Seriation, cluster analysis and NMDS are suitable techniques for use on

binary data, whilst the distribution of genera within higher taxonomic groups can be used as a proxy for abundance data to distinguish meaningful faunal associations using cluster analysis and PCA.

- Seriation can be used to indicate the lithological and environmental gradients of some taxa. Cluster analysis can reveal groups of samples, linking lithology and the diversity and distribution of taxa. PCA can explain the distribution of the clusters in terms of differences in taxonomic composition, trophic structure, lithology and environment.
- Quantitative analysis of the historical BGS collections from the Hurlet and Index limestones confirms the relationship between lithofacies and palaeoenvironment inferred by Wilson (1989) and enables the recognition of more subtle patterns not identifiable by qualitative means.
- The success of this study unlocks the potential for palaeoecological interpretation by multivariate numerical analysis of historical collections not originally intended to investigate palaeoecology. An example of such a collection is that of the BGS, where a vast resource, originally collected for biostratigraphy, now awaits renaissance in palaeoecology.

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Figure captions:

FIG. 1. The geology of the Ayrshire Coalfield Basin including the crop of the Hurlet and Index limestones and the sample localities. Graticule is British National Grid. For full details of the sample localities see Supplementary material.

FIG. 2. Stratigraphical framework for the Ayrshire Coalfield Basin including up-to-date lithostratigraphical nomenclature. Based on Browne *et al.* (1999, table 1); Holliday & Molyneux (2006, fig. 1).

FIG. 3. Hurlet Limestone. Species-level seriated matrix for the unique taxa excluded data set. Fitness criterion = 0.721. For locality details see Supplementary material.

FIG. 4. Hurlet Limestone. Species-level cluster analyses for the unique taxa excluded data set, using the Dice, Simpson, and Raup-Crick coefficients.

FIG. 5. Hurlet Limestone. Data matrix for the diversity analysis showing the higher taxa, localities and numbers of genera within each taxon at those localities. For locality details see Supplementary material.

FIG. 6. Hurlet Limestone. Plot of first and second components in the PCA of the number of genera in the higher taxa. The numbered localities are listed in Figure 4. Contours delimit the number of higher taxa in each group.

FIG. 7. Hurlet Limestone. Species-level seriated matrix for the unique taxa excluded

data set. Fitness criterion = 0.635. Lithological abbreviations: CMdst = calcareous mudstone; CSlst = calcareous siltstone; Dst = dolostone; Lst = limestone; Mdst = mudstone/claystone (undifferentiated); MLst = argillaceous limestone; Slst = siltstone; Sst = sandstone. For sample and taxonomic details see Supplementary material.

FIG. 8. Hurlet Limestone. Genus-level unconstrained seriated matrix for the unique taxa excluded data set. Fitness criterion = 0.617. For lithological abbreviations see Figure 7. For sample and taxonomic details see Supplementary material.

FIG. 9. Hurlet Limestone. Species-level seriation to observe lithological groupings of taxa using all samples constrained, for the unique taxa excluded data set. Fitness criterion = 0.403. For lithological abbreviations see Figure 7. For sample and taxonomic details see Supplementary material.

FIG. 10. Hurlet Limestone. Genus-level seriation to observe lithological groupings of taxa using all samples constrained, for the unique taxa excluded data set. Fitness criterion = 0.426. For lithological abbreviations see Figure 7. For sample and taxonomic details see Supplementary material.

FIG. 11. Hurlet Limestone. Cluster analysis for the higher taxa data set used in the diversity analysis, using the Raup-Crick coefficient. For sample details see Supplementary material. Ht 1–3: major clusters of samples; Ht 1.1–3.1: nested clusters of samples; Ht 1.1.1–3.1.2: close pairings of localities.

FIG. 12. Hurlet Limestone. Plot of: (a) the first and second principal components, and (b) the second and third principal components in the PCA of the numbers of genera present in higher taxa showing the fields occupied by samples belonging to the three major clusters (Ht 1–3) identified in Figure 11. For sample details see Supplementary material.

FIG. 13. Index Limestone. Cluster analysis for the higher taxa data set used in the diversity analysis, using the Raup-Crick coefficient. For sample details see Supplementary material. Ix 1–2: major clusters of samples; Ix 1.1–2.6: nested clusters of samples. Note that Ix 1.1 and Ix 1.2 together contain most of the argillaceous limestone samples, with Ix 1.2 containing most of the calcareous mudstone samples. Ix 2.1–2.6 contain most of the siltstone and sandstone samples.

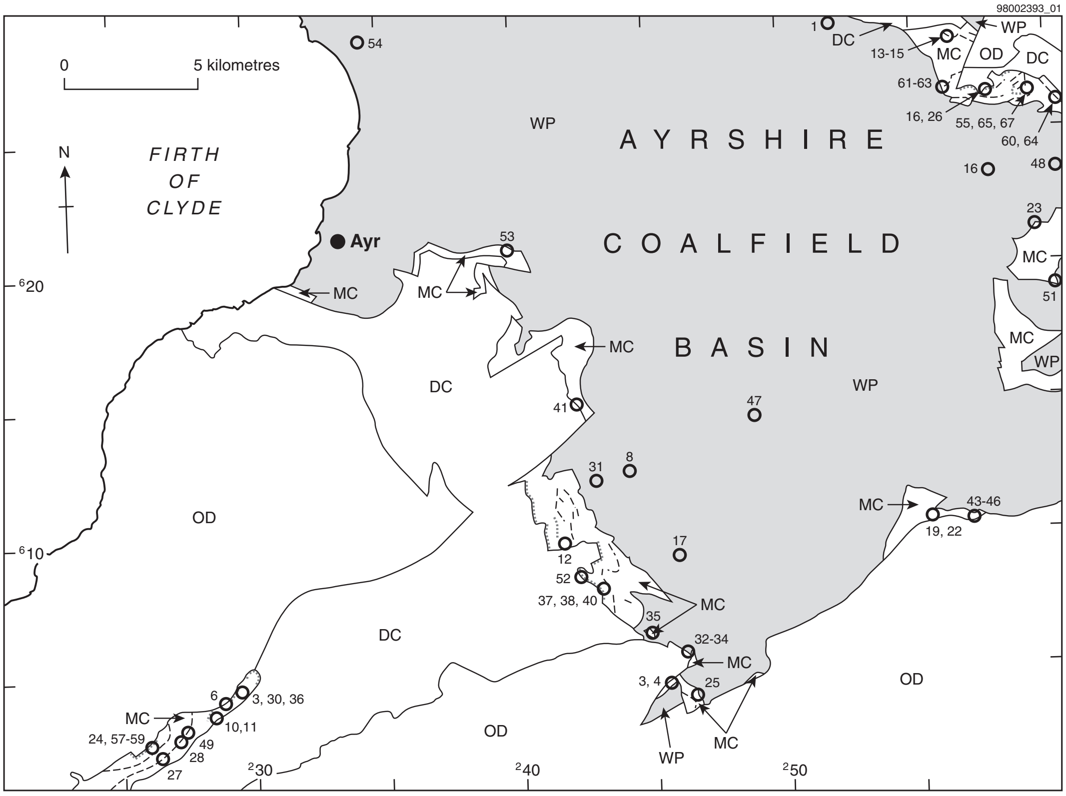
FIG. 14. Index Limestone. Plot of: (a) the first and second principal components, and (b) the second and third principal components in the PCA of the numbers of genera present in higher taxa showing the fields occupied by the two major clusters (Ix 1–2) identified in Figure 13. For sample details see Supplementary material.

FIG. 15. Hurlet Limestone. Ranges of lithofacies and environments of the taxa selected from the genus-level seriation using all samples constrained, for the unique taxa excluded data set. The dotted lines indicate interpolated presence.

FIG. 16. Index Limestone. Faunal gradients of taxa that have the most extensive range within the carbonate depositional environment and extend increasingly into the siliciclastic depositional environment. Based on a seriation of all the consolidated

genus-level data, the samples being constrained to the order obtained by seriating the limestone samples alone. The dotted lines indicate interpolated presence.

FIG. 17. Index Limestone. Faunal gradients of taxa that have a limited range within the carbonate depositional environment and extend furthest into the coarse siliciclastic depositional environment. Based on the seriation of all the consolidated genus-level data, the samples being constrained to the order obtained by seriating the limestone samples alone. The dotted lines indicate interpolated presence.



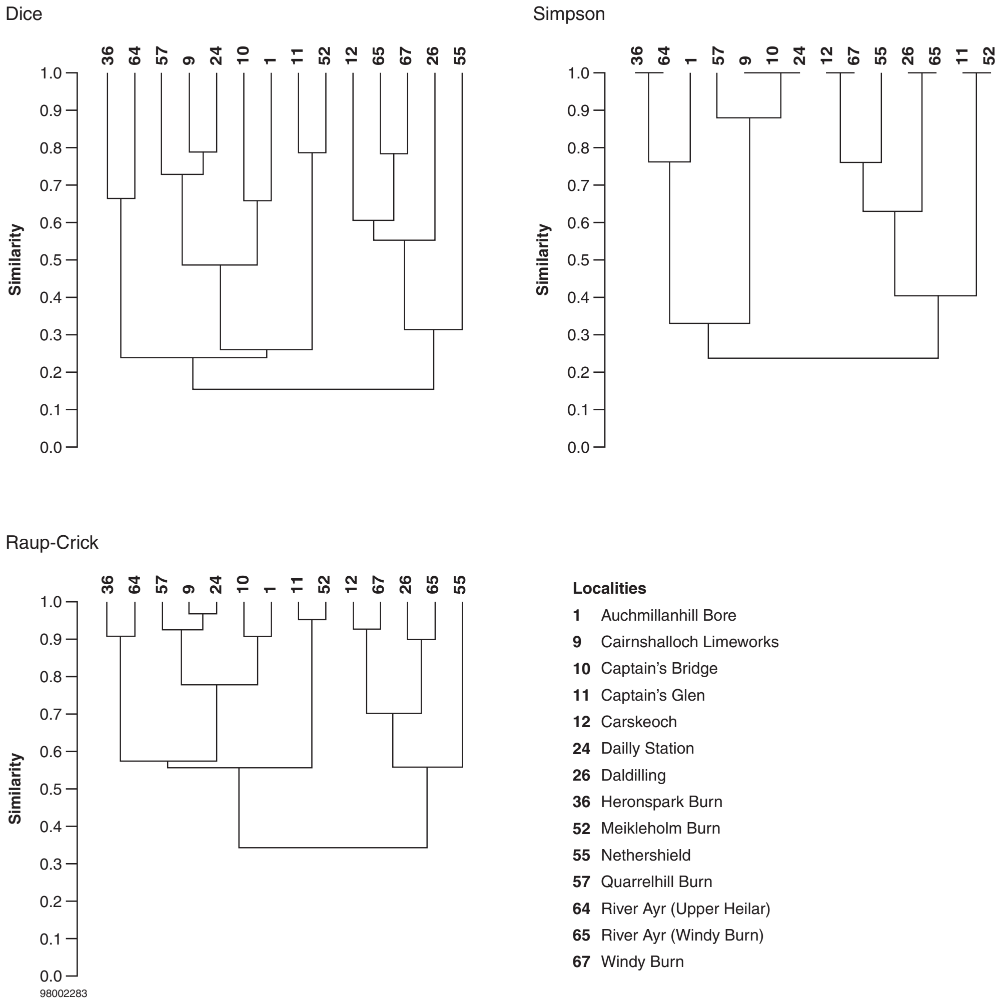
WP	Westphalian-Permian rocks	DC	Devono-Carboniferous (including Courceyan to Brigantian) rocks	········	Crop of the Hurlet Limestone
MC	Middle Carboniferous (including Brigantian to Arnsbergian) rocks	OD	Ordovician-Devonian rocks	- - - -	Crop of the Index Limestone
				o	Sampling locality

Standard Divisions: Sub-system	Standard Divisions: Series	Standard Divisions: Stage	Subsystem (obsolete)	Regional Divisions: Series		Regional Divisions: Stage	Lithostratigraphical Units: Formations	Lithostratigraphical Units: Groups
Pennsylvanian	Middle (*pars*)	Moscovian (*pars*)	Silesian	Westphalian	C	Bolsovian	Scottish Upper Coal Measures	Scottish Coal Measures Group
	Lower	Bashkirian			B	Duckmantian	Scottish Middle Coal Measures	
					A	Langsettian	Scottish Lower Coal Measures	
				Namurian		Chokierian-Yeadonian	Passage Formation	Clackmannan Group
Mississippian	Upper	Serpuk-hovian				Arnsbergian	Upper Limestone Formation	
							Index Limestone	
						Pendleian	Limestone Coal Formation	
	Middle	Viséan	Dinantian	Viséan		Brigantian	Lower Limestone Formation	
							Hurlet Limestone	
							Lawmuir Formation	Strathclyde Group
						Asbian	Kirkwood Formation	
						Arundian-Holkerian	Clyde Plateau Volcanic Formation	
	Lower	Tournaisian		Tournaisian		Chadian	Clyde Sandstone Formation	Inverclyde Group
						Courceyan	Ballagan Formation	
							Kinnesswood Formation	

98002457

Locality / **Taxon**	*Buxtonia* sp.	*?Pugilis* sp.	trepostomatous bryozoa	*Avonia youngiana*	orthotetoid	gigantoproductoid	athyrid	spiriferid	crinoid columnals	*Pleuropugnoides* sp.	productoid	*Spirifer bisulcatus?*
65	■	■	■	■	■	■	■		■			
26	■			■	■				■			
67		■	■	■	■	■		■	■			
55				■				■				
12					■	■		■	■			
52							■		■			
11							■		■	■		
24								■	■		■	
57									■	■	■	
9									■		■	
36									■			■
10											■	
1											■	■
64												■

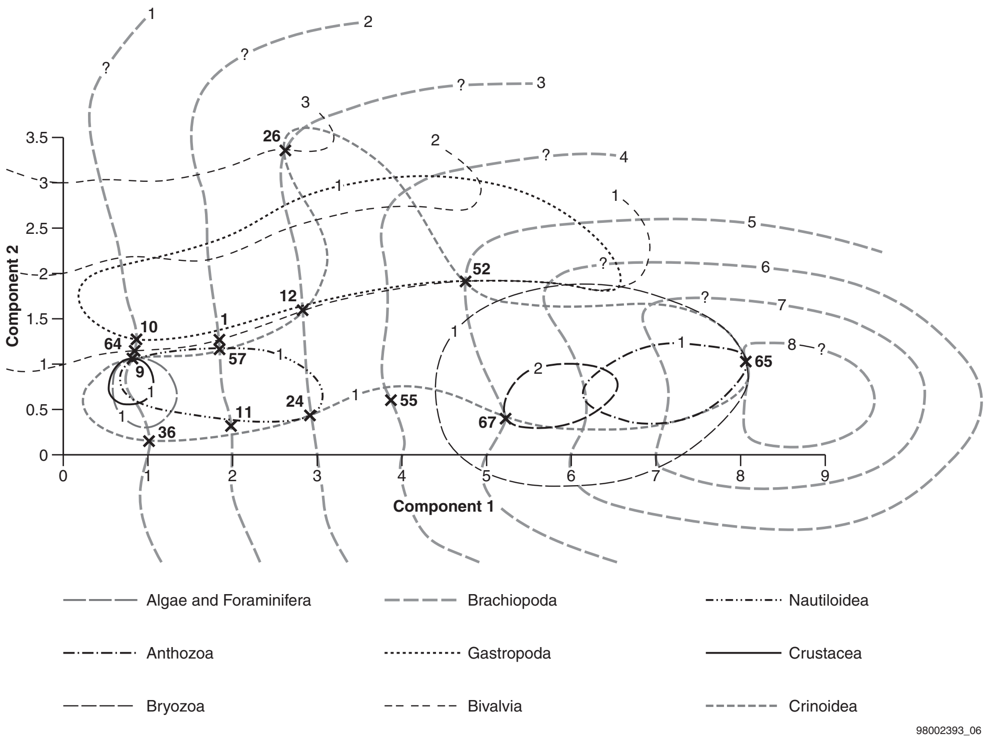
98002393_03



Dice
36 64 57 9 24 10 1 11 52 12 65 67 26 55
Similarity
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Simpson
36 64 1 57 9 10 24 12 67 55 26 65 11 52
Similarity
Raup-Crick
36 64 57 9 24 10 1 11 52 12 67 26 65 55
Similarity
98002283
Localities
1 Auchmillanhill Bore
9 Cairnshalloch Limeworks
10 Captain's Bridge
11 Captain's Glen
12 Carskeoch
24 Dailly Station
26 Daldilling
36 Heronspark Burn
52 Meikleholm Burn
55 Nethershield
57 Quarrelhill Burn
64 River Ayr (Upper Heilar)
65 River Ayr (Windy Burn)
67 Windy Burn

Locality / Taxon	ALGAE	FORAMINIFERIDA	ANTHOZOA	BYROZOA	BRACHIOPODA	GASTROPODA	BIVALVIA	NAUTILOIDEA	CRUSTACEA	CRINOIDEA
1	0	0	0	0	2	0	1	0	0	0
9	1	1	0	0	1	0	1	1	1	1
10	0	0	0	0	1	1	1	0	0	0
11	0	0	0	0	2	0	0	0	0	1
12	0	0	0	0	3	1	1	0	0	1
24	0	0	0	0	3	0	0	1	0	1
26	0	0	0	0	3	0	3	0	0	1
36	0	0	0	0	1	0	0	0	0	1
52	0	0	0	0	5	1	1	0	0	1
55	0	0	0	0	4	0	0	0	0	0
57	0	0	0	0	2	0	1	1	0	1
64	0	0	0	0	1	0	1	0	0	0
65	0	0	1	1	8	0	0	0	0	1
67	0	0	0	2	5	0	0	0	0	1

98002393_05


Component 1
Component 2
Algae and Foraminifera
Brachiopoda
Nautiloidea
Anthozoa
Gastropoda
Crustacea
Bryozoa
Bivalvia
Crinoidea
98002393_06

Sample \ Taxon	gigantoproductoid	*?Pugilis* sp.	trepostomatous bryozoa	*Avonia* sp.	*Buxtonia* sp.	orthotetoid	athyrid	rhynchonellid	*Avonia youngiana*	crinoid columnals	*Camarotoechia* sp.	orthocone nautiloid	*Composita* sp.	spiriferid	productoid
67aMLst	■														
12bLst	■					■									
65aLst	■	■	■	■	■	■	■	■		■					
67bLst		■	■			■			■	■					
26aMLst				■	■					■					
52aLst							■	■		■					
65cCSlst								■	■						
11aLst							■			■	■				
36aLst										■					
12aMdst										■					
1aMdst/CMdst						■		■		■		■	■	■	■
55aLst									■					■	
57aLst										■	■	■	■		■
9aLst										■					■
65bMLst													■		
24aLst										■				■	■
67cSlst														■	
64aSlst														■	
10bMLst															■
10aDst															■

98002393_10

Sample / Taxon	gigantoproductoid	*Buxtonia*	trepostomatous bryozoa	*?Pugilis*	*Avonia*	orthotetoid	athyrid	rhynchonellid	crinoid columnals	*Camarotoechia*	orthocone nautiloid	*Composita*	spiriferid	productoid
67aMLst	■													
12bLst	■					■								
65aLst	■	■	■	■	■	■	■	■	■					
26aMLst		■			■				■					
67bLst			■	■	■	■			■					
55aLst	■				■								■	
65cCSlst					■			■						
52aLst							■	■	■					
11aLst							■		■	■				
12aMdst									■					
36aLst									■					
1aMdst/CMdst						■		■	■		■	■	■	■
57aLst									■	■	■	■		■
9aLst									■					■
65bMLst												■		
24aLst									■				■	■
64aSlst													■	
67cSlst													■	
10aDst														■
10bMLst														■

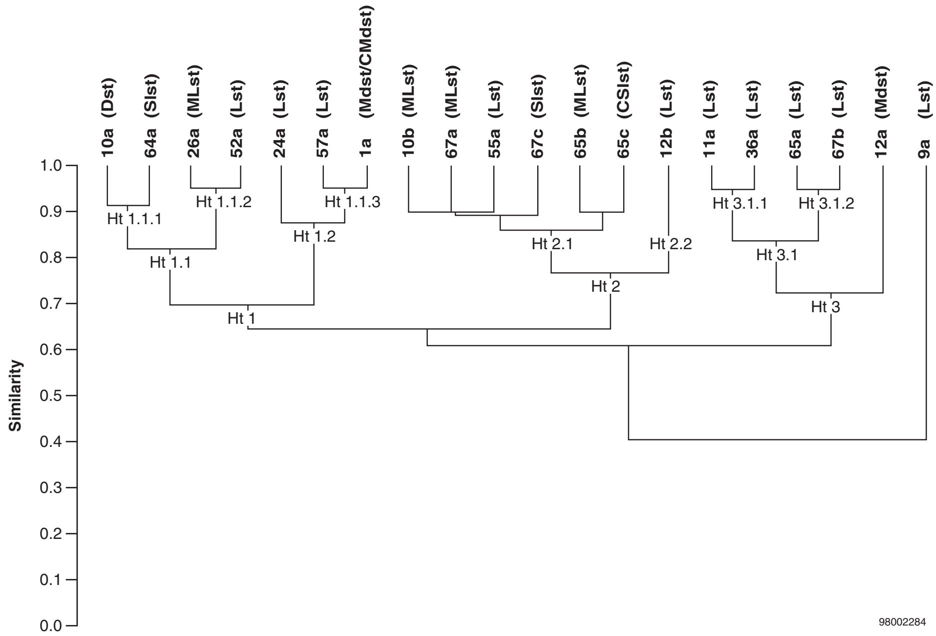
98002393_11

Taxon / Sample	10aDst	57aLst	9aLst	24aLst	11aLst	36aLst	55aLst	52aLst	67bLst	65aLst	12bLst	1aMdst/CMdst	65bMLst	67aMLst	10bMLst	26aMLst	12aMLst	64aSlst	67cSlst	65cCSlst
Camarotoechia sp.		■			■															
productoid	■	■	■	■								■			■					
orthocone nautiloid		■										■								
athyrid					■			■		■										
crinoid columnals		■	■	■	■	■		■	■	■		■				■	■			
Composita sp.		■										■	■							
trepostomatous bryozoa									■	■										
?*Pugilis* sp.									■	■										
orthocone nautiloid									■	■	■	■								
gigantoproductoid										■	■			■						
Avonia youngiana							■		■											■
spiriferid				■			■					■						■	■	
rhynchonellid								■		■		■								■
Avonia sp.										■						■				
Buxtonia sp.										■						■				

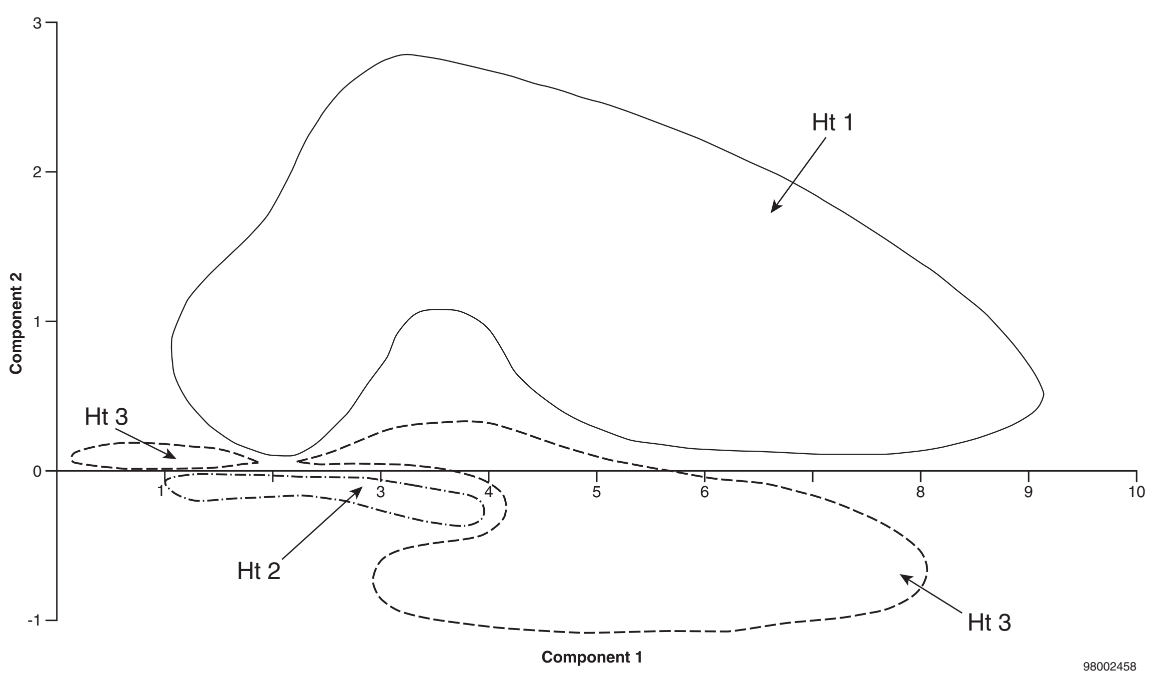
98002393_12

Taxon / Sample	10aDst	57aLst	9aLst	24aLst	36aLst	11aLst	52aLst	55aLst	65aLst	67bLst	12bLst	1aMdst/CMdst	10bMLst	26aMLst	65bMLst	67aMLst	12aMdst	64aSlst	67cSlst	65cCSlst
Camarotoechia		■				■														
productoid	■	■	■	■								■	■							
orthocone nautiloid		■										■								
athyrid						■	■		■											
crinoid columnals		■	■	■	■	■	■		■	■		■		■			■			
trepostomatous bryozoa									■	■										
?Pugilis									■	■										
Composita		■										■			■					
orthotetoid									■	■	■	■								
gigantoproductoid								■	■		■					■				
Buxtonia									■					■						
rhynchonellid							■		■			■								■
spiriferid				■				■				■						■	■	
Avonia								■	■	■				■						■

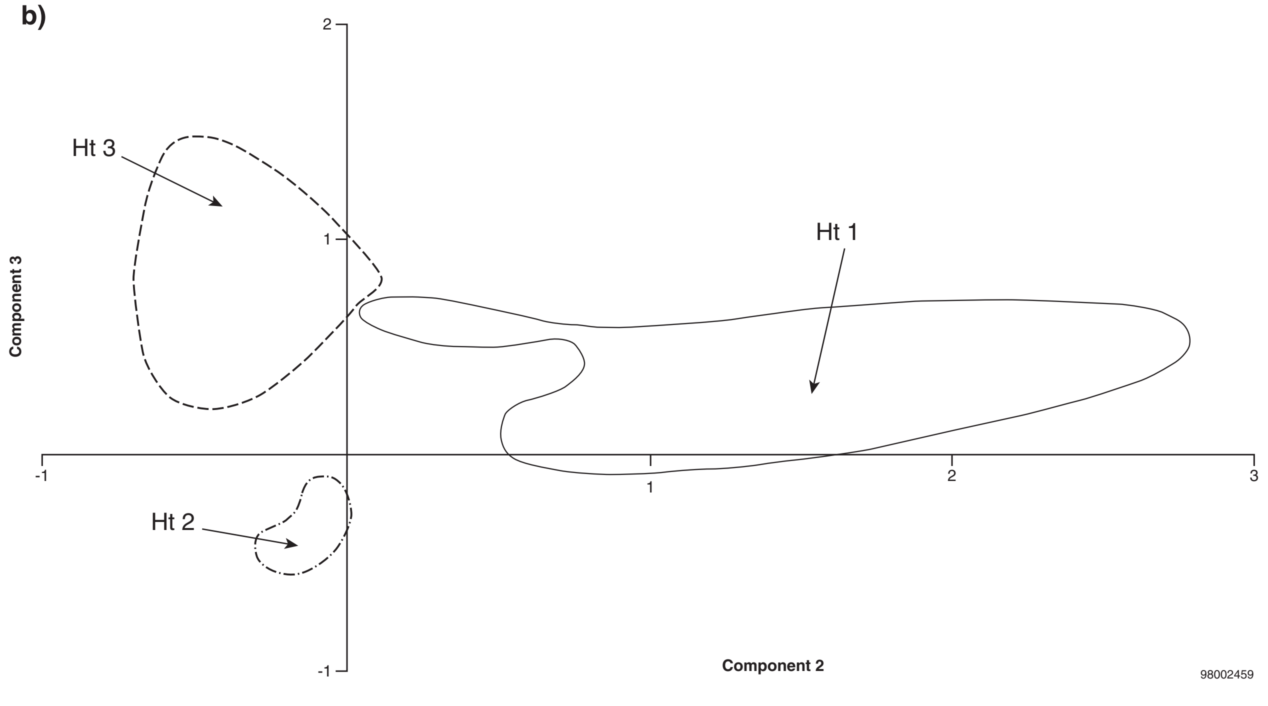
98002393_13

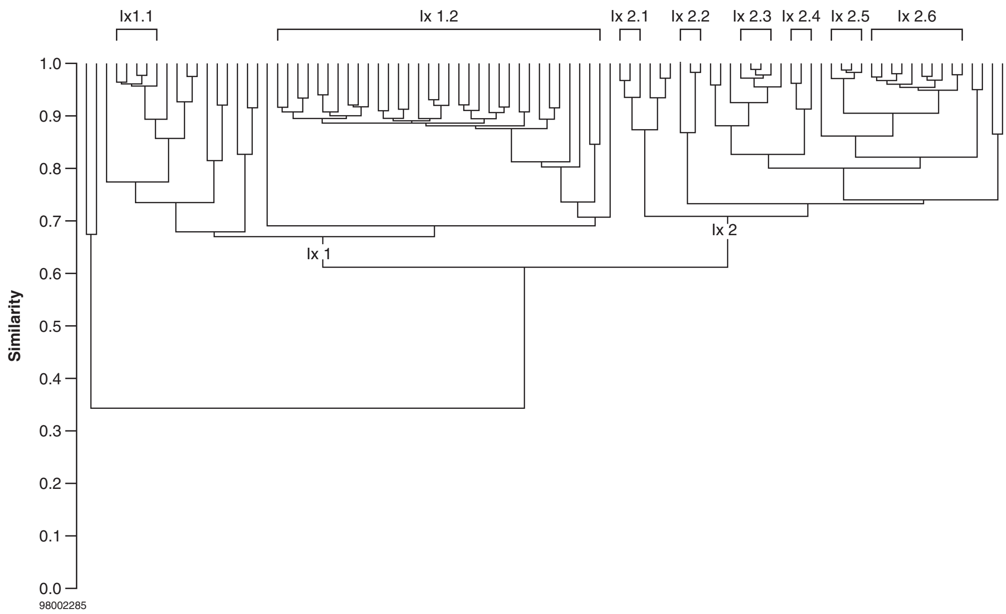

10a (Dst)
64a (Slst)
26a (MLst)
52a (Lst)
24a (Lst)
57a (Lst)
1a (Mdst/CMdst)
10b (MLst)
67a (MLst)
55a (Lst)
67c (Slst)
65b (MLst)
65c (CSlst)
12b (Lst)
11a (Lst)
36a (Lst)
65a (Lst)
67b (Lst)
12a (Mdst)
9a (Lst)
Similarity
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Ht 1.1.1
Ht 1.1.2
Ht 1.1.3
Ht 1.2
Ht 1.1
Ht 1
Ht 2.1
Ht 2.2
Ht 2
Ht 3.1.1
Ht 3.1.2
Ht 3.1
Ht 3
98002284

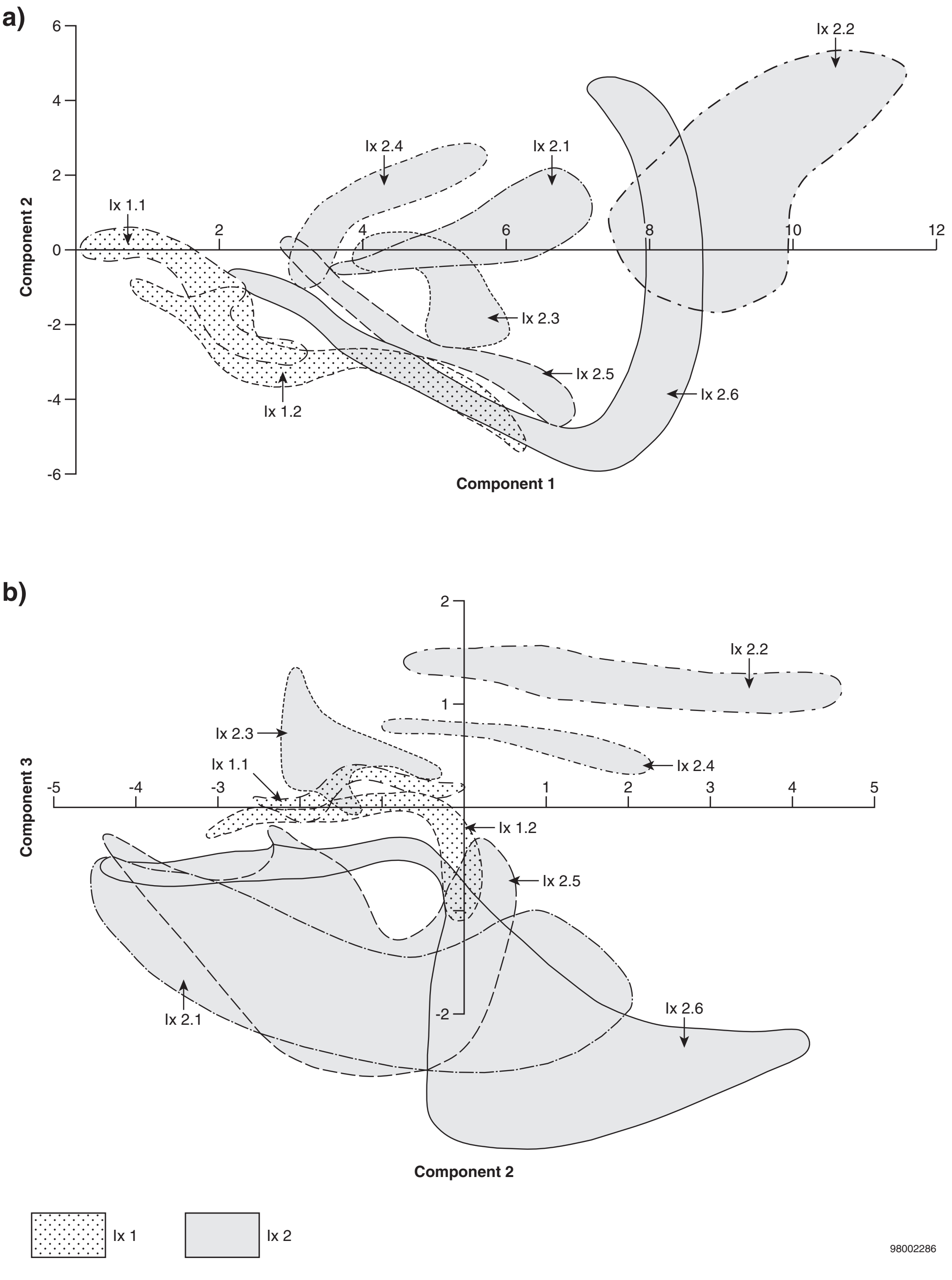
a)

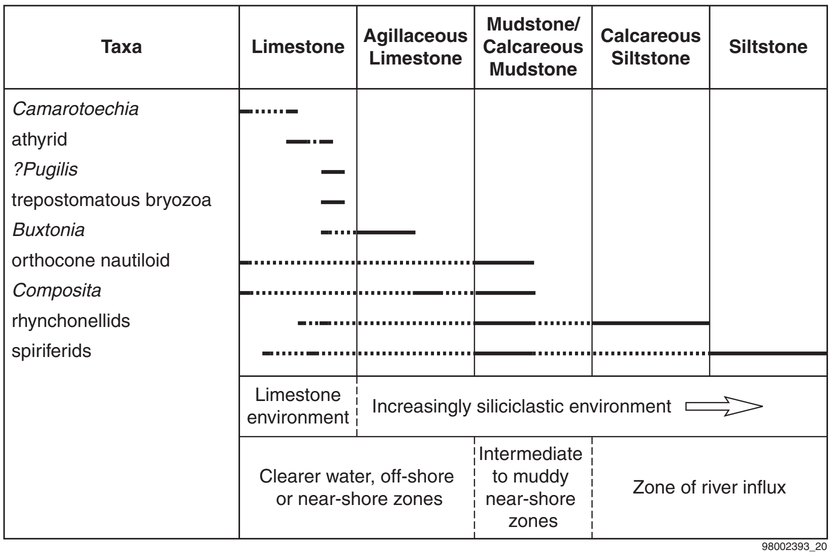

3
2
1
0
-1
Component 2
1
3
4
5
6
8
9
10
Component 1
Ht 1
Ht 2
Ht 3
Ht 3
98002458

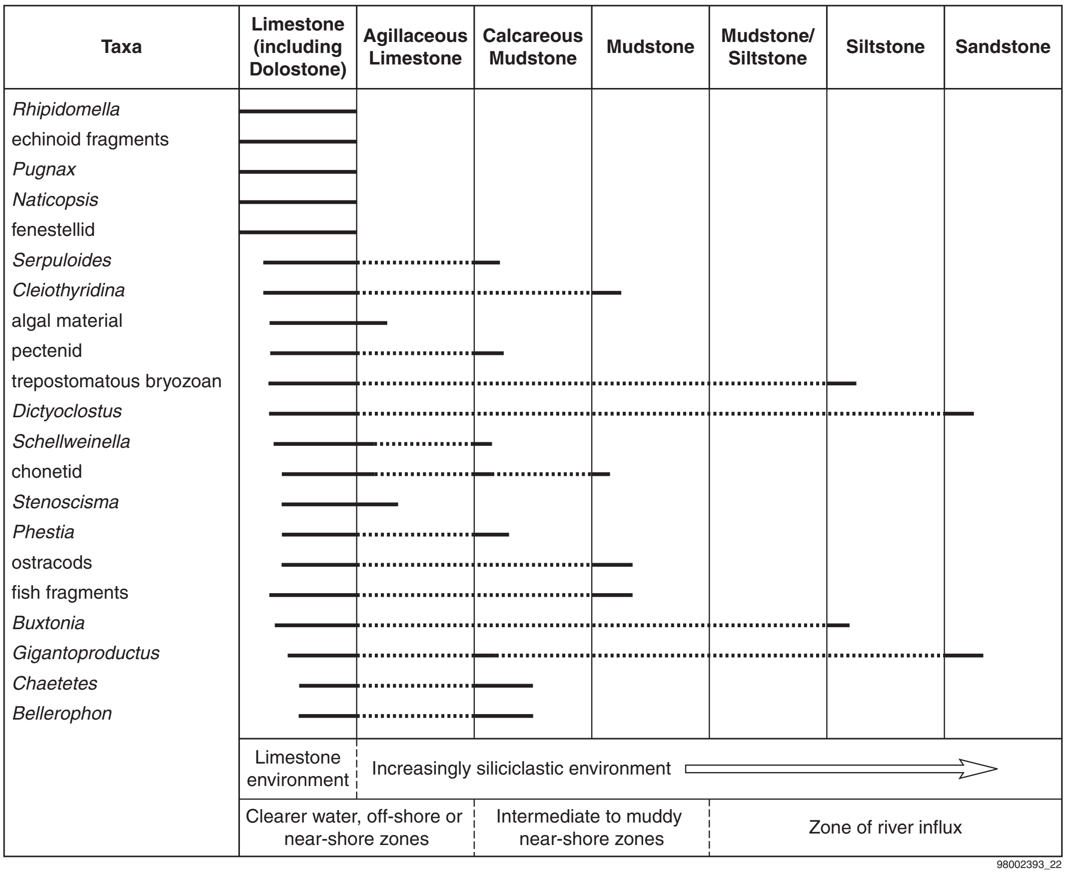
b)

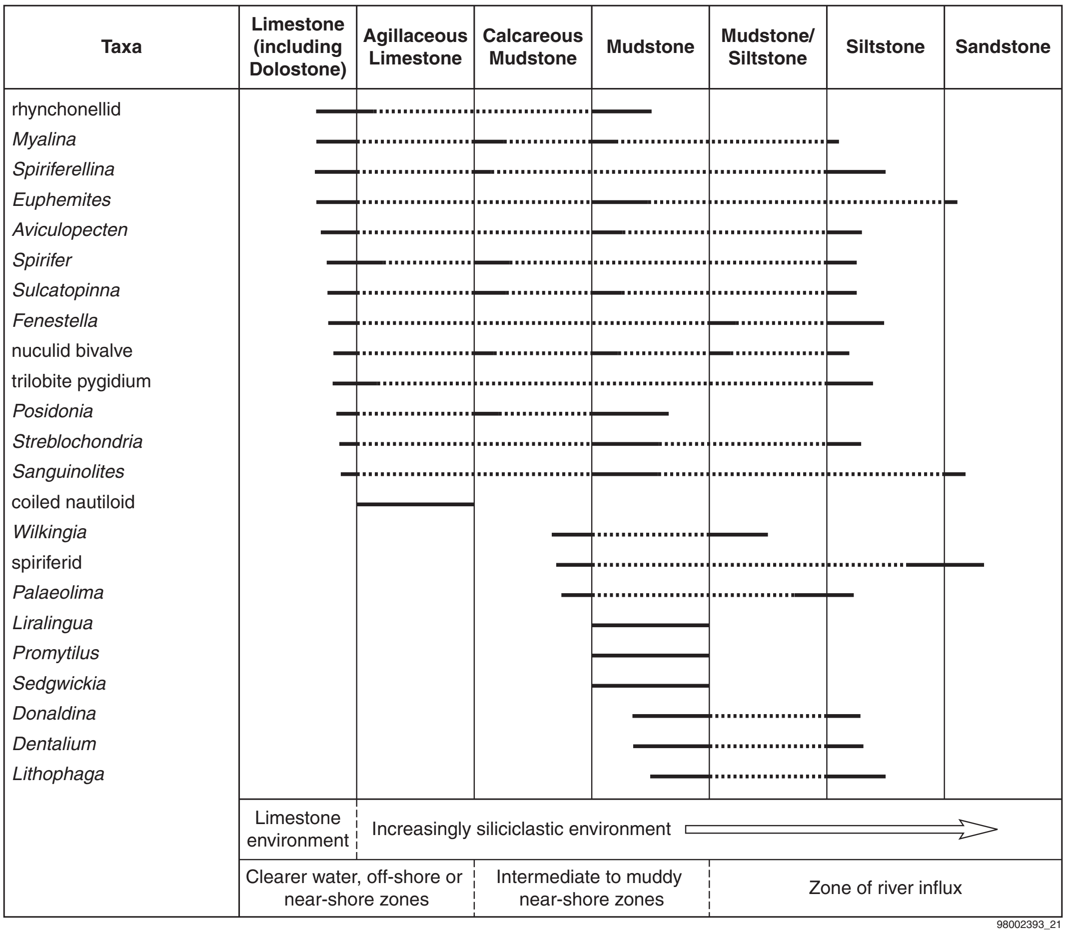

2
1
-1
Component 3
-1
1
2
3
Component 2
Ht 1
Ht 2
Ht 3
98002459


Ix1.1
Ix 1.2
Ix 2.1
Ix 2.2
Ix 2.3
Ix 2.4
Ix 2.5
Ix 2.6
Ix 1
Ix 2
Similarity
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
98002285


a)
Component 2
Component 1
Ix 1.1
Ix 1.2
Ix 2.1
Ix 2.2
Ix 2.3
Ix 2.4
Ix 2.5
Ix 2.6
b)
Component 3
Component 2
Ix 1
Ix 2
98002286


Taxa
Limestone
Agillaceous Limestone
Mudstone/ Calcareous Mudstone
Calcareous Siltstone
Siltstone
Camarotoechia
athyrid
?Pugilis
trepostomatous bryozoa
Buxtonia
orthocone nautiloid
Composita
rhynchonellids
spiriferids
Limestone environment
Increasingly siliciclastic environment
Clearer water, off-shore or near-shore zones
Intermediate to muddy near-shore zones
Zone of river influx
98002393_20


Taxa
Limestone (including Dolostone)
Agillaceous Limestone
Calcareous Mudstone
Mudstone
Mudstone/ Siltstone
Siltstone
Sandstone
Rhipidomella
echinoid fragments
Pugnax
Naticopsis
fenestellid
Serpuloides
Cleiothyridina
algal material
pectenid
trepostomatous bryozoan
Dictyoclostus
Schellweinella
chonetid
Stenoscisma
Phestia
ostracods
fish fragments
Buxtonia
Gigantoproductus
Chaetetes
Bellerophon
Limestone environment
Increasingly siliciclastic environment
Clearer water, off-shore or near-shore zones
Intermediate to muddy near-shore zones
Zone of river influx
98002393_22


Taxa
Limestone (including Dolostone)
Agillaceous Limestone
Calcareous Mudstone
Mudstone
Mudstone/ Siltstone
Siltstone
Sandstone
rhynchonellid
Myalina
Spiriferellina
Euphemites
Aviculopecten
Spirifer
Sulcatopinna
Fenestella
nuculid bivalve
trilobite pygidium
Posidonia
Streblochondria
Sanguinolites
coiled nautiloid
Wilkingia
spiriferid
Palaeolima
Liralingua
Promytilus
Sedgwickia
Donaldina
Dentalium
Lithophaga
Limestone environment
Increasingly siliciclastic environment
Clearer water, off-shore or near-shore zones
Intermediate to muddy near-shore zones
Zone of river influx
98002393_21

Localities, taxa and sample lithologies used on the diagrams

Localities				Taxa			
Number	Name	Limestone	Grid Reference [NS]	Taxon	Abbreviation		
1a	Auchmillan	Hurlet	[5171 2894]		Hurlet Limestone Anal		Index Lime
2a	Auldcraigo	Index	[4561 0421]		Species	Genus	Species
3a	Auldcraigo	Index	[4515 0439]	PLANTAE			
4a	Auldcraigo	Index	[4523 0441]	Lepidophyllum sp.			LEPI
4b	Auldcraigo	Index	[4523 0441]	Odontopteris sp.			ODON
4c	Auldcraigo	Index	[4523 0441]	ALGAE			
5a	Auldcraigo	Index	[4511 0442]	algal mater	alga	alga	alga
5b	Auldcraigo	Index	[4511 0442]	FORAMINIFERIDA			
5c	Auldcraigo	Index	[4511 0442]	foraminifer	fora	fora	
5d	Auldcraigo	Index	[4511 0442]	PORIFERA			
6a	Baldrennar	Index	[2880 0407]	'Chaetetes tumidus'			CHAt
7a	Blairmulloc	Index	[5605 2820]	ANTHOZOA			
8a	Bowhill Bo	Index	[4381 1231]	clisiophyllid			clis
8b	Bowhill Bo	Index	[4381 1231]	Dibunophyllum sp.			DIBU
9a	Cairnshallo	Hurlet	[4080 1006]	zaphrentid			zaph
10a	Captains B	Hurlet	[2851 0356]	coral indete	cora	cora	cora
10b	Captains B	Hurlet	[2851 0356]	BRYOZOA			
11a	Captains G	Hurlet	[2851 0355]	Fenestella	FENs	Fene	FENS
12a	Carskeoch	Hurlet	[4150 0966]	fenestellid			fene
12b	Carskeoch	Hurlet	[4150 0966]	trepostoma	t-br	t-br	t-br
13a	Cleuch Bur	Index	[5604 2817]	ANNELIDA			
14a	Cleuch Bur	Index	[5613 2813]	Serpuloides sp.			SERP
15a	Cleuch Bur	Index	[5605 2818]	?Serpuloides sp.			?SER
16a	Common E	Index	[5734 2322]	BRACHIOPODA			
16b	Common E	Index	[5734 2322]	Actinoconchus sp.			ACTs
16c	Common E	Index	[5734 2322]	Angiospirife	A1ct	Angi	A1ct
16d	Common E	Index	[5734 2322]	Antiquatonia muricata (Phillips)			A2mu
17a	Corbie Cra	Index	[4553 0920]	Antiquaton	A2m?	Anti	A2m?
17b	Corbie Cra	Index	[4553 0920]	Antiquatonia cf. muricata (Phillips)			A2cm
17c	Corbie Cra	Index	[4553 0920]	Antiquatonia sulcata (J Sowerby)			A2sg
18a	Craighouse	Index	[5487 1046]	Antiquatonia sp.			A2sp
19a	Craighouse	Index	[5483 1038]	?Antiquatonia sp.			?A2s
19b	Craighouse	Index	[5483 1038]	?Athyris sp.			?ATHs
20a	Craighouse	Index	[5482 1041]	athyrid	Athd	athy	Athd
21a	Craighouse	Index	[5489 1047]	athyrid?	Atd?	athy	Atd?
22a	Craighouse	Index	[5486 1043]	?Avonia davidsoni (Jarosz)			?Avd
22b	Craighouse	Index	[5486 1043]	Avonia you	Avy	Avon	
22c	Craighouse	Index	[5486 1043]	Avonia sp.	Avsp	Avon	
23a	Craigston I	Index	[5908 2130]	?Avonia sp	?Avs	Avon	
23b	Craigston I	Index	[5908 2130]	?Beecheria sp.			?BEEs
23c	Craigston I	Index	[5908 2130]	Brachythyr	BRAC	Brac	
24a	Dailly Stati	Hurlet	[2601 0246]	Buxtonia scabricula (Martin)			B1sc
25a	Dalcairnie I	Index	[4614 0387]	Buxtonia scabricula (Martin)?			B1s?
26a	Daldilling	Hurlet	[5738 2625]	Buxtonia aff. scabricula (Martin)			B1as
27a	Dalquharra	Index	[2653 0206]	Buxtonia s	B1sp	Buxt	B1sp
27b	Dalquharra	Index	[2653 0206]	?Buxtonia sp.			?B1s
28a	Dalquharra	Index	[2721 0274]	Camarotoe	CAMA	Cama	CAMA
28b	Dalquharra	Index	[2721 0274]	chonetid	chon	chon	chon
28c	Dalquharra	Index	[2721 0274]	Cleiothyridina deroissyi (Léveillé)			C1de
29a	Drumgranç	Index	[4310 0946]	Cleiothyridina deroissyi (Léveillé)?			C1d?
30a	Drummoch	Index	[2955 0444]	Cleiothyridina cf. fimbriata (Phillips			C1cf
30b	Drummoch	Index	[2955 0444]	Cleiothyridina glabistria (Phillips)			C1gl
31a	Drysdales I	Index	[4263 1200]	Cleiothyridina sp.			C1sp

31b	Drysdales	Index	[4263 1200]	?Cleiothyridina sp.			?C1s
31c	Drysdales	Index	[4263 1200]	Composita ambigua (J Sowerby)			c2am
32a	Glenhead	Index	[4590 0560]	Composita ambigua (J Sowerby)?			C2a?
32b	Glenhead	Index	[4590 0560]	Composita cf. ambigua (J Sowerb			C2ca
32c	Glenhead	Index	[4590 0560]	?Composita ambigua (J Sowerby			?C2a
33a	Glenhead	Index	[4590 0561]	Composita	C2sp	Comp	C2sp
33b	Glenhead	Index	[4590 0561]	?Composit	?C2s	Comp	?C2s
34a	Glenhead	Index	[4590 0562]	Crurithyris urii (Fleming)			CRUi
34b	Glenhead	Index	[4590 0562]	Dictyoclostus semireticulatus (Ma			DICs
35a	Grimmet F	Index	[4463 0627]	Dielasma sp.			DIEs
36a	Heronsparl	Hurlet	[2939 0456]	Echinoconchus sp.			ECHs
37a	Keirs Burn	Index	[4298 0802]	?Echinoconchus sp.			?ECH
37b	Keirs Burn	Index	[4298 0802]	Eomarginif	Ello	Eoma	Ello
38a	Keirs Burn	Index	[4309 0809]	Eomarginifera cf. longispina (J So			E1cl
38b	Keirs Burn	Index	[4309 0809]	?Eomarginifera cf. longispina (J S			?E1l
39a	Keirs Burn	Index	[4279 0803]	Eomarginifera praecursor (Muir-W			E1pr
40a	Keirs Glen	Index	[4310 0805]	Eomarginifera praecursor (Muir-W			E1p?
41a	Kerse Park	Index	[4218 1485]	Eomarginifera cf. praecursor (Mui			E1cp
41b	Kerse Park	Index	[4310 0805]	Eomarginifera sp.			E1sp
42a	Knockburn	Index	[5634 1032]	'Fusella convoluta'			FUSc
42b	Knockburn	Index	[5634 1032]	Gigantopro	GIGg	Giga	GIGg
43a	Knockburn	Index	[5634 1029]	Gigantopro	GIGs	Giga	GIGs
43b	Knockburn	Index	[5634 1029]	gigantopro	giga	Giga	giga
44a	Knockburn	Index	[5634 1028]	Krotovia aculeata (J Sowerby)			KROa
45a	Knockburn	Index	[5634 1027]	Latiproductus latissimus (J Sowerl			L1la
46a	Knockburn	Index	[5634 1024]	Latiproductus latissimus (J Sowerl			L1l?
46b	Knockburn	Index	[5634 1024]	Latiproduct	L1cl	Lati	L1cl
47a	Knockguld	Index	[4833 1425]	Latiproductus sp.			L1sp
47b	Knockguld	Index	[4833 1425]	?Latiproductus sp.			?L1s
48a	Lands of M	Index	[5984 2337]	Lingula mytilloides J Sowerby			L2my
48b	Lands of M	Index	[5984 2337]	Lingula squamiformis Phillips			L2sq
49a	Maxwell C	Index	[2746 0298]	Lingula cf. squamiformis Phillips			L2cs
50a	Maxwell R	Index	[2742 0296]	Lingula sp.	L2sp	Ling	L2sp
51a	Meikle Auc	Index	[5982 1899]	Liralingua indicis Graham			LIRi
51b	Meikle Auc	Index	[5982 1899]	Martinia sp.			MART
51c	Meikle Auc	Index	[5982 1899]	?Martinia sp.			?MAR
52a	Meikleholm	Hurlet	[4205 0848]	Orbiculoidea cincta (Portlock)			ORBc
53a	Millcraig	Index	[3959 2081]	Orbicoloidea cincta (Portlock)?			?ORB
54a	Monktonhil	Index	[3457 2849]	Orbiculoidea cf. nitida (Phillips)			ORBn
54b	Monktonhil	Index	[3457 2849]	orthid			orth
55a	Nethershie	Hurlet	[5881 2626]	orthotetoid	orto	orth	orto
56a	Polquhairn	Index	[4733 1499]	orthotetoid?			ort?
57a	Quarrelhill	Hurlet	[2602 0246]	Phricodothyris lineata (J Sowerby)			P1li
58a	Quarrelhill	Index	[2601 0246]	Phricodothyris lineata (J Sowerby)			P1l?
59a	Quarrelhill	Index	[2630 0250]	Phricodothyris cf. lineata (J Sowe			P1cl
60a	River Ayr	Index	[5977 2585]	Phricodothyris sp.			P1sp
61a	River Ayr	Index	[5593 2626]	?Phricodothyris sp.			?P1s
61b	River Ayr	Index	[5593 2626]	Pleuropugnoides pleurodon (Philli			PLEp
61c	River Ayr	Index	[5593 2626]	Pleuropugr	G		PLEs
61d	River Ayr	Index	[5593 2626]	Productus cf. carbonarius de Koni			P2ca
62a	River Ayr	Index	[5588 2629]	Productus concinnus J Sowerby			P2co
62b	River Ayr	Index	[5588 2629]	Productus cf. concinnus J Sowerb			P2co
63a	River Ayr (	Index	[5568 2636]	Productus	P2sp	Prod	P2sp
64a	River Ayr (	Hurlet	[5997 2599]	?Productus sp.			?P2s
65a	River Ayr (	Hurlet	[5886 2627]	productoid	prod	Prod	prod
65b	River Ayr (	Hurlet	[5886 2627]	Pugilis cf. pugilis (Phillips)			PUGp

65c	River Ayr ('	Hurlet	[5886 2627]
66a	Watston Bu	Index	[5985 1725]
67a	Windy Burr	Hurlet	[5874 2629]
67b	Windy Burr	Hurlet	[5874 2629]
67c	Windy Burr	Hurlet	[5874 2629]

Pugilis sp.			PUGs
?Pugilis sp	?PUG	Pugi	
Pugnax cf. pugnus (Martin)			P3cp
?Pugnax sp.			?P3s
?Punctospi	?PUN	Punc	?PUN
Pustula cf. pustulosa (Phillips)			PUSP
Pustula sp.			PUSs
Rhipidomella michelini Léveillé?			RHm?
?Rhipidomella michelini Léveillé			?RHm
rhynchonel	rhyn	rhyn	rhyn
Rugosochonetes hardrensis (Phill			RUGh
Rugosochc	RUGs	Rugo	
Rugosochonetes sp.			Rusp
Schellweinella crenistria (Phillips)			SCHc
Schellweinella sp.			SCHs
?Schellweinella sp.			?SCH
Schizophoria resupinata (Martin)			S1re
Schizophoria cf. resupinata (Marti			S1cr
Schizophoria sp.			S1sp
?Schizophoria sp.			?S1s
Spirifer bisı	SPb?	SPl1	
Spirifer bisulcatus J de C Sowerb			SPbg
?Spirifer sp.			?SPs
Spiriferellina octoplicata (J de C S			S2oc
Spiriferellina cf. perplicata (North)			S2cp
Spiriferellina sp.			S2sp
spiriferid	spir	spir	spir
Stenoscisn	STEs	Sten	STEs
?Stenoscisma sp.			?STE
brachiopod	brac	brac	brac
GASTROPODA			
Bellerophon sp.			BELs
?Bellerophon sp.			?BEL
bellerophontid			bell
Donaldina sp.			DONs
Euphemites ardenensis (Weir)?			EUa?
Euphemites cf. hindi (Weir)			EUch
Euphemites urii (Fleming)			EUur
Euphemites sp.			EUsp
Glabrocingulum sp.			GLAB
'Loxonema curvilineum'			LOXc
loxonematiid			loxo
Meekella sp.			MEEK
Naticopsis variata (Phillips)			NATv
?Naticopsi:	?NAT	Nati	
pleurotomariid?			pleu
Porcellia sp.			PORC
Retispira decussata (Fleming)?			REd?
Retispira cf. decussata (Fleming)			REcd
Retispira striata (Fleming)?			REst
Retispira sp.			REsp
Soleniscus sp.			SOLE
Straparollus carbonarius (J de C S			STRc
pupaeform gastropod			pupa
gastropod i	gast	pupa	gast
SCAPHOPODA			

Dentalium s.l.			DENT
?Dentalium s.l.			?DEN
BIVALVIA			
Actinopteria persulcata (McCoy)			A3pe
Anthraconeilo laevirostrum (Portlo			A4la
?Anthraconeilo pentonensis (Hind			?A4p
?Anthraconeilo sp.			?A4s
Aviculopec	AVIs	Avic	AVIs
?Aviculopecten sp.			?AVI
Aviculopinr	AVIm	Avpl	
Cardiomorp	CARe	Card	CARe
Edmondia maccoyi Hind?			Edm?
Edmondia sulcata (Fleming)			Edsu
?Edmondia sulcata (Fleming)			?EDS
Edmondia sulcata (Fleming)?			EDS?
Edmondia sp.			EDsp
?Edmondia	?Eds	Edmo	?EDs
Euchondria sp.			EUCs
?Euchondria sp.			?EUC
Leiopteria sp.			LEIs
?Leiopteria sp.			?LEI
?Limipecte	?LIM	Limi	
Lithophaga lingualis (Phillips)			LIli
Lithophaga lingualis (Phillips)?			LIl?
Myalina verneuili (McCoy)?			MYv?
Myalina cf. verneuili (McCoy)			MYcv
Myalina sp.			MYsp
Nuculopsis gibbosa (Fleming)			NUCg
nuculid?			nucu
Palaeolima cf. simplex (Phillips)			PAcs
Palaeolima sp.			PAsp
?Palaeolima sp.			?PSa
Parallelodon semicostatus (McCo			PARs
pectenid			pect
Phestia attenuata (Fleming)			PHEa
Posidonia corrugata (Etheridge ju			POCo
Posidonia corrugata (Etheridge ju			POc?
?Posidonia corrugata (Etheridge j			?POc
?Posidonia sp.			?POs
?Promytilus sp.			?PRs
Prothyris sp.			PROs
Saguinolites cf. clavatus Etheridge			SAcc
Sanguinolites plicatus (Portlock)			SApl
Sanguinolites cf. plicatus (Portlock			SAcp
Sanguinolites striatolamellosus de			SAst
Sanguinolites variabilis McCoy gro			SAvg
Sanguinolit	SAsp	Sang	SAsp
?Sanguinolites sp.			?SAs
Schizodus sp.			SCsp
?Schizodus sp.			?SCs
?Sedgwickia sp.			?SED
Solemya primaeva Phillips?			SOLp
Solemya sp.			SOLs
Streblochondria sp.			STRE
Streblopteria ornata (Etheridge jur			STor
?Streblopteria sp.			?STs

Sulcatopinı	SUfl	Sulc	SUfl
Sulcatopinna flabelliformis (Martir			SUf?
Sulcatopinna sp.			SUsp
Wilkingia elliptica (Phillips)			WILe
?Wilkingia	?WIL	Wilk	?WIL
bivalve frag	biva	biva	biva
NAUTILOIDEA			
Orthoceras sp.			ORTH
'cf. Soleno	cSOL	SOLN	
orthocone ı	nauo	naut	nauo
coiled nautiloid			nauc
nautiloid indeterminate			naui
AMMONOIDEA			
goniatite indeterminate			goni
?goniatite indeterminate			goni
ARTHROPODA			
Paladin mucronatus (McCoy)			PALA
trilobite pygidium			tril
trilobite fragments indeterminate			tril
CRUSTACEA			
crustacean			crus
ostracods	ostr	ostr	ostr
ECHINOIDEA			
echinoid fragment			echi
CRINOIDEA			
Poteriocrinus sp.			POTc
crinoid colı	crin	crin	crin
PISCES			
Petalodus psittacinus (McCoy)?			PETA
fish fragments			fish
TRACE FOSSILS			
worm burrows			worm

	Lithologies		
	Abbreviatic	Lithology	
stone Analyses			
Genus	CMdst	Calcareous mudstone	
	CSlst	Calcareous siltstone	
Lepi	Dst	Dolostone	
Odon	Lst	Limestone	
	Mdst	Mudstone/Claystone (undifferentiated)	
alga	MLst	Argillaceous limestone	
	Slst	Siltstone	
	Sst	Sandstone	
Chae			
	Figure 13		
clis	Major Clus	Nested Clu	Sample Number
Dibu			
zaph			
cora	Ix 1		29a Lst
	Ix 1		41a Mdst
Fene	Ix 1		6a Lst
fene	Ix 1	Ix 1.1	15a Lst
t-br	Ix 1	Ix 1.1	48a Mdst
	Ix 1	Ix 1.1	49a MLst
Serp	Ix 1	Ix 1.1	54b Lst
Serp	Ix 1	Ix 1.1	28c Mdst
	Ix 1		66a Dst
Acti	Ix 1		16c Lst
Angi	Ix 1		16d MLst
Anti	Ix 1		42a Lst
Anti	Ix 1		19a Lst
Anti	Ix 1		20a Slst
Anti	Ix 1		50a MLst/Lst
Anti	Ix 1		7a Lst
Anti	Ix 1		23a Mdst
Athy	Ix 1		62b Lst
athy	Ix 1		17a Lst
athy	Ix 1	Ix 1.2	5b CMdst
Avon	Ix 1	Ix 1.2	5c MLst
	Ix 1	Ix 1.2	47a Mdst
	Ix 1	Ix 1.2	48b Lst
	Ix 1	Ix 1.2	22b CMdst
Beec	Ix 1	Ix 1.2	61b CMdst
	Ix 1	Ix 1.2	46b CMdst
Buxt	Ix 1	Ix 1.2	44a Lst/MLst
Buxt	Ix 1	Ix 1.2	63a Lst
Buxt	Ix 1	Ix 1.2	46a Lst
Buxt	Ix 1	Ix 1.2	33a MLst
Buxt	Ix 1	Ix 1.2	62a Mdst
Cama	Ix 1	Ix 1.2	34b Lst
chon	Ix 1	Ix 1.2	43a Lst
Clei	Ix 1	Ix 1.2	4c CMdst
Clei	Ix 1	Ix 1.2	4a Lst
Clei	Ix 1	Ix 1.2	17b CMdst
Clei	Ix 1	Ix 1.2	17c Mdst
Clei	Ix 1	Ix 1.2	23b MLst

Clei	Ix 1	Ix 1.2	61c MLst
Comp	Ix 1	Ix 1.2	54a Mdst
Comp	Ix 1	Ix 1.2	25a Lst
Comp	Ix 1	Ix 1.2	28a Lst
Comp	Ix 1	Ix 1.2	34a CMdst
Comp	Ix 1	Ix 1.2	22c Lst
Comp	Ix 1	Ix 1.2	23c CMdst
Crur	Ix 1	Ix 1.2	37b MLst
Dict	Ix 1	Ix 1.2	61d Slst
Diel	Ix 1	Ix 1.2	45a CMdst
Echi	Ix 1	Ix 1.2	22a Mdst
Echi	Ix 1	Ix 1.2	13a Mdst/CMdst
Eoma	Ix 1	Ix 1.2	14a CMdst
Eoma	Ix 1	Ix 1.2	30a MLst
Eoma	Ix 1		5a Slst
Eoma	Ix 2	Ix 2.1	5d Mdst/Slst
Eoma	Ix 2	Ix 2.1	35a Lst
Eoma	Ix 2	Ix 2.1	51c Slst
Eoma	Ix 2		31c Lst
Fuse	Ix 2		38b Lst
Giga	Ix 2		51b Dst
Giga	Ix 2	Ix 2.2	8a Mdst
Giga	Ix 2	Ix 2.2	31a Mdst
Krot	Ix 2	Ix 2.2	32a Slst
Lati	Ix 2		16a Mdst
Lati	Ix 2		39a Lst
Lati	Ix 2		42b CMdst
Lati	Ix 2	Ix 2.3	3a Sst
Lati	Ix 2	Ix 2.3	28b CMdst
Ling	Ix 2	Ix 2.3	58a Lst
Ling	Ix 2	Ix 2.3	37a Lst
Ling	Ix 2		61a Mdst
Ling	Ix 2	Ix 2.4	16b CMdst
Lira	Ix 2	Ix 2.4	59a Lst
Mart	Ix 2	Ix 2.4	41b Lst
Mart	Ix 2		18a Lst
Orbi	Ix 2	Ix 2.5	27a Mdst
Orbi	Ix 2	Ix 2.5	30b Lst
Orbi	Ix 2	Ix 2.5	40a Lst
orth	Ix 2	Ix 2.5	38a CMdst
orth	Ix 2	Ix 2.6	4b Slst
orth	Ix 2	Ix 2.6	60a Lst
Phri	Ix 2	Ix 2.6	27b MLst
Phri	Ix 2	Ix 2.6	31b CMdst
Phri	Ix 2	Ix 2.6	8b Lst
Phri	Ix 2	Ix 2.6	33b Slst
Phri	Ix 2	Ix 2.6	43b Mdst
Pleu	Ix 2	Ix 2.6	53a MLst
Pleu	Ix 2	Ix 2.6	19b Slst
Prod	Ix 2	Ix 2.6	51a Lst
Prod			32b Mdst
Prod			2a Sst
Prod			32c Lst
Prod			56a Mdst
Prod			
Pugi			

Pugi

Pugn
Pugn
Punc
Pust
Pust
Rhip
Rhip
rhyn
Rugo

Rugo
Sche
Sche
Sche
Schi
Schi
Schi
Schi

SPl1
SPl1
SPl2
SPl3
SPl4
spir
Sten
Sten
brac

Bell
Bell
bell
Dona
Euph
Euph
Euph
Euph
Glab
Loxo
loxo
Meek
Nati

pleu
Porc
Reti
Reti
Reti
Reti
Sole
Stra
pupa
pupa

Dent
Dent

Acti
Anth
Anth
Anth
Avic
Avic

Card
Edmo
Edmo
Edmo
Edmo
Edmo
Edmo
Euch
Euch
Leio
Leio

Lith
Lith
Myal
Myal
Myal
Nucu
nucu
PALE
PALE
PALE
Para
pect
Phes
Posi
Posi
Posi
Posi
Prom
Prot
Sagu
Sang
Sang
Sang
Sang
Sang
Sang
SCH2
SCH2
Sedg
SOLM
SOLM
Steb
Steb
Steb

Sulc
Sulc
Sulc
Wilk
Wilk
biva

ORTH

naut
naut
naut

goni
goni

PALA
tril
tril

crus
ostr

echi

Pote
crin

PETA
fish

worm