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**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 Hurler 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 Hurler 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), Nethersfield (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 preference 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 preference 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.

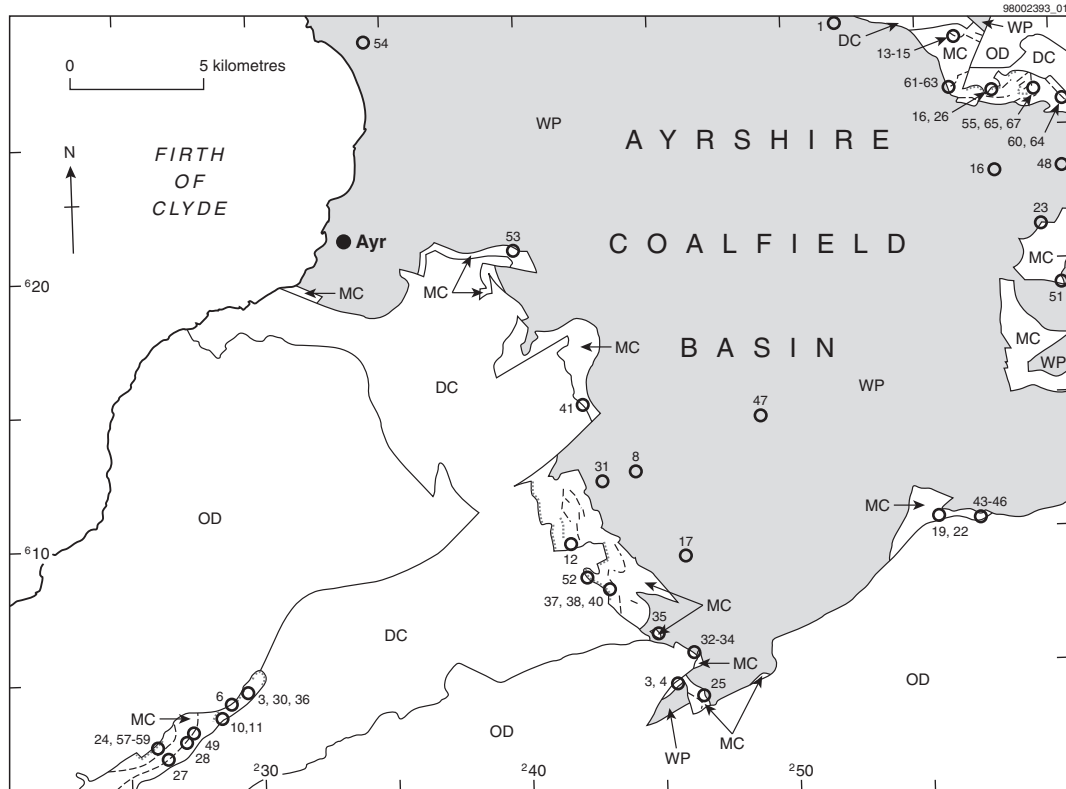
FIG. 14. Index Limestone. Plot of: (a) the first and second principal components, and (b) the second and third principal components in the PCA of the numbers of genera present in higher taxa showing the fields occupied by the two major clusters (Ix 1–2) identified in Figure 13. For sample details see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



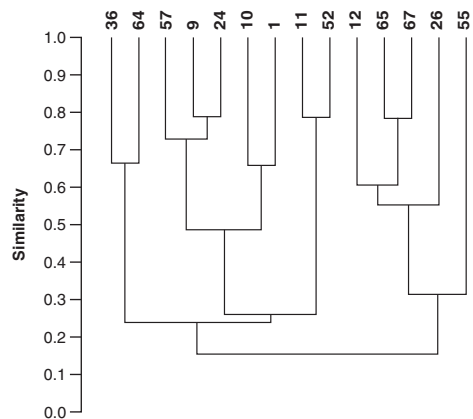
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|----|--|----|---|-------|------------------------------|
| WP | Westphalian-Permian rocks | DC | Devono-Carboniferous (including Courcyezan to Brigantian) rocks | | Crop of the Hurlet Limestone |
| MC | Middle Carboniferous (including Brigantian to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

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

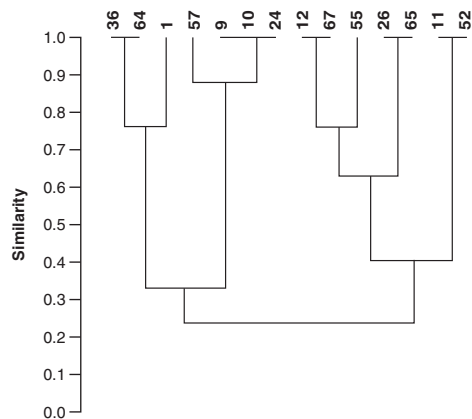
Locality	Taxon	<i>Buxtonia</i> sp.	? <i>Pugilis</i> sp.	trepostomatous bryozoa	<i>Avonia youngiana</i>	orthotetoid	gigantoproductoid	athyrid	spiriferid	crinoid columnals	<i>Pleuropugnoides</i> sp.	productoid	<i>Spirifer bisulcatus</i> ?
65		■	■	■	■	■	■	■		■			
26		■			■	■				■			
67			■	■	■	■	■		■	■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

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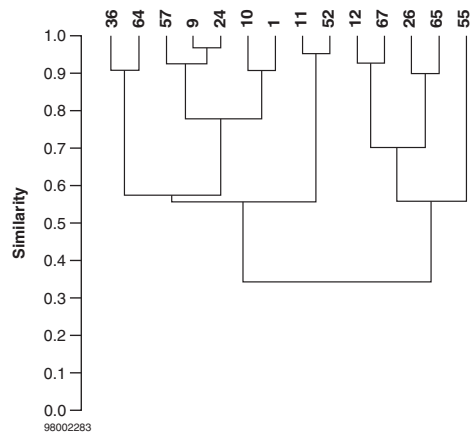
Dice



Simpson



Raup-Crick

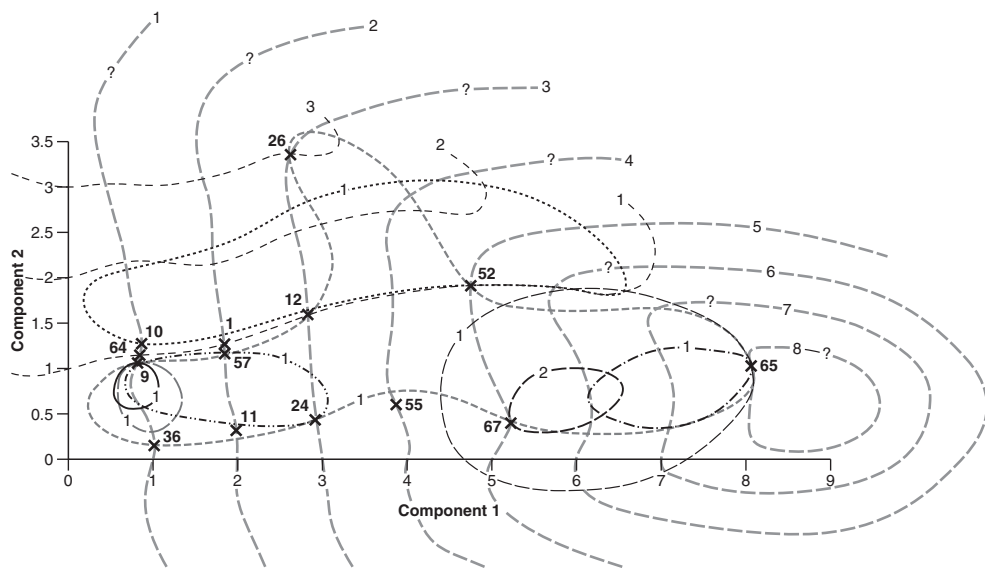


Localities

- 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 Nethersield
- 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

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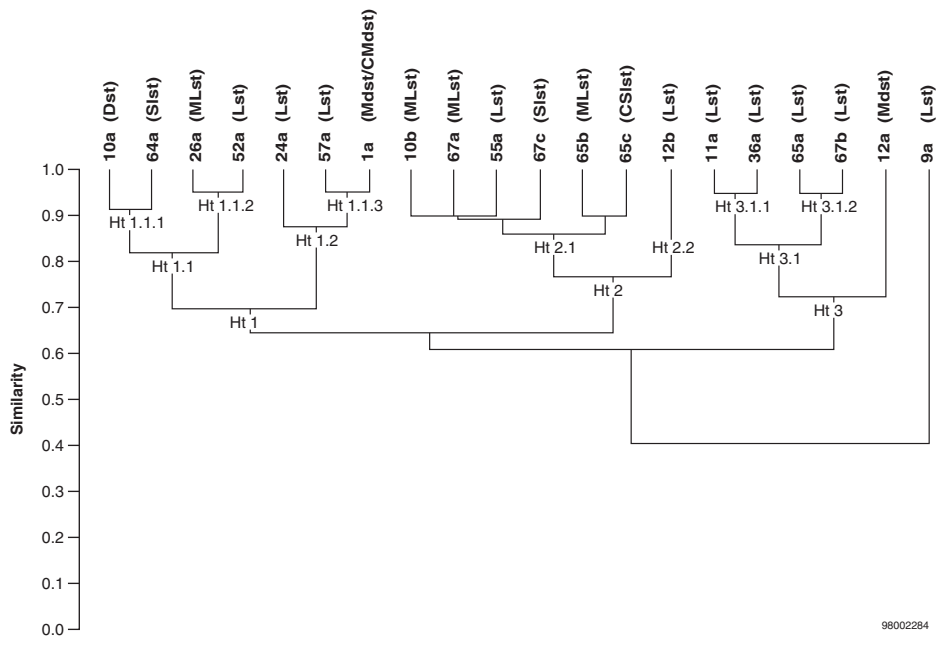
- | | | |
|--------------------------|------------------|-----------------|
| — Algae and Foraminifera | — Brachiopoda | — Nautiloidea |
| - - - Anthozoa | Gastropoda | — Crustacea |
| — Bryozoa | - - - Bivalvia | - - - Crinoidea |

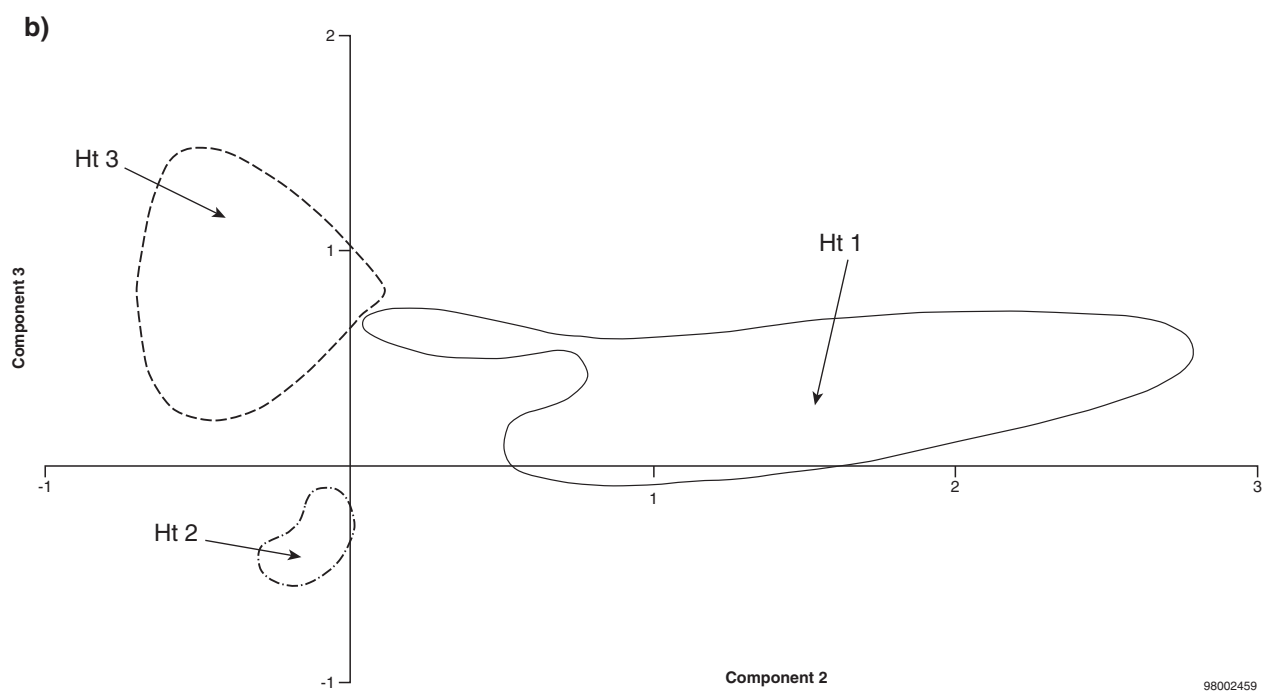
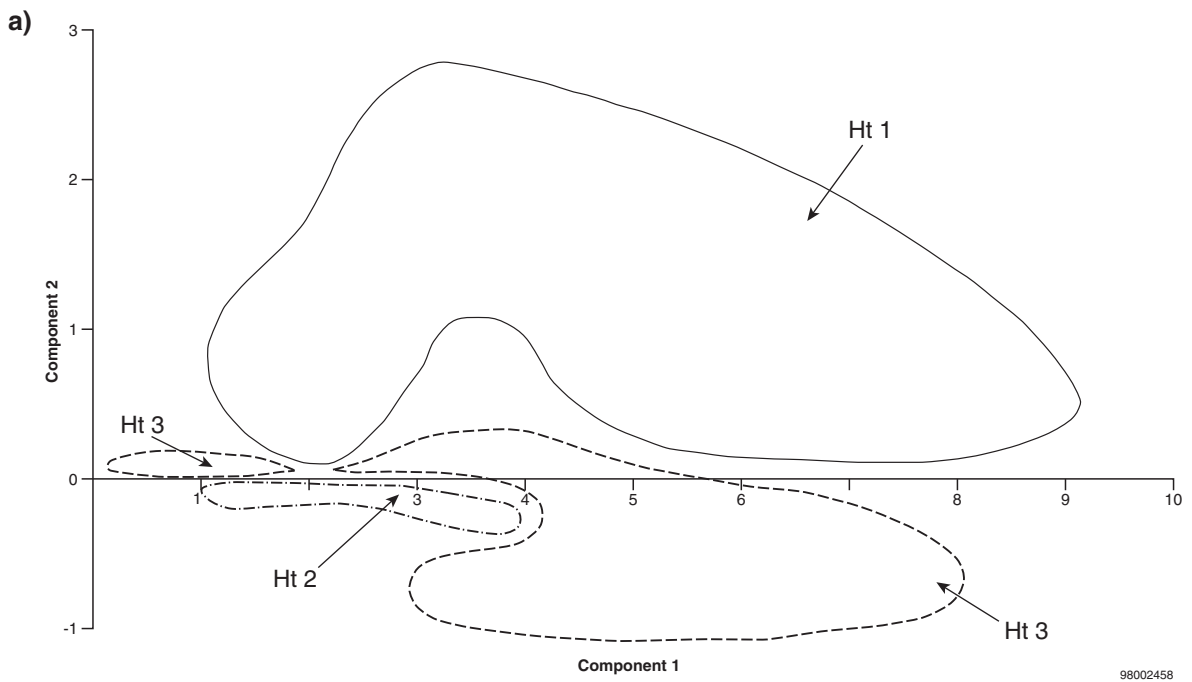
Sample	Taxon	gigantoproductoid	? <i>Pugilis</i> sp.	trepostomatous bryozoa	<i>Avonia</i> sp.	<i>Buxtonia</i> sp.	orthotetoid	athyrid	rhynchonellid	<i>Avonia youngiana</i>	crinoid columnals	<i>Camarotoechia</i> sp.	orthocone nautiloid	<i>Composita</i> sp.	spiriferid	productoid
67aMLst		■													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

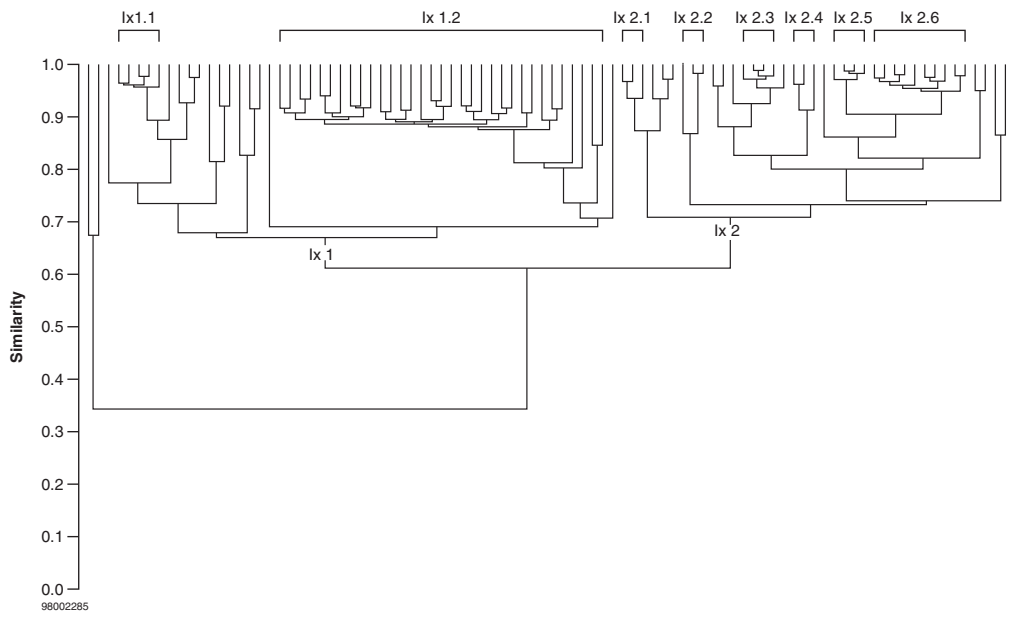
Sample	Taxon	gigantoproductoid	Buxtonia	trepostomatous bryozoa	?Pugilis	Avonia	orthotetoid	athyrid	rhynchonellid	crinoid columnals	Camartoechia	orthocone nautiloid	Composita	spiriferid	productoid
67aMLst		■													
12bLst		■					■								
65aLst		■	■	■	■	■	■	■	■	■					
26aMLst			■			■				■					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

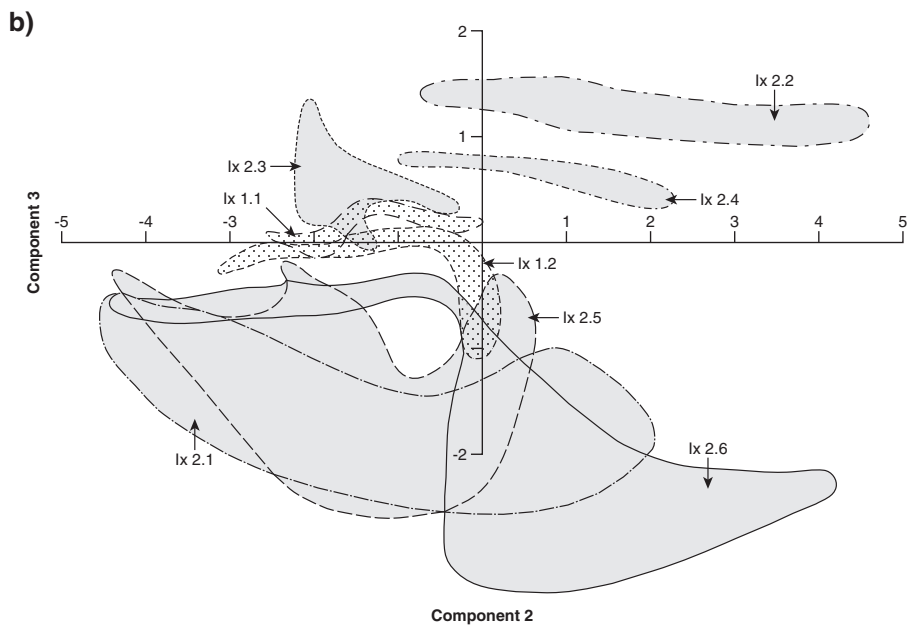
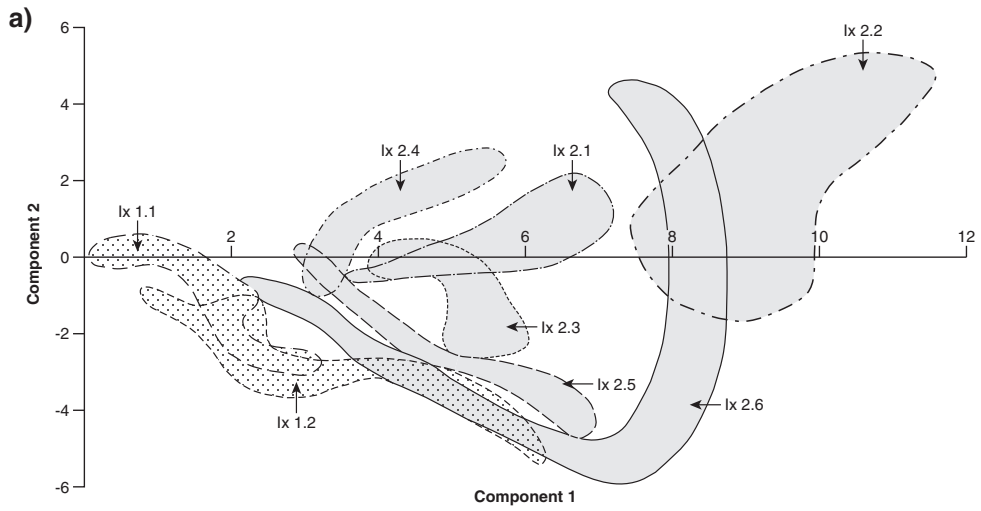
Taxon	Sample	10aDst	57aLst	9aLst	24aLst	11aLst	36aLst	55aLst	52aLst	67bLst	65aLst	12bLst	1aMdst/CMdst	65bMLst	67aMLst	10bMLst	26aMLst	12aMLst	64aS1st	67cS1st	65cCS1st	
<i>Camarotoechia</i> sp.			■			■																
productoid		■	■	■	■								■			■						
orthocone nautiloid			■										■									
athyrid						■			■		■											
crinoid columnals			■	■	■	■	■		■	■	■		■				■	■				
<i>Composita</i> sp.			■										■	■								
trepostomatous bryozoa										■	■											
? <i>Pugilis</i> sp.										■	■											
orthocone nautiloid										■	■	■										
gigantoproductoid											■	■			■							
<i>Avonia youngiana</i>								■		■												■
spiriferid				■				■					■						■	■		
rhynchonellid									■		■		■									■
<i>Avonia</i> sp.																	■					
<i>Buxtonia</i> sp.											■						■					

Taxon	Sample	10aDst	57aLst	9aLst	24aLst	36aLst	11aLst	52aLst	55aLst	65aLst	67bLst	12bLst	1aMdst/CMdst	10bMLst	26aMLst	65bMLst	67aMLst	12aMdst	64aS1st	67cS1st	65cCS1st	
<i>Camarotoechia</i>			■				■															
productoid		■	■	■	■								■	■								
orthocone nautiloid			■										■									
athyrid							■	■		■												
crinoid columnals			■	■	■	■	■	■		■	■		■		■			■				
trepostomatous bryozoa										■	■											
? <i>Pugilis</i>										■	■											
<i>Composita</i>			■										■			■						
orthotetoid										■	■	■	■									
gigantoproductoid										■	■	■					■					
<i>Buxtonia</i>										■	■		■		■							
rhynchonellid							■		■	■			■									
spiriferid				■				■	■				■						■	■		
<i>Avonia</i>								■	■	■				■							■	■











Taxa	Limestone	Agillaceous Limestone	Mudstone/ Calcareous Mudstone	Calcareous Siltstone	Siltstone
<i>Camarotoechia</i>	-----				
athyrid	-----				
? <i>Pugilis</i>	-----				
trepostomatous bryozoa	-----				
<i>Buxtonia</i>	-----	-----			
orthocone nautiloid	-----	-----	-----		
<i>Composita</i>	-----	-----	-----		
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		

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

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

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	Auld craigo Index		[4561 0421]		Species	Genus	Species
3a	Auld craigo Index		[4515 0439]	PLANTAE			
4a	Auld craigo Index		[4523 0441]	Lepidophyllum sp.			LEPI
4b	Auld craigo Index		[4523 0441]	Odontopteris sp.			ODON
4c	Auld craigo Index		[4523 0441]	ALGAE			
5a	Auld craigo Index		[4511 0442]	algal mater alga	alga		alga
5b	Auld craigo Index		[4511 0442]	FORAMINIFERIDA			
5c	Auld craigo Index		[4511 0442]	foraminifer: fora	fora		
5d	Auld craigo Index		[4511 0442]	PORIFERA			
6a	Baldrennar Index		[2880 0407]	'Chaetetes tumidus'			CHAt
7a	Blairmulloc Index		[5605 2820]	ANTHOZOA			
8a	Bowhill Boi Index		[4381 1231]	clisiophyllid			clis
8b	Bowhill Boi Index		[4381 1231]	Dibunophyllum sp.			DIBU
9a	Cairnshalc 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]	Angiospirifer 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 F Index		[5908 2130]	?Avonia sp ?Avs	Avon		
23b	Craigston F Index		[5908 2130]	?Beecheria sp.			?BEEs
23c	Craigston F Index		[5908 2130]	Brachythyris BRAC	Brac		
24a	Dailly Statii Hurlet		[2601 0246]	Buxtonia scabricula (Martin)			B1sc
25a	Dal cairnie 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	Drumgrang 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	Drysdale I Index		[4263 1200]	Cleiothyridina sp.			C1sp

31b	Drysdale Index	[4263 1200]	?Cleiothyridina sp.	?C1s
31c	Drysdale 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 Sowerby)	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]	?Composita ?C2s	Comp ?C2s
34a	Glenhead Index	[4590 0562]	Crurithyris urii (Fleming)	CRUi
34b	Glenhead Index	[4590 0562]	Dictyoclostus semireticulatus (Muir)	DICs
35a	Grimmet F. Index	[4463 0627]	Dielasma sp.	DIEs
36a	Heronsp. Hurlet	[2939 0456]	Echinoconchus sp.	ECHs
37a	Keirs Burn Index	[4298 0802]	?Echinoconchus sp.	?ECH
37b	Keirs Burn Index	[4298 0802]	Eomarginifera Ello	Eoma Ello
38a	Keirs Burn Index	[4309 0809]	Eomarginifera cf. longispina (J Sowerby)	E1cl
38b	Keirs Burn Index	[4309 0809]	?Eomarginifera cf. longispina (J Sowerby)	?E1l
39a	Keirs Burn Index	[4279 0803]	Eomarginifera praecursor (Muir-Wood)	E1pr
40a	Keirs Glen Index	[4310 0805]	Eomarginifera praecursor (Muir-Wood)	E1p?
41a	Kerse Park Index	[4218 1485]	Eomarginifera cf. praecursor (Muir-Wood)	E1cp
41b	Kerse Park Index	[4310 0805]	Eomarginifera sp.	E1sp
42a	Knockburn Index	[5634 1032]	'Fusella convoluta'	FUSc
42b	Knockburn Index	[5634 1032]	Gigantoproductus GIGg	Giga GIGg
43a	Knockburn Index	[5634 1029]	Gigantoproductus GIGs	Giga GIGs
43b	Knockburn Index	[5634 1029]	gigantoproductus giga	Giga giga
44a	Knockburn Index	[5634 1028]	Krotovia aculeata (J Sowerby)	KROa
45a	Knockburn Index	[5634 1027]	Latiproductus latissimus (J Sowerby)	L1la
46a	Knockburn Index	[5634 1024]	Latiproductus latissimus (J Sowerby)	L1l?
46b	Knockburn Index	[5634 1024]	Latiproductus 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 Cr. 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	Meikleholr Hurlet	[4205 0848]	Orbiculoidea cincta (Portlock)	ORBc
53a	Millcraig Index	[3959 2081]	Orbiculoidea 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 Sowerby)	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 (Phillips)	PLEp
61c	River Ayr Index	[5593 2626]	Pleuropugnoides G	PLEs
61d	River Ayr Index	[5593 2626]	Productus cf. carbonarius de Koning	P2ca
62a	River Ayr Index	[5588 2629]	Productus concinnus J Sowerby	P2co
62b	River Ayr Index	[5588 2629]	Productus cf. concinnus J Sowerby	P2co
63a	River Ayr (1) Index	[5568 2636]	Productus P2sp	Prod P2sp
64a	River Ayr (1) Hurlet	[5997 2599]	?Productus sp.	?P2s
65a	River Ayr (1) Hurlet	[5886 2627]	productoid prod	Prod prod
65b	River Ayr (1) Hurlet	[5886 2627]	Pugilis cf. pugilis (Phillips)	PUGp

65c	River Ayr (' Hurlet	[5886 2627]	Pugilis sp.	PUGs
66a	Watston Bt Index	[5985 1725]	?Pugilis sp ?PUG Pugi	
67a	Windy Burr Hurlet	[5874 2629]	Pugnax cf. pugnus (Martin)	P3cp
67b	Windy Burr Hurlet	[5874 2629]	?Pugnax sp.	?P3s
67c	Windy Burr Hurlet	[5874 2629]	?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 (Martii	S1cr
			Schizophoria sp.	S1sp
			?Schizophoria sp.	?S1s
			Spirifer bisi SPb? SPI1	
			Spirifer bisulcatus J de C Sowerby	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
			?Naticopsis: ?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	
Cardiomorj 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)		LIII
Lithophaga lingualis (Phillips)?		LII?
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 (McCoy)		PARs
pectenid		pect
Phestia attenuata (Fleming)		PHEa
Posidonia corrugata (Etheridge jui	POCo	
Posidonia corrugata (Etheridge jui	POC?	
?Posidonia corrugata (Etheridge ji	?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 grc	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

Sulcatopina	SUfl	Sulc	SUfl
Sulcatopinna flabelliformis (Martini)	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	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 colu	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
Major Clus: Nested Clu Sample Number

clis			
Dibu			
zaph			
cora	lx 1		29a Lst
	lx 1		41a Mdst
Fene	lx 1		6a Lst
fene	lx 1	lx 1.1	15a Lst
t-br	lx 1	lx 1.1	48a Mdst
	lx 1	lx 1.1	49a MLst
Serp	lx 1	lx 1.1	54b Lst
Serp	lx 1	lx 1.1	28c Mdst
	lx 1		66a Dst
Acti	lx 1		16c Lst
Angi	lx 1		16d MLst
Anti	lx 1		42a Lst
Anti	lx 1		19a Lst
Anti	lx 1		20a Slst
Anti	lx 1		50a MLst/Lst
Anti	lx 1		7a Lst
Anti	lx 1		23a Mdst
Athy	lx 1		62b Lst
athy	lx 1		17a Lst
athy	lx 1	lx 1.2	5b CMdst
Avon	lx 1	lx 1.2	5c MLst
	lx 1	lx 1.2	47a Mdst
	lx 1	lx 1.2	48b Lst
	lx 1	lx 1.2	22b CMdst
Beec	lx 1	lx 1.2	61b CMdst
	lx 1	lx 1.2	46b CMdst
Buxt	lx 1	lx 1.2	44a Lst/MLst
Buxt	lx 1	lx 1.2	63a Lst
Buxt	lx 1	lx 1.2	46a Lst
Buxt	lx 1	lx 1.2	33a MLst
Buxt	lx 1	lx 1.2	62a Mdst
Cama	lx 1	lx 1.2	34b Lst
chon	lx 1	lx 1.2	43a Lst
Clei	lx 1	lx 1.2	4c CMdst
Clei	lx 1	lx 1.2	4a Lst
Clei	lx 1	lx 1.2	17b CMdst
Clei	lx 1	lx 1.2	17c Mdst
Clei	lx 1	lx 1.2	23b MLst

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

Pugi

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naut

goni
goni

PALA
tril
tril

crus
ostr

echi

Pote
crin

PETA
fish

worm